Minot (C. S.)

Proceedings of the Boston Society of Natural History.
Vol. 28, No. 10,
p. 265–274.

ON THE VEINS OF THE WOLFFIAN BODIES IN THE PIG.

By Charles Sedgwick Minot.

With One Plate.

BOSTON:
PRINTED FOR THE SOCIETY.
July, 1898.

No. 10. — *On the Veins of the Wolffian Bodies in the Pig.*

By Charles Sedgwick Minot.

In transverse sections of pig embryos of 10 mm. and upwards in length, representing stages in which the Wolffian bodies (Mesonephroi) are well developed, no cardinal veins can be distinguished on the dorsal side of the Wolffian bodies. As we rely principally upon pig embryos for the class work in embryology at the Harvard Medical School, it was important to elucidate the history of the cardinal veins. During this undertaking I found certain relations of the veins, which seem to me worthy of description and illustration.

The material studied consists of twenty-five series of sections of pig embryos of from 6.0–24.0 mm. in length, corresponding in range approximately to Figs. 14–29 inclusive of Keibel's Normentafeln I. Embryos of 12.0 mm. were found to be especially instructive as regards the transformation of the cardinal veins, and accordingly the following descriptions are based chiefly on that stage. To render verification of the observations feasible, the sections are referred to by the number of the series, and the number of the section in the series. For example, Fig. 3 is taken from *Series* 6, *section* 423. The collection is the property of the Harvard Embryological Laboratory and is open to qualified investigators.

In pig embryos of 12.0 mm. the cardinal vein is a large stem, which may be said to end abruptly at the cephalic end of the Wolffian body, Fig. 1, although a prolongation of small caliber may sometimes be traced a short distance on the dorsal side of the body. The vena cava inferior is a large vessel a little to the right of the median line, Fig. 3, and receives its blood almost exclusively from the Wolffian bodies. The primitive kidneys have at this stage two large veins. The renal and iliac branches of the cava inferior commence their development in slightly older embryos. The left umbilical vein is a large blood channel, Fig. 5, which passes from the umbilicus, directly through the liver to the heart; it has numerous side branches in the liver. The right umbilical vein is markedly smaller than the left; in series 5 (transverse sections) it has a wide connection inside the liver with the portal vein; in series 6 (sagittal sections) the connection can be made out, but it is of small diameter; in series 7 (frontal sections) the connection is absent, and the right umbilical vein breaks up and is lost in the liver substance. From these observations we must conclude that it is at about this stage that the abortion of the right umbilical vein as a continuous blood channel through the liver is completed, but it varies in individual embryos. The portal vein is a well-developed vessel, which enters the right upper lobe of the liver, and there ramifies.

The relations of the cardinal veins are essentially alike upon the two sides. As shown in Fig. 1, the cardinal, *Card*, and jugular, *Jug*, veins unite and form the Ductus Cuvieri, *D. C.*, which descends obliquely towards the liver; on the right side, Fig. 1, the Ductus Cuvieri is joined also by the Vena Cava Inferior, *V. C. I.*, which ascends through the liver — compare also, Figs. 2 and 3 — to the heart. Between the liver and the heart the venous channel is homologous with the sinus venosus. A sagittal section, such as Fig. 1, shows the wide cardinal vein abruptly closed by the mass of tubules of the Wolffian body, *W. B.*, so that one receives the impression that the vein suddenly becomes a sinus in which the tubules are lodged. Closer examination with higher powers reveals that this conception is essentially correct.

Fig. 2 represents a sagittal section from the same series as Fig. 1, but is from the opposite side of the embryo, namely the left. It illustrates the connection of the vascular channels of the primitive kidney with the Vena Cava Inferior, *V. C. I.* This connection is established on the medial side of each mesonephros by a short wide channel, which shows well in transverse sections, Fig. 4, in frontal, Fig. 3, and also of course in reconstructions, Fig. 5. If we consider the Wolffian body as to its length the mesonephric branches of the cava inferior will be found near the middle so that they may be said to divide the cephalad from the caudad half of the organ. These venous stems being of enormous size, see Fig. 2, in comparison with the Wolffian body, renders this division a true anatomical division, and later when the true kidney grows headwards from its position at the caudal end of the Wolffian body, where it lies at this stage, it approaches the branches of the vena cava, and there results a complete interruption of the continuity of the Wolffian body, which thereafter is represented by a cephalic division and a caudal division. The former is presumably the anlage of the organ of Rosenmüller (Parovarium, Epididymis), and the latter is presumably the anlage of the organ of Giraldès (Paradididymis, Paroöphoron). Unfortunately, I have not been able to follow the further history of these parts, so that the homologies indicated must be left for future investigations to verify or deny.

