# THE PRONEPHROS AND EARLY DEVELOPMENT OF THE MESONEPHROS IN THE CAT

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Comparatively few observations have been made on the early development of the excretory system in the Mammalia. The existence of a pronephros was first recorded in the rabbit and rat by Renson ('83), and later Janosik ('85) described pronephric canals in the rabbit. A more detailed investigation of the anterior end of the excretory organ (called by this author *mesonephros*) in the same animal has been given by Martin ('88), and a few observations were made by Rabl ('96) in 1896. The most complete accounts of the mammalian pronephros are those of Kerens ('07) in both the rabbit and the mole, and of Felix ('12), who has described in some detail both pro- and mesonephros in the human embryo. Embryos of the marmot have been studied by Janosik ('04), and van der Stricht ('13) has recorded the existence of a pronephros in an embryo of the bat, *Rhinolophus hipposideros.*

The anterior end of the organ which gives rise to the Wolffian duct shows varying stages of degeneration in different genera; the course of development is much abbreviated, and events follow each other with great rapidity. The correct interpretation of what takes place is therefore not easy, and whilst more knowledge of the conditions in other mammals is greatly needed, the exact significance of these rudimentary structures can only be appreciated after careful comparison with the corresponding parts of the organ in lower vertebrates.

Owing to the rapidity at which development takes place in early stages, a very complete and well preserved series of embryos is an essential factor for accurate observations. The series of cat embryos in the possession of Professor J. P. Hill, from which my investigations are taken, is an excellent one, and the embryos are mostly in a good state of preservation. I should like to express my gratitude to Professor Hill and to thank him for his kind criticism.

In stages possessing 17 to 35 somites and older, the sequence is a very close one, and moreover consists of many individuals of the same age. It is thus quite adequate for a study of the excretory system during this period. The number of embryos with 9 to 16 somites, during which time the Wolffian duct first makes its appearance, is smaller, and, though fairly complete, does not justify a definite and final conclusion as to the exact mode of origin of the duct at this early stage. The observations of these early stages were made from one embryo of each of the stages with 8, 9, 10, and 12 somites, two embryos with 14, and two with 16 somites.

These investigations were begun in 1918 during my tenure of a research assistantship under the Department of Scientific and Industrial Research.

I am much indebted to Mr F. Pittock of University College for the beautiful microphotographs on plates XXXVI, XXXVII, and XXXVIII.

## DESCRIPTION OF STAGES

8 *to* 10 *somites*. The primordium of the excretory organ in the cat first appears in embryos with 8 to 10 somites. At this stage a central cavity is beginning to appear in the somites, and each one is united with the lateral plate by a narrow somitic stalk or intermediate cell mass. In the more cranial portion, that is opposite the first six somites, the somitic stalk appears to consist of two single layers of cells, separated by a lighter portion extending inwards from the coelom, with indications here and there of a definite lumen. More posteriorly the stalk increases in thickness and more definite cavities can be seen within it, although these never extend into the cavity of the somite itself.

At the anterior end of the 7th somite, almost simultaneously with the formation of the intermediate cell mass, the somatic wall of the latter, about midway between the somite and the lateral plate, becomes slightly thickened, and consists of two or three layers of cells which extend up dorsally towards the ectoderm. The thickening becomes very distinct between the 7th and 8th somites, and forms a marked swelling on the somatic side of the stalk; behind this level it gradually increases in size, becoming more prominent. Plate XXXV, fig. 1, shows the swelling in the region of the 8th somite. Although, perhaps most developed at the cranial end of the 9th somite (plate XXXV, fig. 2), the whole somatic wall of the stalk is much thickened throughout this somite, and at the end of the latter and opposite somite 10 (plate XXXVI, fig. 3) it extends out towards the ectoderm as a definite dorsal outgrowth, which is still well marked posterior to the segmented region of the embryo. Although at the cranial end, opposite somites 7 and 8, the swellings may be slightly more marked at some points than at others, no definite metamerism can be distinguished, the thickenings posteriorly forming a continuous ridge.

At the beginning of the 8th somite for a few sections, and again opposite the 9th, the intermediate cell mass becomes isolated from the somite, and is at the same time marked off from the lateral plate by a constriction; in a cross section through one of these points the mid-region of the stalk appears as a somewhat tubular structure, being composed of cells surrounding a latent lumen (plate XXXV, fig. 1 *a*).

Between the somites and again opposite the middle of each, from the level of the sixth somite backwards, a small portion of the coelom becomes partially cut off from the general body cavity just laterally to the somitic stalk. From between the 8th and 9th somites backwards to the hinder end of the embryo this portion closes in to form a small vesicular chamber, lying immediately to one side of the thickened region of the intermediate cell mass (plate XXXV, fig. 2, *c.ch.*); in front of the 8th somite cranially this structure is less well developed, and opposite the 6th somite can hardly be distinguished. The cavity of the chamber may occasionally extend inwards into the intermediate cell mass.

12 *somites.* The central cavity of the somite is more distinct, and the hinder end of each is united with the lateral plate by the intermediate cell mass, whilst the mid-region of the somite is again connected with the latter by a few cells. Opposite the 6th somite a few cells extend up dorsally from the somatic layer of the stalk, but these disappear, and no thickening is present in the region of the 7th somite. Opposite the 8th and 9th, the middle portion of the stalk remains attached to the lateral plate in the form of a circular mass as in the last stage, its component cells surrounding a lightly staining area in which a central cavity may be distinctly visible (plate XXXV, fig. 4). From the 8th somite posteriorly, this mass increases in size, its somatic wall thickens and extends out towards the ectoderm. This thickening becomes gradually more conspicuous, continuing throughout somite 10 (plate XXXV, fig. 5), and forming opposite the 11th (plate XXXVI, fig. 6 *a*, 6 *b*) and beginning of the 12th somites a prominent solid outgrowth, which lies closely adjacent to the ectoderm, pressing the latter slightly outwards. For some distance behind the segmented region of the embryo, a well marked swelling is to be seen on the somatic side of the intermediate cell mass which is thick in this region. Except opposite the anterior part of the 9th somite, where the swelling appeared to be less marked, no segmentation could be distinguished.

The vesicular chambers, described in the last stage, are now much better developed. They are present opposite somites 10 (plate XXXV, fig. 5), 11 (plate XXXVI, fig. 6 *a*, 6 *b*), and 12, and continue behind the segmented region of the embryo as far back as the shortened primitive streak region or tail bud, forming a series of coelomic chambers, which are becoming separated off from the general body at intervals one behind the other. Some are larger than others, as for example opposite somite 10 (plate XXXV, fig. 5, *c.ch.*) where we find a well marked chamber with a wide central cavity lying ventro-laterally to the thickened portion of the somitic stalk. Fig. 7 *a* and *b* shows the condition near the hinder end of the embryo. I put forward the suggestion, which seems to me a probable one, that these structures represent vestigial pronephric chambers, each one communicating with the general coelom by a peritoneal funnel. In some places, as opposite somite 10, a distinct lumen can be seen passing in from the coelom all along the intermediate cell mass as far as the wall of the somite.

14 *somites.* The sections of this embryo are unfortunately rather oblique, thus making a correct interpretation of the swellings of the intermediate cell mass more difficult in the region of the 8th to the 10th somites on that side.

