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CONTRIBUTIONS TO THE EMBRYOLOGY

of the

MARSUPIALIA

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II On a further Stage in the Placentation of Perameles.

Introduction.

In the present paper I deal with a stage in the placentation of Perameles, somewhat later than my previous Stage D. (1) Beyond the demonstration of the persistence of the entire yolk-sac wall, no strikingly new facts have been brought to light in the investigation but I have been enabled to essentially confirm my previous account and to add additional information on certain points of detail, especially as regards the yolk-sac vessels. In addition I give an account, in the sequel, of the foetal membranes of a species of Macropus, for comparison with those of Perameles and I also take this opportunity of giving a somewhat extended account of the female urogenital organs in Perameles with especial reference to the phenomena of parturition. This is all the more necessary since the examination of further material has convinced me that the structures to which in my previous paper I gave the name of "uterine canals" are, in reality, not exclusively uterine but comprise portions derived from the lateral vaginal canals, and which form a median vaginal apparatus homologous with that existing in other Marsupials. It is with much satisfaction, in view of my interpretation of the allantoic placenta of Perameles as a primitive feature of its organisation, that I am thus enabled to bring its apparently peculiar parturition phenomena into line with those occurring in certain other Marsupials. And I believe that the present investigation demonstrating as it does the extremely primitive condition of the genital organs of Perameles serves materially to strengthen the position I have taken up as regards the significance of the occurrence of an allantoic placenta in the genus.

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(1) The Placentation of Perameles. Q. J. M. S. Vol.40 p.411.

Stage D'. P. obesula.

The female, a specimen of the short-nosed Bandicoot, P. obesula, upon the examination of whose genital organs, the account of the present stage is based, came into my hands a few hours after death. Post-mortem change however was not at all apparent and the genital organs were at once cut out and preserved in picro-nitric acid.
Both uteri were much enlarged; the right measured 22 mm. in length by 11 mm. in breadth, the left 21 mm. by 15 mm. Each contained a single embryo (Plate II fig. 3.) measuring in greatest length, 12·5 mm and in head length 6·5 mm. The structural characteristics of the embryo of this stage are given in the appendix.
Both uteri were submitted to macroscopical examination, while the right uterus and its embryo were alone examined microscopically.

Foetal Membranes.

In Fig 1. Plate I, the embryo is shown in situ in the right uterus, the ventral wall of which has been removed. It was noticed at once that the yolk-sac wall was not even slightly adherent to the surface of the mucosa. Whether this non-adherence is due to post-mortem change or to natural causes I am unable to decide. It is quite possibly due to the latter latter since the yolk-sac placenta is now in a largely degenerate condition.
In the figure, the vascular omphalopleure and the yolk-sac splanchnopleure which were cut through along their line of attachment to the margin of the allantoic-placental area, have been reflected outwards. The embryo is seen lying on its right side with its head end next the anterior end of the uterus and its long axis in the antero-posterior axis of the same. In the left uterus the head of the embryo lay next the posterior end of the uterus so that its position is an inconstant one. The embryo is situated of course, in the extra-embryonic splanchno-coele which has been opened into by the reflection of the yolk-sac splanchnopleure and is invested by the amnion. The latter is reflected from the distal end of the thick stalk which arises from the mid-region of the ventral abdominal wall. This stalk - the umbilical stalk - (fig 1. u.s.) is a tubular prolongation of the abdominal wall which encloses a portion of the coelom and the upper ends of the allantoic and yolk stalks (fig 4. Plate II). From the yolk stalk, the yolk-sac splanchnopleure is reflected closely round the embryo. It becomes continuous with the vascular omphalopleure along the line of union of the latter with the marginal zone of chorion which is present round the allantoic placental area.
The allantoic stalk (fig 1. all. s.) on leaving the umbilical stalk, passes outwards and forwards, and then curving mesially forms a single loop upon itself, hence it passes over the