The mesonephric branches from the end of the cava inferior abut partly directly upon the Wolffian tubules, and partly indirectly, since they are each continued by a headward or upper and a tailward or lower branch, as illustrated in the reconstruction, Fig. 5. These branches lie upon the dorsal side of the organ and take an arching course. They were originally portions of the cardinal veins, and their connection with vena cava inferior is secondary. This change in the connections of the distal parts of the cardinal veins was described by Rathke long ago, **30.1, 38.3**, and has been studied more recently by Hochstetter, **87.2, 88.1, 88.3, 92.1, 92.3, 93.1, 94.3, 97.2**, and Zumstein, **96.1, 97.1**. I must point out that the diagram given by O. Hertwig in his Entwickelungsgeschichte, Fünfte Auflage, p. 537, and which I have reproduced in my Human Embryology, p. 543, represents the transformations of the veins incorrectly. It is incorrect especially in failing to show that each cardinal vein becomes discontinuous, and that the caudad segment of the cardinal vein becomes connected near its own middle with the end of the vena cava inferior, so that this segment is transformed into what appear as the two branches of the mesonephric vein. This change of connection is so important that the vessels of the new arrangement deserve a special name, and I propose therefor the term mesonephric vein (*vena mesonephrica*). The trunk of this vein is a new connecting stem established between the end of vena cava inferior and the cardinal vein; the two main branches of the vein are the remnants of the caudad division of the cardinal vein, and they may be conveniently styled the *superior* and *inferior* branches respectively, the superior being that lying nearest the head.

The Wolffian body of the pig is then remarkable for being furnished with two very large veins, both receiving their blood supply practically exclusively from the Wolffian body. It seems possible that this peculiar condition, which does not obtain in Guinea pigs or in man, is connected with the great functional activity of the mesonephros in the ungulates, which develop an enormous allantoic sack and fill the sack with a urinary excretion. Guinea pigs have a small, man a minimal allantois, and it must be assumed that the mesonephric functions are correspondingly reduced. As regards the veins in these two types Zumstein, **96.1**, **97.1**, has shown that the general course of the development is the same as in the pig, the mesonephric veins arising in the same way by the median fusion of the cardinals for a short distance. But as regards the size of the veins there is a marked difference from the pig. Thus in human embryos of 14 and 16 mm. the cardinal veins are not only smaller in width than the umbilical veins but smaller even than the dorsal aorta,— see Zumstein, **96.1**, p. 592–593. So also in the Guinea pig the relatively small size of the cardinal veins is recorded by Zumstein, **97.1**, in his figures 5–12, from embryos of 18–24 days. These observations justify the inference of a direct correlation between the functional activity of the mesonephroi on the one hand and the size of the two pairs of veins and of the allantois on the other.

The character of the circulation within the Wolffian bodies is not yet quite clear, for, although the connection of the blood channels between the tubules with veins is easily determined, the pathways of the arterial inflow are obscure. One sees readily the small arteries, which bring the blood from the aorta directly to the glomeruli. I have not studied the arterial supply carefully, and can therefore only state that the arteries running to the glomeruli are the only mesonephric arteries which I have noticed, without however being able to affirm that no others are present. If my supposition as to the vascular arrangements are correct, then the course of the circulation must be from the aorta through the numerous small glomerular arteries, into the glomeruli, from the glomeruli into the intertubular vessels of the mesonephros, and thence into either the mesonephric or the cardinal veins.