The pronephric ridge extends from the 8th somite posteriorly. The anterior portion, from the 8th to the mid-region of the 9th somite, is separated from the remainder by a gap of ·04 mm.; behind this gap the ridge extends continuously backwards, gradually increasing in thickness to the end of the 14th somite, marking the limit of the segmented region. Here and there a central cavity may be observed within it. Plate XXXVI, fig. 8, *p.r.* shows the ridge at the level of the 13th somite.

The coelomic chambers, so well developed in the last stage, cannot be recognised anteriorly, but from behind the 10th somite posteriorly there is present what appears as a thickened region of the somitic stalk, somewhat circular in cross section, lying immediately ventro-laterally to the pronephric ridge (plate XXXVI, fig. 8, *th.*). It has a solid connection with the coelomic epithelium, and within it at intervals small central cavities, often very indistinct, may be observed. Opposite this connection a slight groove in the coelomic wall may sometimes be seen. After running for some distance behind the last somite the thickened portion of the stalk disappears, and from this region backwards to near the hinder end of the embryo, we find a series of small coelomic chambers, similar to those of the last stage, in process of separating off from the general body cavity. If we compare fig. 8 with fig. 6 *a* and *b* of the preceding stage, there seems great probability that this thickened region of the stalk represents the united coelomic chambers of the earlier embryo, which have become closed off from the coelom.

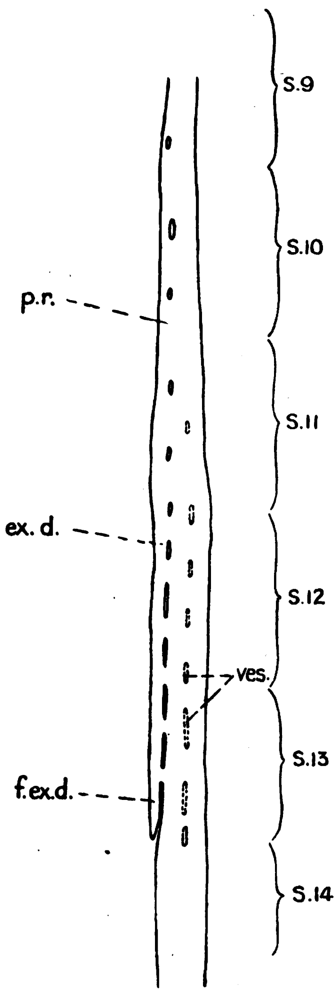
The first indication of the formation of the excretory duct occurs at this stage. On the right side opposite somite 10, the solid dorsal margin of the pronephric ridge is continued backwards for ·03 mm. as a free cellular cord lying close to the ectoderm, the tip of which, only a few cells in thickness, unites once more with the ridge near the end of the somite. Small portions are again separated off from the dorsal margin of the ridge for ·01 or ·02 mm. opposite somites 11 and 12, and at this level they appear to be simply split off at intervals from the ridge, remaining connected with the latter at the intervening points. Whether the condition opposite somite 10, where the distal end of the free portion is distinctly tapering, represents a definite segmental outgrowth, is a question which must be left undetermined until more embryos of exactly this stage are available. In the next stage, an embryo of 16 somites, the dorsal margin of the ridge from near the anterior end of the 13th somite continues posteriorly quite free from the intermediate cell mass as far as the hinder region of the 15th somite. In one embryo of this age, however, its free tip terminates at the level of the anterior end of the 14th somite on the left side. The free portion forms a thin strip of cells, often distinctly tubular, and elongated in a dorso-lateral direction above the somitic stalk.

17 *somites*. The hinder end of each somite is united with the intermediate cell mass, except in the case of the first somite, which is smaller and quite isolated. Opposite the posterior end of the 7th somite there is a slight out-

growth from the dorsal side of the somitic stalk, but this is quite divided off from the ridge behind.

As in the embryo with 14 somites the coelomic chambers have completely disappeared in front of the 11th somite, but from the hinder end of the latter backwards there is present a thickened region of the stalk as described in the last stage. The small central cavities within it have now become more distinct, so that the region from the 11th to the end of the 15th somite takes the form of definite vesicles, attached end to end by solid cellular connections (text-fig. 1, *ves.*). There are two or three vesicles opposite each somite, though they are less developed opposite somite 11; each has a well marked central cavity and is attached to the coelomic epithelium by a solid mass of cells, opposite which a narrow slit-like peritoneal funnel may be present (plate XXXVII, figs. 12 and 13). Behind the level of the 15th somite, the vesicles run back into a solid swollen region of the somitic stalk, and only at about the level at which the 21st somite will later develop do we find small coelomic chambers still being cut off from the general coelom.

The pronephric ridge, from the 8th as far as the anterior portion of the 11th somite, is seen as in preceding stages in the form of a thickening of the intermediate cell mass, but from this level to the end of the 13th somite, where the coelomic chambers have completely closed in, and have become transformed into a longitudinal cord of vesicles, as above described, the ridge passes on to this cord, and appears as a thickening on its dorsal wall, and where vesicles are developed, on the dorsal wall of the latter. This condition is well seen in plate XXXVII, fig. 14, which represents a section through the region of the 12th somite in an older embryo of 19 somites.



TEXT-FIG. 1. Embryo with 17 somites. Diagram of the pronephric ridge (*p.r.*) and primordium of the excretory duct (*ex.d.*), which has split off at intervals from the dorsal side of the ridge. *f.ex.d.* = free distal end of duct. *S* 9, 10, ... = level of somite 9, 10, .... *ves.* = vesicles in the thickened region of the somitic stalk.

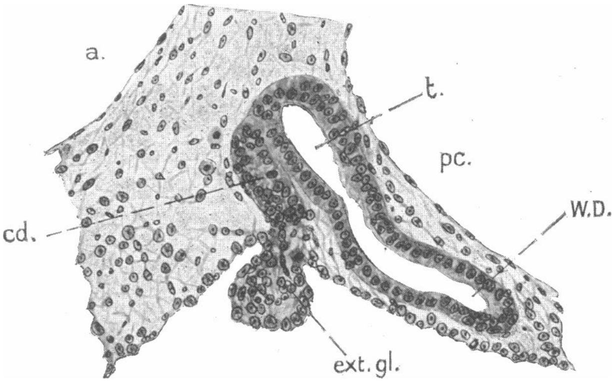
The separation of the excretory duct now is more pronounced. At the anterior end of the 8th somite a few cells pass off from the dorsal wall of the thickened side of the stalk and disappear without again uniting with the latter, but posterior to this level once opposite the end of the 9th somite, twice opposite the 10th (plate XXXVII, fig. 9, *ex.d.*), and three times opposite the 11th and 12th, alternating with the vesicles, the dorsal margin of the ridge becomes split off, anteriorly as a small, posteriorly as a larger mass of cells, elongated in the direction of the long axis of the somitic stalk, and wedged in between the ridge and the ectoderm (text-fig. 1, *ex.d.*). The cells are for the most part radially arranged surrounding either a definite or a latent lumen. Proceeding in the caudal direction, the duct is divided off for longer intervals, so that opposite the 12th somite it is free throughout the greater part of the somite, union only occurring in odd sections. It is, however, very difficult to determine exactly when the duct is completely free, as a dividing line is often not easy to see. The duct is last connected with the ridge at the posterior end of the 13th somite where it terminates on the left, but on the right side it continues back near to the end of the 14th somite as a few cells almost embedded in the ectoderm, the latter at this point being very thin. An excretory tubule later arises opposite each vesicle where the connection with the duct is retained.