right side of the embryo to reach the centre of the allantoic placental area (fig. 1. pl.a.) a portion of which is visible behind the back of the embryo.
In fig. 2 Plate I, the embryo has been removed to expose the placental area. In both uteri the placental area is roughly oval in shape as in Stage D and situated on the mesial side of the uterus. It is bounded by a continuous ridge-like thickening of the mucosa so that the area itself appears depressed below the general level of the inner surface of the uterus. Through the thin walls of the vesicular portion of the allantois, the irregularly ridged surface of the placental syncytium could be made out. The inner surface of the mucosa of the rest of the uterus also presents a ridged appearance.
The placental area of the right uterus measures approximately 8 mm in length by 6 mm in breadth - that of the left uterus was somewhat larger, measuring 8.5 mm by 9 mm. The allantoic stalk has now a length of about 16 mm. i.e. just double the length of the stalk in the preceding Stage D, and it is now also just about double as thick as in that stage.
As in previous stages, the outer or placental surface of the vesicular part of the allantois is found not to occupy the entire extent of the original chorionic area so that there is left outside its margin i.e. outside the margin of the placental area, a narrow annular zone of persistent pure chorion which surrounds the placental area and which is attached on the one side around the margin of that area and on the other passes into the vascular omphalopleure along the line of junction of the latter with the yolk-sac splanchnopleure (Plate III fig 6. ch.)
The placental area of the present stage as seen in surface view is essentially similar to that of Stage D. The allantoic stalk (Plate 1. fig 2. all. s.) is seen to join the inner surface of the flattened vesicular portion of the allantois near its centre. In the stalk run the two allantoic arteries and the single vein. The latter is situated above the two arteries and is hence not visible in the figure. At the distal end of the stalk, the vessels branch out over the inner (coelomic) wall of the vesicular part of the allantois. The two arteries - the one running forwards to supply the anterior portion of the placental area, the other passing back to similarly supply the posterior portion of the area - eventually divide, each into two branches. These pass outwards, dividing as they go, to the margin of the allantoic vesicle round which they and their branches pass to reach its outer or placental surface where they break up into capillaries in the allanto-chorionic mesenchyme.
The allantoic vein is formed by the union of two main factors (fig. 2. all. v.) which accompany the corresponding arteries. The main arterial branches are each accompanied by a corresponding venous trunk but the smaller arterial

branches may or may not be so accompanied. The vitelline artery (fig. 2, vit. art.) emerging from under the distal margin of the umbilical stalk. passes in the yolk-sac splanchnopleure, at first almost directly backwards, then curves mesially and slightly forwards to reach the margin of the chorionic zone where it passes over into the vascular omphalopleure. There it at once divides into its two branches which diverging in opposite directions form the sinus terminalis (figs 1 & 2 s.t.). the two branches being united by a delicate anastomosis.
The vascular omphalopleure (figs 1 & 2, vasc.omph.) is readily distinguishable macroscopically from the bilaminar omphalopleure (figs 1 & 2. bil. omph.) lying outside the sinus, by its more opaque appearance and yellowish colour. Owing to the fact that the vitelline artery at once divides on reaching the vascular omphalopleure, the vascular area has at this point no existence but as the two branches of the artery pass out, they at the same time diverge away from the margin of the placental area and the vascular area thus gradually increases in width until a maximum of 5 mm. is reached about opposite the point of bifurcation of the vitelline artery. The vascular area has a maximum diameter of 12.5 mm. It will be shown later that the extent of the vascular area of the Perameles embryo of this stage is considerably less than that of a Macropod embryo at a somewhat earlier stage of development. What, however, especially characterises the vascular area of this stage as well as that of my preceding stage D is its relatively extremely poorly developed capillary system. Branches are, indeed, given off from the sinus into the vascular area but these are small and by no means numerous and apparently undergo very little secondary branching.
Below, I describe the foetal membranesof an embryo of Macropus parma and from that account and the accompanying figure (Plate IV. fig. 1,), it will readily be seen that the branches given off from the sinus terminalis into the vascular area are not only numerous but richly branched. They form a highly developed capillary system, almost entirely unrepresented in Perameles, in correspondence with the fact that in Macropus, the embryonal nutrition is carried on solely by means of the yolk-sac vessels of the vascular area,while in the Perameles embryo of this stage, the allantoic circulation is now playing the dominant part in the nutrition of the embryo, only an insignificant proportion of the nourishment necessary for the growth of the latter being conveyed through the yolk-sac vessels. In my previous paper, I put forward the suggestion that probably the entire yolk-sac wall disappeared before the end of intra-uterine life. The present stage, however shows that at all events up to this period of development the entire yolk-sac wall remains intact, although greatly reduced in functional importance as shown by the poor development of its vessels.
The yolk-sac splanchnopleure is supplied with blood by numerous fine wavy vessels (fig 1. a.v.) which arise