The intertubular vessels of the mesonephros of the pig are highly characteristic. They communicate freely with one another and with the veins, and they are in no sense capillaries. In Figures 1, 2, 3, and 4, the representation of the Wolffian body is in each case in so far diagrammatic that many details are omitted, including most of the blood spaces. Fig. 6 is from a drawing much magnified of a small part of the left Wolffian body (to the right in the figure) of Fig. 3. It illustrates the character of all the intertubular vessels. Their walls consist for the most part solely of a thin endothelium, so thin as to be merely a line except where the nuclei are lodged; the nuclei are large, granular, and protuberant, and are indeed similar to those of the adult vascular endothelium, although conspicuously less flattened. This endothelium, *endo*, lies for the most part immediately in contact with the epithelium, *Ep*, of the Wolffian tubules. Occasionally, as at *mnch* in the figure, a thin layer of mesenchyma intervenes between the vascular endothelium and the tubular epithelium, but the total amount of mesenchyma is insignificant. Almost everywhere the vascular endothelium is closely fitted against the tubules. It results that the mesonephros does not have a series of blood vessels in the ordinary sense, but is rather a single complex sinus, imperfectly subdivided by the Wolffian tubules. Hence every tubule is almost (or even for a certain part absolutely) completely bounded by a blood space, and accordingly bathed in blood from which it is parted only by the exceedingly thin endothelium. The circulation is therefore very unlike that through the capillary network of the pig's kidney, for in the true kidney the capillaries are much smaller in caliber than the renal tubules,[1] and consequently only a small proportion of the epithelial excretory cells are in *immediate* proximity to the circulating blood. In the mesonephros of the pig, on the contrary, the great majority of the excretory cells are in actual contact with the attenuated vascular endothelium.

In pig embryos, older than those of 12 mm., the Wolffian tubules are found increasing in length and (by budding) in number, but since the volume of the organ does not increase in the same measure, the tubules become more crowded, so that the intertubular sinus becomes more subdivided, and the vascular spaces of the sinus are reduced. Moreover the tubules occasionally become closely appressed, and then the blood space between them may be obliterated. The general result of these changes is to cause the blood spaces to appear in sections less like parts of a great sinus, and more like separated vessels. An attentive study, however, of pigs of 14, 17, and 20 mm. shows conclusively that the circulation is only modified, and preserves the essential characteristics which it presents in pigs of 12.0 mm.

The entire absence of capillaries and the sinus-like disposition of the blood channels characterize the circulation of blood between the tubules of the Wolffian body of the pig. This fact has already been confirmed, since the preliminary announcement of my results (Science, N. S., vol. 7, p. 229), by Parker and Tozier, **98.1**. My observations show that both characteristics recur equally well

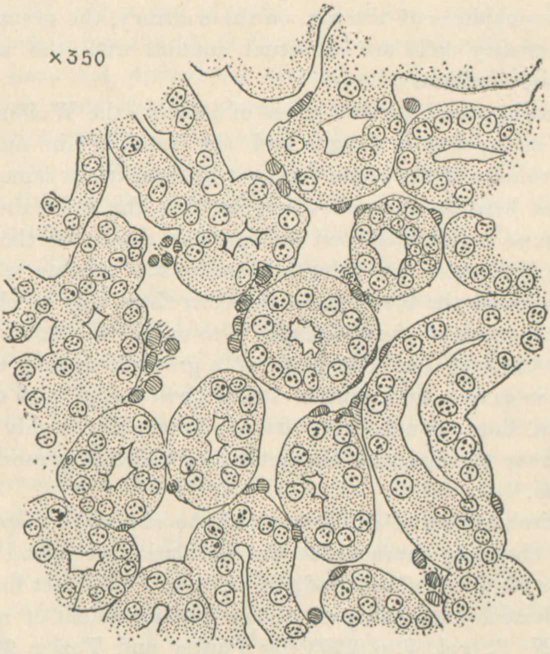
---

[1] Except of course the small portion of Henle's loop, which is almost as narrow as a capillary.

marked in the embryos of man, the cat, the rabbit, and the chick. Hence it seems to me fair to suppose that this feature is characteristic of the mesonephros of all amniote embryos, and marks a sharp distinction to be drawn between the mesonephros and the true kidney or metanephros.

It is inevitable to deduce the supposition that the mesonephros has no true intertubular capillaries in any species, not even in such types as preserve the mesonephros as the renal organ of adult life. Attractive as this supposition appears, it is evidently necessarily to be tested by more accurate and extended observations than are yet at our disposal.