19 *somites.* The cranial end of the excretory primordium is now undergoing degeneration. A small solid outgrowth arises from the intermediate cell mass opposite the anterior portion of the 9th somite, but this is quite disconnected from the rest of the organ, the cranial end of which lies on a level with the hinder end of the 9th somite (plate XXXVIII, fig. 20, *p.r.*). The excretory duct is free behind the end of the 14th somite on the right, and behind the mid-region of this somite on the left side (plate XXXVIII, fig. 16), and running posteriorly, diminishes to a few cells which disappear behind the level of the 18th somite. It is noteworthy that posterior to the mid-region of the 14th somite on the left side a definite outgrowth was observed, extending out from the vesicle towards the duct, but failing to reach the latter. The region, therefore, which gives rise to the Wolffian duct, certainly does not extend posteriorly beyond the mid-region of the 14th somite, and very possibly not beyond the 13th somite.

The coelomic vesicles are well marked, three being present opposite the 11th, 12th, and 13th somites (plate XXXVII, fig. 14, plate XXXVIII, fig. 15, *ves.*), and two opposite each succeeding one up to the 16th, where they become less distinct, continuing back into a thickened area of the somitic stalk, which soon becomes solid, and which can be followed to the hinder end as a slightly swollen region of the mesoderm lying immediately adjacent to the coelom. Each vesicle is connected with the coelomic epithelium (plate XXXVIII, fig. 16, *con.*) by a solid mass of cells, opposite which a groove may be present.

In embryos with 20 somites, the vesicles opposite the 16th and 17th somites are already united with the Wolffian duct, the latter extending a short distance behind the 20th somite. Plate XXXVIII, fig. 17 shows the duct (*ex.d.*) near its posterior end in an embryo of 21 somites, lying in an indentation in the ectoderm. In some cases, as was observed in embryos of 22 to 23 somites, solid sprouts appear to grow out from the ventro-lateral wall of the duct towards the vesicle, although more usually, the union between the two is effected by outgrowths from the dorso-lateral wall of the vesicle towards the duct.

*Later stages.* In succeeding stages the pronephric ridge disappears opposite the 8th somite, whilst in the region of the 9th, 10th, and cranial part of the 11th somites small tubular remnants are found, sometimes connected with the coelomic epithelium by a few cells. Behind this level definite mesonephric tubules are developed, although they are only small and vestigial opposite the 11th somite. In embryos of 27 somites for example, three or four are developing opposite the 11th somite, three opposite the 12th and 13th (plate XXXVIII, fig. 18), two or three opposite the 14th, and two opposite each succeeding somite; each is connected with the coelomic epithelium by a short solid band of cells, these bands being more distinct at some places than at others.



TEXT-FIG. 2. Embryo with 45 somites. Transverse section (composite) through the external glomerulus (*ext.gl.*) and first excretory tubule (*t*) in the region of the 9th somite and 6th spinal ganglion. Left side. *a* = aorta. *cd.* = degenerate cord of cells connecting the tubule with the glomerulus. *pc.* = posterior cardinal vein. *W.D.* = Wolffian duct.
(Sl. 5–5–4 to 7)

From the 18th somite backwards the vesicles are no longer united with the excretory duct; they gradually run into each other and their central cavities become reduced. The duct reaches the wall of the cloaca about this stage, and actually opens into the latter in embryos with 36 to 37 somites.

The mesonephric tubules are formed in the typical manner. The vesicle becomes flattened and invaginated, and develops into the Malpighian body, whilst the connection between the latter and the Wolffian duct becomes elongated and coiled to form the tubule. Definite glomeruli first appear in embryos with 35 to 36 somites, from the region of the 12th somite posteriorly; small and very rudimentary glomeruli may develop, opposite the end of the 11th somite, but these always remain vestigial. Plate XXXVIII, fig. 19, shows a well marked glomerulus developing in the region of the 12th somite in the embryo with 35 to 36 somites. At this stage the first somite is very small but apparently has not yet disappeared.

The primordium of the ureter first appears in an embryo of 38 to 39 somites as a slight dilatation on the dorsal side of the excretory duct, some distance behind the last tubule. At this stage, excluding about five tubular remnants at the anterior end, there are altogether 43 tubules on the left side, the last four not yet united with the duct. In an embryo with 50 to 51 somites, where the distal end of the ureter is expanding into the thick walled pelvis, surrounded by a dense layer of mesenchyme, about 50 tubules were counted; of these, one or two at the cranial end possessed only rudimentary glomeruli, whilst two or three glomeruli at the posterior end were very small and poorly developed. At one stage with 45 somites a very small but definite external glomerulus was present on a level with the first degenerate tubule of the left side, in the region of the 9th somite and the 6th spinal ganglion. A solid degenerate cord of cells connected the distal end of the tubule with the glomerulus (text-fig. 2, *ext.gl.*). In no other embryo was an external glomerulus observed.

In the oldest stage examined (about 55 somites) the Malpighian capsules were still connected with the coelomic epithelium either by strands of cells, or, more rarely, by a diffuse cellular mass.

## SUMMARY AND DISCUSSION

The cranial end of the excretory system in the cat is first developed in the form of a continuous ridge, the pronephric ridge, which arises as a thickening of the somatic layer of the intermediate cell mass or somitic stalk uniting the somite with the lateral plate. This thickening, which first appears in embryos with 8 to 9 somites, begins in the region of the 7th somite and increases gradually in thickness from before backwards to the level of the 13th or 14th somite. During the same time as the formation of the ridge, in embryos with 9 to 17 somites, a series of coelomic chambers becomes cut off from the general body cavity. They are very poorly developed anteriorly, but from the 9th somite backwards to the region of the shortened primitive streak, they form a well marked series one behind the other, being most conspicuous in the embryo of 12 somites. I have suggested that these structures represent vestigial pronephric chambers. When best developed (plate XXXV, fig. 5), each forms a well defined chamber lying immediately ventro-laterally to the pronephric ridge and communicating with the general body cavity by a narrow passage, the peritoneal funnel. In older embryos the coelomic chambers disappear completely in front of the 10th somite, probably becoming once more a part of the general coelom, but from this level down to the posterior end, they appear to become closed off from the coelom, and come to form a longitudinal cord of tissue, roughly circular in cross section, the entire cord being connected throughout its length with the coelomic epithelium by a short solid band of cells, representing the united and now closed peritoneal funnels. The cavities of the chambers become very much reduced in the anterior portion from the 11th to the 14th somites but apparently never quite disappear, but behind this level they become completely obliterated. Very soon, however, cavities again appear, and the whole structure becomes divided up into a series of vesicles, three opposite each of the somites from the 11th to the 14th inclusive and two opposite each succeeding somite as far as the latter are developed, each vesicle being united with the coelomic epithelium by a solid column of cells, opposite which vestiges of a funnel may be present as a groove running inwards from the coelom.

In the region in front of the 11th somite the pronephric ridge has the form of a thickening of the dorsal wall of the somitic stalk, but from the hinder part of the 11th to the 13th or 14th somite, it appears as a thickening on the dorsal side of the longitudinal cord of tissue formed by the closed coelomic chambers, and therefore, at the points where vesicles develop, as a swelling on the wall of each vesicle.