directly from the vitelline artery - especially from its first part - as it courses over that membrane. In fig.2. one main branch is seen passing from under the free margin of the umbilical stalk. It divides up into numerous small wavy branches which pass up parallel with the vitelline veins. Behind this numerous branches arise separately from both sides of the artery (fig. 2. vit. art.) In the terminal part of the course of the latter fewer and shorter branches are given off. The blood from these fine vessels apparently passes over into the vascular area at the line of junction of the splanchnopleure with the vascular omphalopleure.

Semon (1) has also described the occurrence of similar fine branches of the vitelline artery in the two forms examined by him (**Phascolarctus cinereus & Aepyprymnus rufescens**) Such also occur in Macropus parma. The blood from the vascular area is returned by two vitelline veins (figs. 1 & 2, vit. v.) each of which is formed by the union of two main factors, shortly after they enter the yolk-sac splanchnopleure. As in Stage D. the 2 vitelline veins run back in the splanchnopleure over the left side of the head of the embryo (fig. 1), enclosing between them a narrow triangular area altogether devoid of vessels. The two veins gradually approximate as they pass back and eventually run side by side. In this region the amnion is found connected with the yolk-splanchnopleure by a narrow wedge-shaped band of mesoderm which separates the two veins,(Plate II, fig. 5, mes.). This narrow connection is all that is now left of the much larger proamniotic remnant seen in Stage D. Not only in the area now less in extent but the mesoderm has penetrated completely across it. The ectoderm of the amnion over the remnant is thickened,(fig 5,ect.) the cells being club-shaped in form with the nucleus situated in the outer projecting part of the cell. The entoderm of the yolk-sac splanchnopleure over the remnant is likewise thickened but irregularly. (fig.5,ent .)

As the vitelline veins are traced back towards the umbilical stalk they gradually become smaller and at the same time pass over from the yolk splanchnopleure towards the amnion in the now greatly thinned bridge of mesoderm of the proamniotic remnant which posteriorly becomes continuous with the thin, and attenuated yolk stalk carrying the vitelline artery. At the anterior margin of the umbilical stalk the two veins unite to a single trunk. This runs up in a thin fold of mesoderm continuous with that of the proamniotic remnant and which connects the yolk-stalk with the inner surface of the tubular umbilical stalk.(fig.4). In the upper part of the umbilical stalk the vitelline vein becomes considerably reduced in size and is a much smaller vessel than the allantoic vein. In this stage the vitelline vein is very remarkably reduced as compared with the same vessel in Stages C & D. The vitelline artery in the upper part of the umbilical stalk is also a quite insignificant trunk, about half the size of one of the allantoic arteries, although

(1). Semon. "Die Embryonalhüllen der Monotremen u. Marsupialier" Zool. Forsch.in Australien. Bd. II.

its diameter is considerably greater as it courses over the yolk-sac splanchnopleure. These facts are sufficient to show that at this stage the yolk-sac vessels play a quite insignificant part in the nutrition of the embryo as compared with their functional importance in Stages C. & D.

The bilaminar omphalopleure calls for no special mention here beyond the remark that it composes the larger half of the entire surface of the globular embryonic formation.

STRUCTURAL DETAILS.

The following account of the structural features of the uterus and foetal membranes is made very brief in view of the close agreement of this stage with my previous Stage D. In writing up the present paper, I have had after an interval of a year, to carefully re-examine many of my old preparations and compare them with those of this stage, with the result that I am able to substantially confirm my previous account.

1. Uterus - The serosa, muscularis, and corium present essentially the same appearances as in Stage D. The uterine glands are considerably enlarged and lined by a low cubical epithelium. Very numerous blood vessels occur in the much attenuated interglandular connective tissue.