Material already at my command enables me, however, to state positively even now that in the frog (Rana esculenta, R. halecina) the blood channels are not true capillaries but irregular spaces bounded by an endothelium, which is closely fitted against the



Part of a section of the mesonephros of Rana to illustrate the sinus-like arrangement of the blood vessels and the absence of true capillaries. For clearness the nuclei of the vascular endothelium are drawn dark.

epithelial surface of the renal tubules, the curves of which the endothelium follows closely. In a true capillary the endothelium on the contrary follows, so to speak, its own and independent curve. The figure in the text illustrates the facts recorded. [Since this article went to press, I have examined the kidney of *Necturus maculatus*, for which material I am indebted to the kindness of Dr. G. H. Parker. In this representative of the Urodela, I find the same circulatory conditions as in Rana, but with wider sinuses.]

The peculiar type of circulation to which I have called attention has, I believe, greater morphological (and physiological) importance than has been recognized. Comparison with the rete mirabili of various animals, for instance with the carotid gland of the frog, at once suggests itself. Even nearer lies the comparison with the form of circulation in two embryonic organs — the liver and the pronephros. As regards the liver, the comparison is especially facile in those lower types, in which the hepatic cylinders are tubular in form — compare the figure and brief description, which I have given in my "Human Embryology," p. 761, of the liver of an Acanthias embryo. As regards the pronephros, I will record that in tailed Amphibia, teleosts, and ganoids, I have observed the same circulatory conditions. As specific evidence on this point I will put down the references to certain sections in our collection.

These are: —

Necturus,	15.0	mm.	Transverse	Series	78,	Sections	300–330
"	"	"	Frontal	"	80,	"	95– 97
"	18.0	"	Transverse	"	16,	"	335–345
"	"	"	Frontal	"	84,	"	95–100
Ameiurus	9.0	"	Transverse	"	85,	"	55– 60
"	"	"	Frontal	"	87,	"	45– 50
Batrachus	9.5	"	Transverse	"	118,	"	218–236
"	"	"	Frontal	"	120,	"	100–104
Amia,	10.0	"	Transverse	"	19,	"	260–270
"	"	"	Frontal	"	20,	"	60– 67
"	13.0	"	Transverse	"	55,	"	231–240
"	"	"	Frontal	"	57,	"	74– 78

In the two teleostean forms, Ameiurus and Batrachus, and in the ganoid, Amia, the greater part of the space between the pronephric tubules is occupied by the blood channels, but there are also patches of tissue, the "*Pseudolymphoidgewebe*" of W. Felix, **97.1**, p. 443. In these patches the nuclei are crowded together, and they differ by their deep staining and in their minute structure very conspicuously from the nuclei of the pronephric tubules and of the vascular endothelium. In all three forms above mentioned, the pronephros is without capillaries, but has instead sinus-like vessels, the endothelium of which is in large part in close contact with the epithelium of the pronephric tubules.

The peculiarity of the pronephric circulation has been noted by previous writers. For example, the sinus-like character and the intimate relation to the veins were noted by Alexander Götte in 1875, see his *Entwickelungsgeschichte der unke*, p. 760, also by M. Fürbringer, **78.1**, Taf. I, fig. 4. In W. Felix's recent admirable monograph, **97.1**, the similar conditions in teleostean pronephros are referred to. The list of authorities upon this feature of the pronephros in Ichthyopsida might be considerably extended, in short its seems to me that one may safely regard the multifid intertubular venous sinus as an essential characteristic of the well-developed pronephros.

The facts presented bring us to question: Is there a constant and therefore typical difference between the pronephros and mesonephros on the one hand and the true kidney on the other as regards the form of circulation, a blood sinus developing about the tubules of the former, true capillaries about the tubules of the latter? The present possibilities indicate an affirmative answer, and such an answer would, in my opinion, go far towards establishing a morphological difference between the various renal organs and would tend to prove that the true kidney (metanephros) is not phylogenetically related to the mesonephros, but is a wholly new acquisition, not evolved from segmental organs (nephrotomes).

LITERATURE.

Felix, W.