From the pronephric ridge the excretory duct takes its origin. The ridge may be represented by a very slight swelling of the somatic wall of the stalk, consisting of a few cells, opposite the 6th somite, whilst opposite the 7th, it is very small and never contributes towards the formation of the excretory duct, nor are any tubules developed in this region. The rudiment opposite the 8th somite is more definite and may possibly take a small part in the composition of the duct. From this level posteriorly, a small portion becomes split off from the dorsal margin of the ridge at regular intervals, the amount separated off increasing in size from before backwards. The points at which connection is retained later become luminated and constitute the excretory tubules; from the region of the 11th to the 13th somites the tubules develop at the level of the vesicles, the splitting off occurring between the vesicles. Thus the region from the 8th or 9th to the 13th somites gives rise to the Wolffian duct, its main seat of origin being opposite the 11th, 12th, and 13th somites. Behind the 13th somite the duct grows back independently, and its union with the vesicles is a secondary one, occurring either as a solid outgrowth from the dorso-lateral wall of the vesicle towards the duct, or apparently sometimes as an outgrowth of the ventro-lateral wall of the duct towards the vesicle. It must be noted, however, that opposite the 14th somite a vesicle may be found to be united with the duct before the latter has begun to grow freely backwards, as in one embryo of 19 somites, so that the region from which the duct arises may extend as far as the 14th somite, and possibly varies in different embryos. In any case, at this level and also opposite somite 15, the union of the vesicles with the duct occurs very early; moreover, as will be seen from the subsequent discussion, the exact point from which the duct begins its independent growth is probably not of great morphological importance.

Unfortunately, the exact mode of origin of the anterior portion of the duct was not determined with certainty. In one embryo, that of 14 somites, a definite but very short outgrowth from the ridge is present at the level of the 10th somite; this extends dorsally and posteriorly, its hinder tapering end, which consists of only two cells, uniting once more with the ridge. Posterior to this level, however, the duct appears simply to become split off from the ridge between the points at which tubules arise, and all signs of metamerism are absent from the first. Whether the condition opposite somite 10 is the normal one, and whether it represents a segmental outgrowth, it was not possible to decide without more embryos of this age. Definite segmental outgrowths, which unite to form the pronephric duct, have been described in the rabbit and mole by Kerens ('07) and at the cranial end in man by Felix ('12). They may possibly occur in the cat opposite the 8th and 9th somites as well as the 10th, but in this mammal the anterior end of the organ is very degenerate, and if a stage of definite segmental outgrowths is present, it is passed through with great rapidity, and could only be observed by the careful examination of many embryos of the same age.

The excretory duct when first formed is solid or possesses a latent lumen, and appears as a mass of cells lying dorsally to the pronephric ridge and just above the vesicles posteriorly to the ridge. Its posterior free tip consists of a fine cellular strand almost embedded in the ectoderm and sometimes almost indistinguishable from it. There is, however, no definite evidence that the ectoderm takes a part in the formation of the duct. Soon a distinct cavity appears within it, and it reaches the ventro-lateral wall of the cloaca in embryos with 27 to 29 somites, actually opening into the latter in stages with 36 to 37 somites.

The anterior end of the excretory organ in the cat is obviously undergoing atrophy. Opposite the 6th and 7th somites degeneration is almost complete, and neither in this region nor opposite somite 8 are any tubules developed. Isolated tubular remnants are present opposite the 9th somite, and posterior to this level they gradually become larger and more definite. They are still rudimentary and few in number opposite the 10th and beginning of the 11th somite, but towards the hinder region of the latter they increase in size and the first internal glomeruli are apparent, although here the latter are always very small and quite vestigial, the anterior end of the functional mesonephros lying in the region of the 12th somite.

The pronephric region in both reptiles and mammals is usually regarded as that region from which the excretory or Wolffian duct arises. That this distinction has no value is shown by Brauer in the Gymnophionan Hypogeophis. Here the pronephros is probably as well developed as in any other vertebrate, except perhaps the Myxinoids, and stretches from the 4th to the 15th segments; twelve pronephric canals are laid down but only the first three of these form the pronephric duct. The level at which the excretory duct becomes independent does not therefore necessarily mark the hinder limit of the pronephros. According to Kerens ('07), the duct takes its origin in the mole from three tubules arising opposite the 8th, 9th, and 10th somites, whilst in the rabbit an extra one is developed opposite the 7th somite. These tubules, which are thus strictly segmental, are all small and atrophy early. Posteriorly to the

10th somite the last tubule passes back into a cellular cord which becomes entirely separated from the lateral plate.

In the marmot as described by Janosik ('04), the dorsal portions of the "middle plate," connecting the somite with the lateral plate, from the distal end of the 6th to the 12th somites, give rise to a cell mass which eventually forms a cell strand, the latter growing distally as the Wolffian duct. The strand remains connected with the coelomic epithelium at intervals by rudimentary canals, six or seven being present. From the level of the 13th somite to the 15th or 16th, the duct is split off as a whole from the dorsal side of the middle plate, and posterior to this region it grows back independently. The cranial portion, as far as the level of the 12th somite, is regarded as homologous with the pronephros, and that between the 12th and 15th or 16th somite is considered as a region of transition between pro- and mesonephros. Here, and posteriorly to the hinder end of the mesonephros, the middle part separates off both from the somite and the coelomic epithelium, forming a cellular cord, which later divides into a species of dysmetameric vesicles. This process strikingly recalls the conditions in the cat. It is worthy of note that the primordium of the mesonephric canals, both in the marmot and the cat, is regarded as a portion cut off from the coelomic epithelium.

In an embryo of the bat, *Rhinolophus hipposideros*, van der Stricht ('13) has described two pronephric vestiges between the 7th and 8th somites, and one between the 9th and 10th on the left side, whilst on the right one is found opposite the 7th somite and two opposite the 8th and 9th.

The pronephros in man, as observed by Felix ('12), extends from the 7th to the 14th segments. Only the three anterior primordia are completely separated from each other and show some metamerism, whilst the hinder tubules are not segmental, altogether six being present opposite the 10th, 11th, and 12th segments. Whether this dysmetamerism is primary or not was not determined owing to want of sufficient material.

In Echidna (Keibel ('03)) vestiges of eight primordia have been observed in the region of the 4th, 5th, and 6th spinal ganglia, behind which typical mesonephric tubules begin, the first glomeruli appearing between the 7th and 8th spinal ganglia, that is presumably between the 10th and 11th somites, at a level only slightly in front of the anterior glomeruli in the cat.

In the marsupial Trichosurus vulpecula (Buchanan and Fraser ('18)) there are a large number (about 14 to 16) of degenerating excretory tubules, beginning opposite the 4th spinal ganglion and extending as far as the 8th, where rudimentary internal glomeruli are developed. As the necessary early stages were missing it was not possible to ascertain how many of these take part in the formation of the excretory duct. In an embryo of Perameles, however, with 15 to 16 somites, the excretory tubules appear to be primarily connected with the duct as far back as the 13th somite, and it is quite possible that this condition also exists in Trichosurus, for it is evident, from our observations on the cat, that the presence of internal glomeruli does not mark the boundary between so-called pro- and mesonephric tubules, as was supposed in the earlier paper on Trichosurus ('18). In Trichosurus, as in the cat, there was absolutely no evidence of the two kinds of tubules occurring in the same segment.

The mode of origin of the mesonephric tubules in the cat follows that described in other forms. The dorsal wall of each vesicle becomes flattened and then invaginated to form the Malpighian capsule, on the dorsal side of which the glomerulus arises. The solid connection between the vesicle and the Wolffian duct soon becomes tubular and coiled, and eventually develops into the secretory and excretory parts of the organ. The vesicles extending from the level of the hinder end of the 11th to the 13th somites, from which the duct takes its origin, give rise to tubules which are serially homologous with those behind this region; all are typical mesonephric tubules. That being so, the distinction in the cat between pronephric and mesonephric regions is purely arbitrary, for no definite line can be drawn between the two areas. The whole excretory organ must be looked upon as one continuous organ, the anterior portion of which shows progressive deterioration from behind forwards.