97.1. Beiträge zur entwickelungsgeschichte der salmoniden. Anat. hefte, vol. 8, p. 251–466, taf. 34–41.

Fürbringer, M.

78.1. Zur vergleichenden anatomie und entwickelungsgeschichte der excretionsorgane der vertebraten. Morph. jahrb., vol. 4, p. 1–3, taf. 1–2.

Hochstetter, Fr.

87.2. Ueber die bildung der hinteren hohlvene bei den säugethieren. Anat. anz., vol. 2, p. 517–520.

Hochstetter, Fr.

88.1. Beiträge zur entwickelungsgeschichte des venensystems der amnioten. Morph. jahrb., vol. 12, p. 575–585, taf. 24.

Hochstetter, Fr.

88.3. Zur morphologie der vena cava inferior. Anat. anz., vol. 3, p. 867–872.

Hochstetter, Fr.

92.1. Ueber die hintere hohlvene. Verhand. anat. ges., vol. 6 (Wien), p. 181.

Hochstetter, Fr.

92.3. Beiträge zur entwickelungsgeschichte des venensystems der amnioten; II. Reptilien (Lacerta, Tropidonotus). Morph. jahrb., vol. 19, p. 428–501, taf. 15–17.

Hochstetter, Fr.

93.1. Beiträge zur entwickelungsgeschichte des venensystems der amnioten; III. Säuger. Morph. jahrb., vol. 20, p. 543–648, taf. 21–23.

Hochstetter, Fr.

94.3. Entwickelung des venensystems der wirbelthiere. Ergebnisse anat. entwick., vol. 3, p. 461–489.

Hochstetter, Fr.

97.2. Zur entwickelung der venae spermaticae. Anat. hefte, vol. 8, p. 801–810.

Parker, G. H., and Tozier, C. H.

98.1. The thoracic derivatives of the post-cardinal veins in swine. Bull. Mus. comp. zool., vol. 31, p. 133–144.

Rathke, H.

30.1. Ueber die bildung der pfortader und der lebervenen bei säugethieren. Meckel's Arch., 1830, p. 434–438.

Rathke, H.

38.3. Ueber den bau und die entwickelung des venensystems der wirbelthiere. Dritter Bericht naturw. semin. univ. Königsberg, 23 pp.

Zumstein, J.

96.1. Zur anatomie und entwickelung des venensystems des menschen. Anat. hefte, vol. 6, p. 571–608, taf. 26–37.

Zumstein, J.

97.1. Zur entwickelung des venensystems bei dem meerschweinchen. Anat. hefte (Arbeiten), vol. 8, p. 165–190, taf. 21–30.

Printed, *July*, 1898.

EXPLANATION OF THE PLATE.

ABBREVIATIONS.

Ao.	Aorta.	*Mnph. i.*	Inferior mesonephric vein.
Au.	Auricle.	*Port. V.*	Portal vein.
Au. D.	Right Auricle.	*Si.*	Blood sinus.
Au. S.	Left Auricle.	*Sp. C.*	Spinal cord.
bl. c.	Blood corpuscles.	*St.*	Stomach.
Card.	Cardinal vein.	*Sup. mes.*	Superior mesenteric artery.
Con.	Connective tissue.	*S. V.*	Sinus venosus.
D. cho.	Ductus choledochus.	*Um. V.*	Umbilical vein.
Endo.	Endothelium.	*V. C. I.*	Vena cava inferior.
Ent.	Entoderm.	*V. C. I. D.*	Vena cava inferior dextra.
Ep.	Epithelium.	*V. E.*	Eustachian valve.
G. bl.	Gall bladder.	*V. S.*	Valvula sinistra.
Gln.	Ganglion.	*W. B.*	Wolffian body.
Jug.	Jugular vein.	*W. D.*	Wolffian duct.

PLATE 1.

Fig. 1. Pig, 12.0 mm. Sagittal series 7, section 39. (Compare also series 6, section 453.) Through the right Wolffian body. A short branch of the cardinal vein can be followed on the dorsal side of the Wolffian body in neighboring sections; see especially Section 24. × 28 diams.

Fig. 2. Same as above, but from section 51, to show the connection of the vena cava inferior with the right Wolffian body. The Wolffian tubules are not accurately drawn, and the small blood channels between them are omitted. The vena cava inferior shows no branches of any importance outside of the Wolffian body. In section 68, the vein comes very close to the dorsal aorta leaving only a very thin partition. × 28 diams.

Fig. 3. Pig, 12.0 mm. Frontal series 6, section 423, passing through the entire length of the *vena cava inferior.* The section also illustrates the influence of this vein, developed upon the right side, in forcing the stomach to the left. × 13 diams.

Fig. 4. Pig, 12.0 mm. Transverse series 5, section 705. Through the Wolffian bodies at the level of the connection with the vena cava inferior. × 17 diams.

Fig. 5. Pig, 12.0 mm. Frontal series 6. Abdominal veins in frontal view, reconstructed from drawings of every tenth section, but the branches of the umbilical vein in the ventral part of the liver are entirely omitted. × 13 diams.

Fig. 6. Pig, 12.0 mm. Frontal series 6, section 423. Part of the left Wolffian body to show the relation of the venous endothelium to the Wolffian tubules. × 267 diams.

Fig. 1.

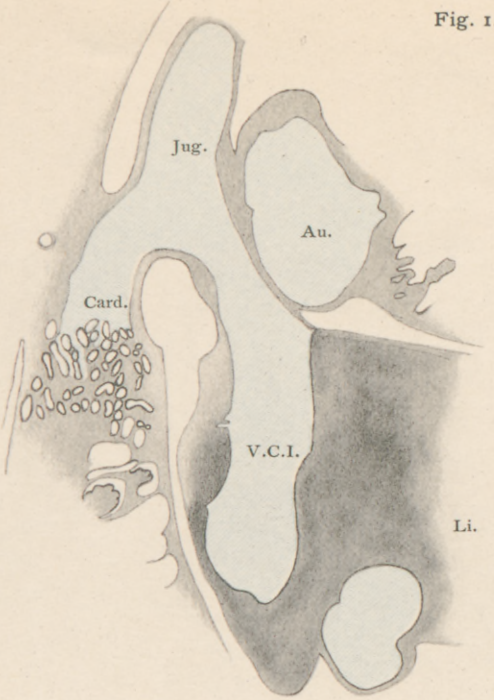


Fig. 2.

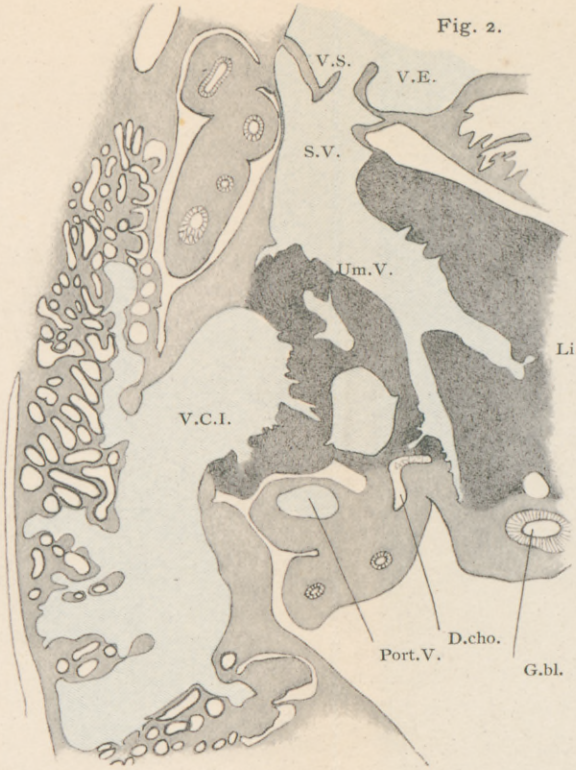


Fig. 3.