The view that pro- and mesonephros are different parts of the same organ was first put forward by Balfour and Sedgwick ('79), was later supported by Renson ('83) and Weldon ('83), and has since been upheld by several recent investigators [Wiedersheim ('90) in reptiles, Field ('91) in Amphibia, Price ('97 and '04) in Myxinoids, Brauer ('02) in the Gymnophiona, Kerens ('07) in Reptilia, Aves and Mammalia, Burland ('13) in Chelonia, and Borcea ('05) in Elasmobranchii]. More recently Graham Kerr ('19) has supported the same theory in his text book on the embryology of Fishes and Sauropsida. Many observers [Rückert ('88), van Wijhe ('89) and Rabl ('96) in Selachii, Semon ('92) in Ichthyophis, Hoffmann ('89) in Lacerta, Felix ('91) in the chick, Maas ('97) in Myxine, Wheeler ('99) and Hatta ('00) in Petromyzon, Gregory ('09) in the Turtle] regard the pronephros as having once extended all down the body, but as having later undergone atrophy, being replaced, except in the cranial region, by another series of tubules forming the mesonephros. These authors contend that both pro- and mesonephric canals may develop in the same segments, the mesonephric primordia arising from a more dorsal part of the somitic stalk than the pronephric. It must be said, however, that the figures given to illustrate so-called mesonephric primordia in the pronephric region are quite unconvincing.

It seems very probable, as Brauer ('02) suggests, that the canal-like connection between the somite and the nephrotome, seen in the last stage of separation between the two, has in some instances, been mistaken for a mesonephric canal. In the cat, the portion of the somitic stalk connecting the hinder end of the somite with the pronephric ridge often contains a distinct central cavity, forming, in cross section, a vesicular region of the stalk. This is especially well marked in embryos with 19 somites (plate XXXVIII, fig. 20, *s.q.*), but later completely disappears. In the cat, however, such structures have no connection whatever with the mesonephric vesicles, which arise laterally to the pronephric ridge.

Borcea ('05), in his studies on Elasmobranchii, also considers that the mesonephric canals arise from a more dorsal part of the nephrotome than the pronephric, but that the limits between the two cannot be definitely determined, and he holds at the same time that pro- and mesonephros are parts of one organ, at first similar, but later undergoing physiological differentiation in two directions. This difference in function has led to a difference in development (Borcea, p. 340).

That the external glomeruli of the pronephros are homodynamous with the internal glomeruli of the mesonephros, the one gradually passing into the other, has been pointed out by Sedgwick ('81), also by Renson ('83) and Mihalkovics ('85), although the latter worker did not consider the homology between the two excretory organs a complete one. Many of the later workers also look upon the Malpighian capsules simply as pronephric chambers or nephrotomes, which have become completely closed off from the body cavity, the external glomerulus thus becoming internal. This view is upheld by Wiedersheim ('90) and Burland ('13) in Reptilia, Field ('91) in Amphibia, Price ('97) in Myxinoidei, Brauer ('02) in Hypogeophis, and Borcea ('05) in Elasmobranchii. The similarity of the two structures is illustrated in Lepidosteus (Balfour and Parker ('82) and Beard ('94)) where the glomerulus of the pronephros lies in a chamber which is cut off from the body cavity, and which is identical with a Malpighian capsule. According to Price, who has investigated Bdellostoma, the homology between the two is a very complete one. In the Mammalia this homology has not been demonstrated, the rudimentary state of the anterior end of the excretory organ and the absence of external glomeruli, except in a very degenerate condition, making a comparison between the latter and the internal glomeruli of the mesonephros almost impossible. In early embryos of the cat there is a series of coelomic chambers extending from the 6th somite to the hinder end of the body. Such structures do not appear to have been previously described in a mammal; they are, however, quite definite in the cat, and it has been suggested that they are equivalent to vestigial pronephric chambers. They are especially well developed in the embryo with 12 somites, but they very soon undergo a change, and from the region of the 11th somite backwards, close off from the coelom and come to form an almost solid cord (corresponding with a nephrogenic cord), attached throughout its length to the coelomic epithelium. This cord later divides up into a series of vesicles, the central cavity in each of which, behind the level of the 13th somite, arises secondarily. Each vesicle remains united with the coelomic epithelium by a solid mass of cells. Though it is difficult to demonstrate conclusively that the longitudinal cord of tissue, in which the vesicles arise, is actually derived from the pronephric chambers, this interpretation seems to be the correct one. If so, then the pronephric chambers are homologous with the Malpighian capsules.

The connections of the vesicles with the coelomic epithelium, representing the closed peritoneal funnels, persist for a considerable period. When the Malpighian body is developed, its ventral wall is seen to be connected with the coelomic epithelium either by a more or less definite cord of cells, or by a diffuse mass of mesenchyme, similar to that described in the marsupial Perameles (Fraser, '19). In the cat, these atrophied funnels are still present in an embryo with about 55 somites, but as I have not yet studied older stages; it is not possible to say whether or not they are transformed directly into the rete tubules as in the case of Perameles. The development of the vasa efferentia has, however, been studied by Sainmont ('06). This author states that the rete first appears in embryos of 24 days, when it arises as outgrowths from the walls of the Malpighian capsules. It is not unusual for the peritoneal connection of the mesonephric tubules to be lost and regained, a secondary union arising as an outgrowth from Bowman's capsule towards the coelomic epithelium, and developing finally into a definite open peritoneal funnel. This condition is found, for example, in Hypogeophis (Brauer, '02) and also in Amphibia (Fürbringer '78). That great variation exists is evident from the divergence of opinion expressed by so many observers, not only in different vertebrates but in one and the same species, some attributing the origin of the rete to outgrowths of the Malpighian bodies, others to evaginations of the peritoneal epithelium, and yet others to a condensation of mesenchyme lying between the peritoneum and Bowman's capsules. Many workers, again, experience great difficulty in distinguishing the exact origin of the cells from which the rete is derived.

In conclusion, it may be said that the anterior region of the excretory system in the cat is as well developed as in other mammals, with the probable exception of the Marsupialia and the Monotremata. The number of rudimentary tubules, although slightly in excess of man, is apparently less than in marsupials. The cranial end is undergoing atrophy as in all mammals, and whilst the incompletely formed tubules in front of the 11th somite may possibly have a segmental origin, behind this level all signs of metamerism have disappeared. Vestigial external glomeruli may develop in later stages (e.g. 45 somites) but only rarely; such structures have been described in man, and in the marsupial Trichosurus, but in the rabbit, mole, and marmot they appear to be completely absent. The whole excretory system is composed of one continuous series of tubules, the structure of which increases in complexity in an antero-posterior direction, there being no clear distinction between the anterior tubules ordinarily regarded as forming the pronephros, and the posterior tubules of the mesonephros.

## CONCLUSIONS

The embryonic excretory system in the cat is one continuous organ, the degenerate anterior end passing posteriorly into the fully developed mesonephros.

In early stages an intermediate cell mass or somitic stalk connects the mesoblastic somite with the lateral plate.

A pronephric ridge is developed as a thickening of the somatic wall of the intermediate cell mass. This ridge extends from the level of the 6th to the 13th or 14th somite increasing in thickness from before backwards. The hinder portion, from the region of the 9th somite posteriorly gives origin to the excretory or Wolffian duct.

During the formation of the pronephric ridge and immediately laterally to it, a series of coelomic chambers become cut off from the general body cavity communicating with the latter by a narrow passage. These extend from about the level of the 6th somite almost to the posterior end of the embryo. It is suggested that they represent vestigial pronephric chambers, each with a peritoneal funnel.

The chambers in front of the 11th somite soon disappear, but behind this region it appears as if they become completely closed off from the body cavity so as to form an almost solid longitudinal cord of tissue, attached throughout its length to the coelomic epithelium by a solid band of cells, representing the closed peritoneal funnels.

Later this cord becomes divided into a series of vesicles each united to the coelomic epithelium by a cord of cells. In the region from about the 11th to the end of the 13th somite the cavities of the coelomic chambers become reduced but nevertheless persist, but posteriorly the vesicles arise secondarily within the cord. There are three vesicles opposite the 11th to the 14th somites, and two opposite each somite posteriorly.

The greater part of the Wolffian duct arises in the region of the 11th to the 13th somites. It becomes split off from the dorsal margin of the ridge between the vesicles, connection being retained opposite the latter where tubules later arise. In front of the 11th somite definite segmental outgrowths may possibly occur from the ridge, the distal ends of which unite to form the anterior end of the excretory duct.

Behind the level of the 13th or 14th somite the duct grows back independently, its free tip lying in an indentation of the ectoderm. There is no direct evidence that the ectoderm takes a part in its formation.

The Wolffian duct reaches the wall of the cloaca in embryos with 29 somites and opens into the latter in embryos with 36 to 37 somites.

From the 11th to the 13th somites the connection of the vesicles with the Wolffian duct is thus primary, behind this level the union is a secondary one.

Each vesicle develops into the Malpighian body of a mesonephric tubule and the connection between the vesicle and the duct becomes the excretory tubule.

Definite mesonephric tubules are present from the level of the hinder end of the 11th somite posteriorly, though the glomeruli at the extreme anterior end are quite rudimentary. In front of this level only vestigial tubules are developed.

An external glomerulus was observed in only one embryo with 45 somites in the region of the 9th somite and the 6th spinal ganglion.

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## REFERENCE LETTERS

*a* = dorsal aorta; *b.c.* = body cavity; *c.ch.* = coelomic chamber; *ect.* = ectoderm; *ent.* = entoderm; *ex.d.* = excretory duct; *m.p.* = medullary plate; *n.* = notochord; *n.t.* = neural tube; *p.f.* = peritoneal funnel; *p.r.* = pronephric ridge; *S*1, 2, ... = somite 1, 2, ... ; *smpl.* = somatopleure; *spl.* = splanchnopleure; *ves.* = coelomic vesicle.

## DESCRIPTION OF PLATES

The figures are reproduced at a magnification of 200 diam.

Fig. 1 *a*. Embryo with 9 to 10 somites. Transverse section at the level of the 8th somite, showing the somitic stalk or intermediate cell mass at the point where it is isolated from the somite. Left side. (Sl. 2–6–14.)

Fig. 1 *b*. Embryo with 9 to 10 somites. ·01 mm. behind *a*, showing the thickening of the dorsal wall (*p.r.*) of the somitic stalk. (Sl. 2–6–15.)

Fig. 2. Embryo with 9 to 10 somites. Transverse section at the level of the 9th somite on the left side, showing the coelomic chamber (*c.ch.*) and thickening of the somitic stalk. The latter in this section is not united with the somite. (Sl. 2–7–8.)

Fig. 3. Embryo with 9 to 10 somites. Transverse section at the level of the 10th somite, showing the thickening of the somitic stalk (*p.r.*). (Sl. 2–7–16.)

Fig. 4. Embryo with 12 somites. Transverse section through the hinder end of the 8th somite, showing the mid-region of the somitic stalk, which is attached to the lateral plate and disconnected from the somite. Left side. (Sl. 2–1–14.)

Fig. 5. Embryo with 12 somites. Transverse section at the level of the 10th somite, showing the well developed coelomic chamber (*c.ch.*) and the pronephric ridge (*p.r.*). The peritoneal funnel does not appear in this section. Left side. (Sl. 2–3–11.)

Fig. 6 *a* and *b*. Embryo with 12 somites. Two consecutive transverse sections at the level of the 11th somite, showing the pronephric ridge (*p.r.*) and the coelomic chamber (*c.ch.*) with its peritoneal funnel (*p.f.*). Left side. (Sl. 2–4–10 and 11.)

Fig. 7 *a* and *b*. Embryo with 12 somites. Two consecutive transverse sections in the region of the shortened primitive streak, showing a coelomic chamber (*c.ch.*) with its peritoneal funnel (*p.f.*). Left side. (Sl. 3–3–10 and 11.)

Fig. 8. Embryo with 14 somites. Transverse section at the level of the 13th somite, showing the pronephric ridge (*p.r.*) and the thickened region of the somitic stalk (*th.*) derived in all probability from a closed coelomic chamber. Right side. (Sl. 3–4–7.)

Fig. 9. Embryo with 17 somites. Transverse section at the level of the 10th somite, showing the separation of the excretory duct (*ex.d.*) from the dorsal margin of the pronephric ridge (*p.r.*). Left side. (Sl. 4–3–8.)

Fig. 10. Embryo with 17 somites. Transverse section showing the pronephric ridge (*p.r.*) at the level of the 10th somite. Right side. (Sl. 4–3–9.)

Fig. 11. Embryo with 17 somites. Transverse section showing the pronephric ridge at the level of the 11th somite. Right side. (Sl. 4–5–7.)

Fig. 12. Embryo with 17 somites. Transverse section at the level of the anterior end of the 13th somite, through the anterior wall of a vesicle (*ves.*), and showing the last vestige of the peritoneal funnel (*p.f.*). The excretory duct (*ex.d.*) lies free above the vesicle. Right side. (Sl. 5–2–3.)

Fig. 13. Embryo with 17 somites. Transverse section, ·03 mm. posterior to fig. 12, showing the central cavity within the vesicle, and the free excretory duct (*ex.d.*) above the latter. (Sl. 5–2–6.)

Fig. 14. Embryo with 19 somites. Transverse section in the region of the 12th somite, showing the pronephric ridge (*p.r.*) forming a thickening of the dorsal wall of the vesicle (*ves.*). (Sl. 1–7–15.)

Fig. 15. Embryo with 19 somites. Transverse section at the level of the 13th somite, showing the free excretory duct lying immediately dorsally to a vesicle, and a short distance behind its last connection with the pronephric ridge. Left side. (Sl. 4–5–10.)

Fig. 16. Embryo with 19 somites. Transverse section between the 14th and 15th somites, showing the solid connection (*con.*) of a vesicle with the coelomic epithelium. The now luminated excretory duct is seen lying dorsally to the vesicle. Left side. (Sl. 1–9–6.)

Fig. 17. Embryo with 21 somites. Transverse section showing the excretory duct (*ex.d.*) near its hinder end lying in an indentation of the ectoderm. *s.mes.* = somitic mesoderm. (Sl. 7–4–5.)

Fig. 18. Embryo with 27 somites. Transverse section through a developing mesonephric tubule at the level of the 13th somite. Right side. *M.c.* = future Malpighian capsule. (Sl. 2–1–17.)