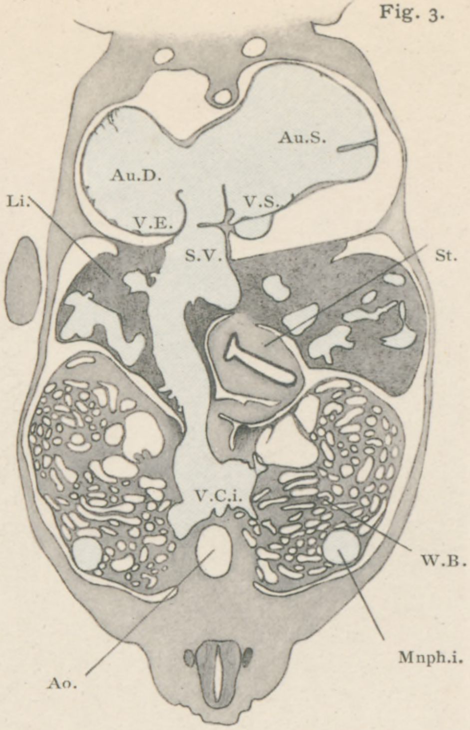


Fig. 4.

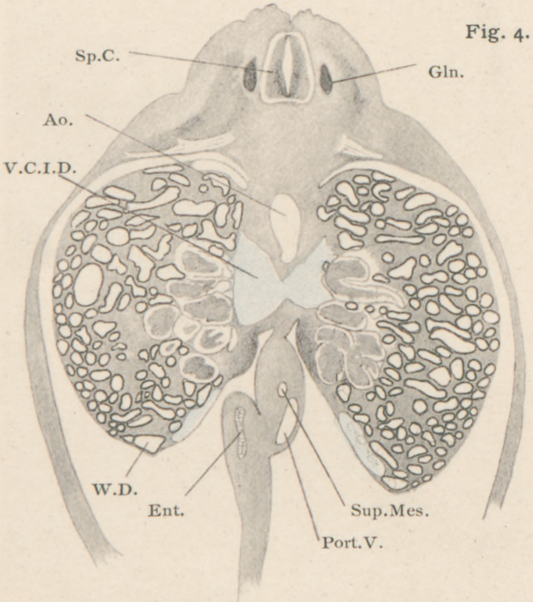


Fig. 5.

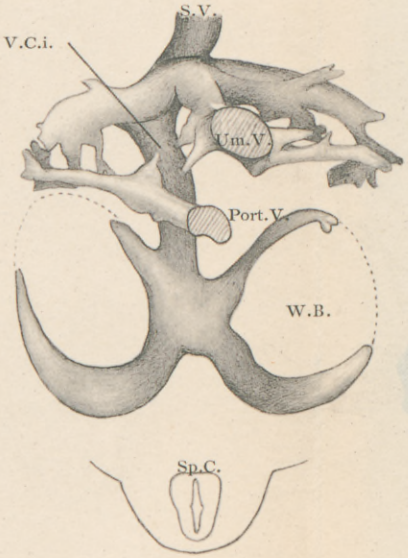
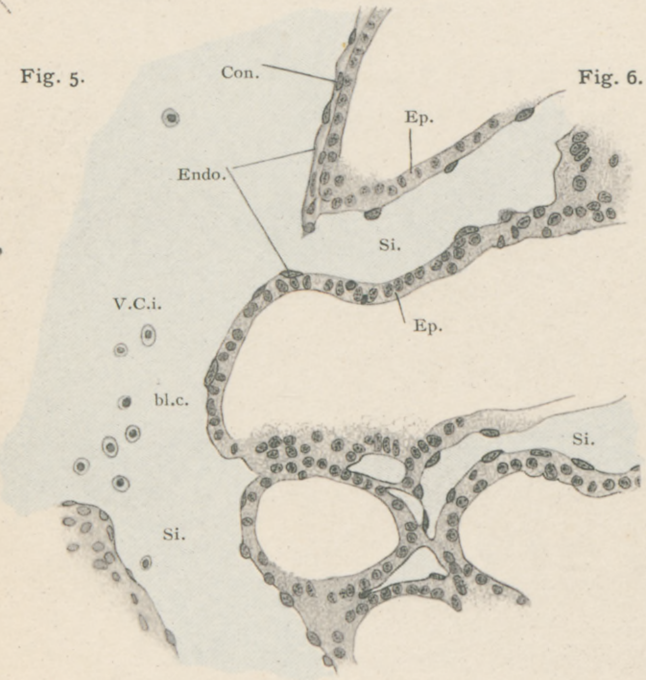


Fig. 6.



THE HELIOTYPE PRINTING CO., BOSTON