Fig. 19. Embryo with 35 to 36 somites. Transverse section at the level of the 12th somite and 9th spinal ganglion, showing an excretory tubule (*ex.t.*) with its developing glomerulus (*gl.*). Left side. (Sl. 3–4–5.)

Fig. 20. Embryo with 19 somites. Transverse section between the 9th and 10th somites, showing the vesicular region (*S.* 9) of the somitic stalk connecting the hinder end of the 9th somite with the pronephric ridge (*p.r.*). Right side. (Sl. 1–5–9.)

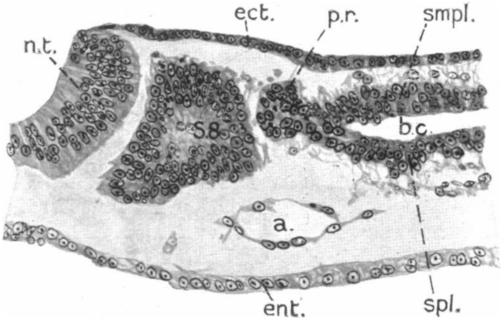
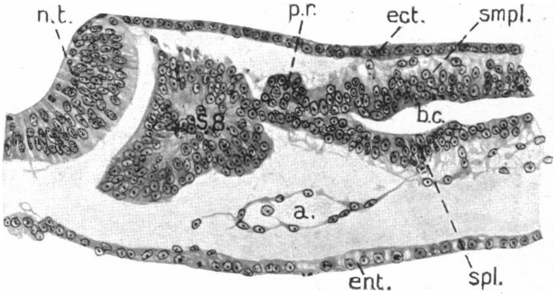


**Fig. 1a.**



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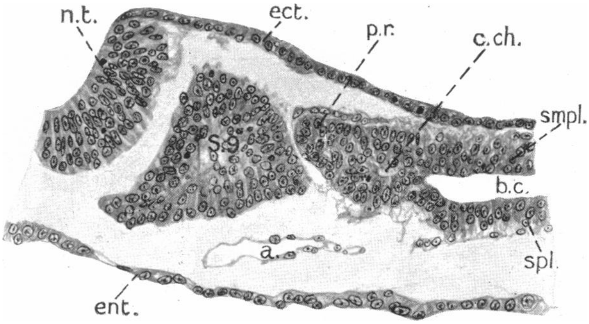

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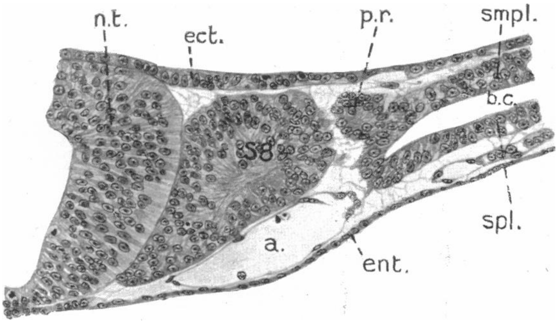

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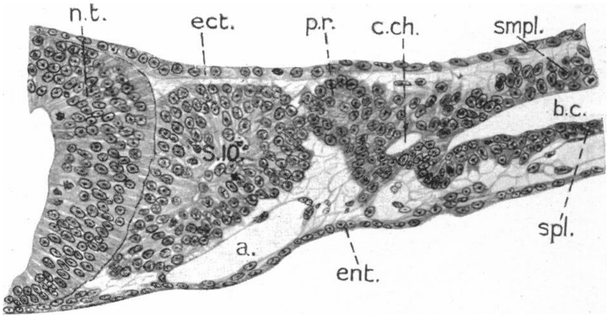

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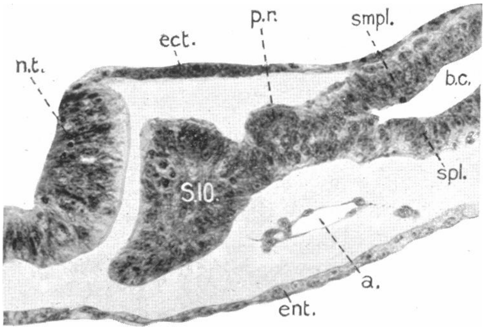

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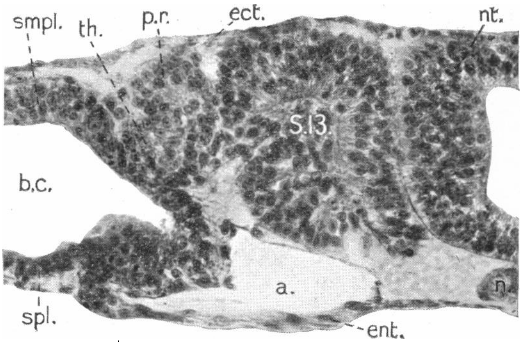

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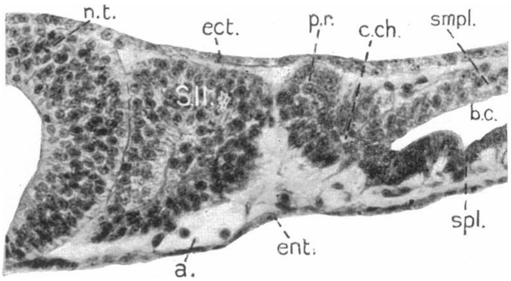


Fig. 6a.

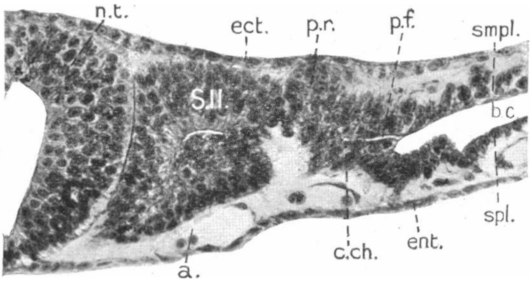


Fig. 6 b.

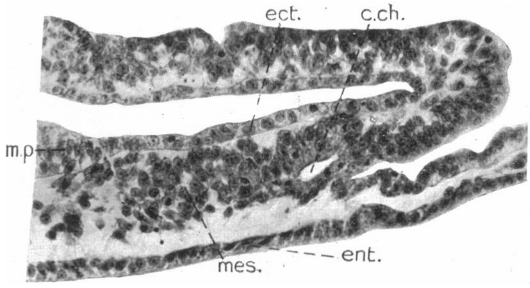
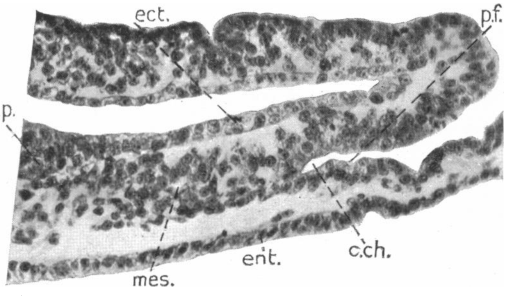


Fig. 7a.



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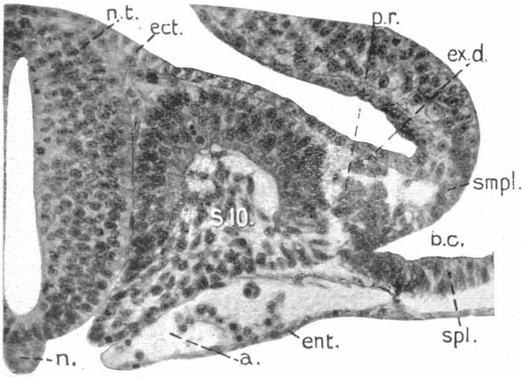


Fig. 9.

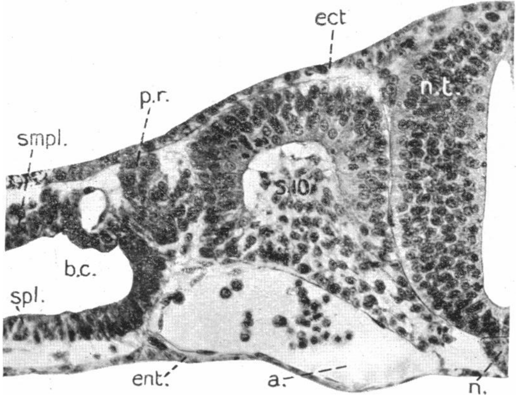


Fig. 10.

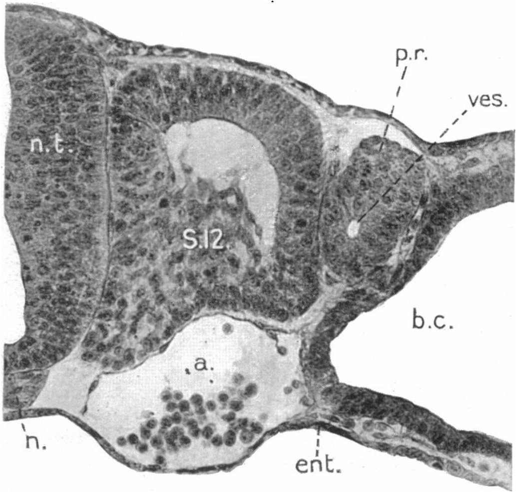


Fig. 14.

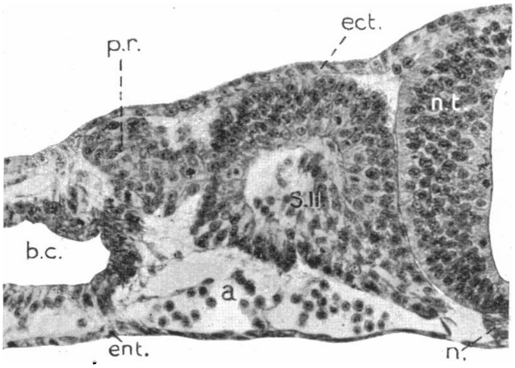
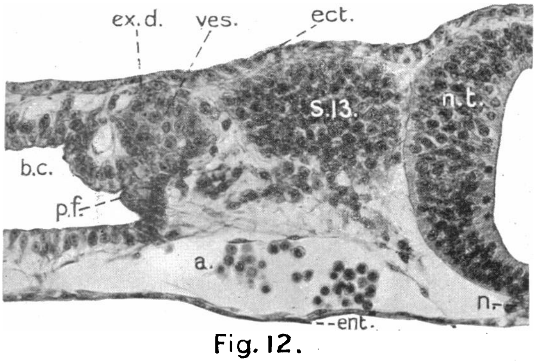


Fig. 11.



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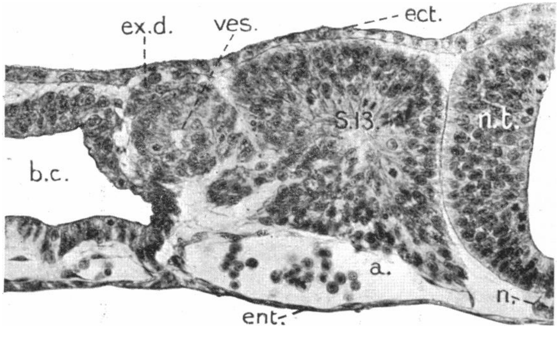

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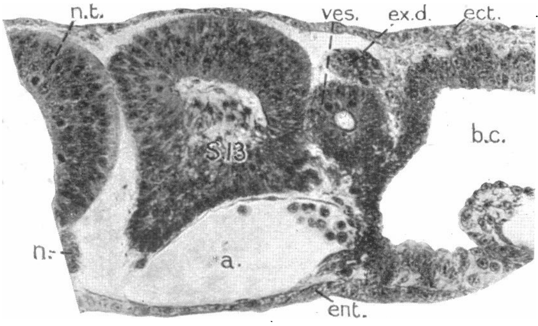

Fig. 15.

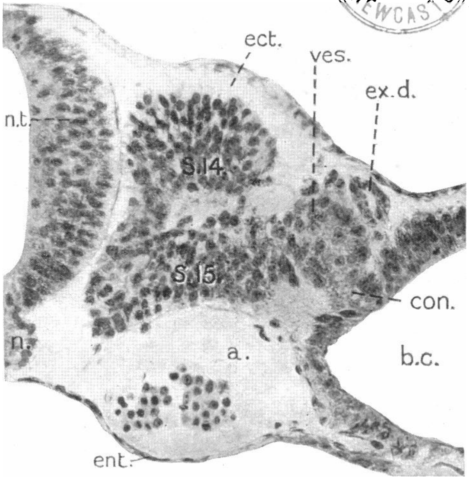

Fig. 16.

Fig. 18.

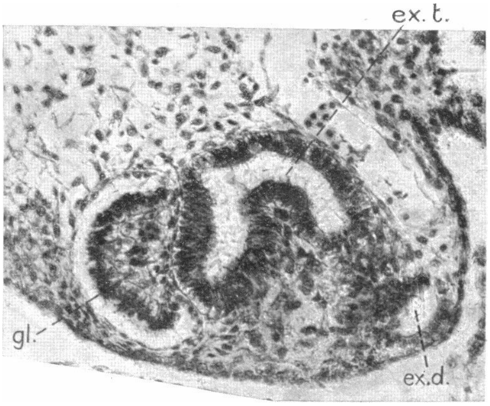

Fig. 19.

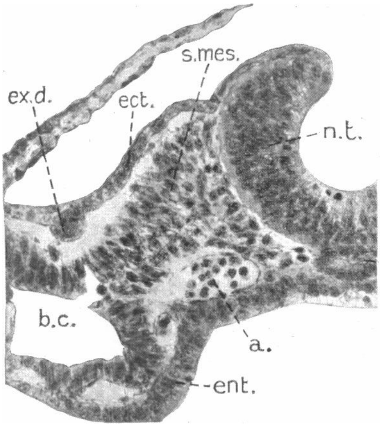

Fig. 17.

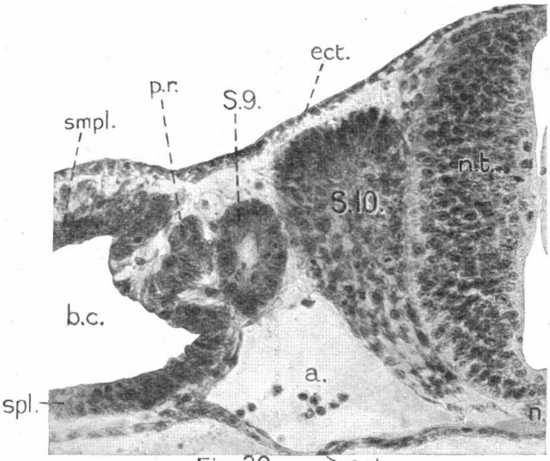

Fig. 20.