(a) Allantoic Placental Syncytium. -This has the same average thickness as in Stage D viz. .12 mm. and shows no differences from that stage worthy of remark, beyond the fact that its capillary system is somewhat better developed, the capillaries being on the whole larger. As in that stage owing to the projection of the superficial capillaries, the syncitial surface presents an irregularly ridged appearance.(Plate III, fig 7. syn. c.).

(b) Syncytium beyond allantoic Placental area. - the portion in contact with the vascular omphalopleure is also of the same average thickness as in Stage D. viz. .09 mm. In other respects also the same features are visible. The superficial capillaries are fairly abundant but on the whole, very much smaller than those of the placental area and not quite so well developed as in Stage D. The Syncytium in contact with the bilaminar omphalopleure is a thinner and much less regular layer and less vascular.

II. Foetal Membranes -

(a) Chorionic Ectoderm - Over the placental area usually single, much degenerated and deeply staining chorionic ectoderm cells are still to be found but are not numerous. Of the marginal zone of chorionic ectoderm seen persistent in Stage D, only traces now remain in the form of isolated and often much altered cells. Occasionally such cells are found forming the transition to the ectoderm of the zone of pure chorion (Plate III. fig. 6. ch.) which exists between the outer margin of the allantois and the vascular omphalopleure (Plate III. fig. 6 ch. ect.). The ectoderm cells of this chorionic zone are usually enlarged close to the margin of the placental area but rapidly diminish in size as they pass outwards.

(b) Allantois and Allantoic Placenta. - The allantoic stalk is more or less rounded in section and where it lies enclosed by the umbilical stalk, has a diameter of .5mm. The allantoic canal (fig. 4. all. c.) is no longer perfectly continuous and its entodermal lining is only recognisable in places. Curiously enough the allantoic vessels appear to be smaller than in Stage D but the difference in size is not so disproportionate as in the case of the vitelline vessels in the two stages. As regards the vesicular portion of the allantois and the allantoic placenta I have little of importance to add to the description already given of the same parts in Stage D. It may be mentioned that small numbers of maternal leucocytes occur in the allantoic cavity.
A fairly typical section of the allantoic placental area is shown in Plate III. fig. 7. from which it will be seen that except perhaps for an increase in size of both foetal and maternal capillaries the description already given of the allantoic placenta in Stage D. holds good certainly up to this stage of gestation and without doubt also for the whole period of intra-uterine life, a conclusion already arrived at from the conditions presented by the post-partum uterus described in my previous paper.

(c) Vascular omphalopleure and yolk-sac placenta.-
The entodermal cells of the vascular omphalopleure, some of which were found in Stage D. to be undergoing enlargement, are now found to have all increased in size, and to form a uniformly much thicker layer than in that stage. The cells are mostly somewhat cubical in form, with rounded projecting ends. (Plate II. fig. 8, ent). Their protoplasm and nuclei stain deeply. Over the sinus terminalis (fig. 8. s.t.) the entoderm cells are also enlarged and as in previous stages are club-shaped in form, with the nucleus situated in the outer projecting part of the cell.
It seems highly probable that this hypertrophy of the entodermal cells of the vascular omphalopleure, commencing as it does about the time the allantoic placenta begins its functional activity, is to be associated with the functional retrogression of the yolk-sac placenta consequent upon the establishment of the allantoic one. For, whether the ectoderm of the vascular omphalopleure be adherent to the surface of the syncytium or not, the condition of the yolk-sac vessels shows us that the yolk-sac placenta, if we can any longer speak of such, is now functionally the mere shadow of its former self. The ectoderm of the vascular omphalopleure though still a comparatively thin layer is slightly thicker than in preceding stages - the cell bodies being richer in protoplasm (Plate II fig.8. ect.

(d) Bilaminar Omphalopleure. -
The ectoderm of the bilaminar omphalopleure (Plate II

fig 8, ect.) is just about double as thick as that of stage C. The cells are large and somewhat irregular in shape with projecting outer ends. Their protoplasm is considerably vacuolated. In Didelphys, according to Selenka(1), the ectodermal cells of both the vascular and bilaminar omphalopleure undergo enlargement during the last two days of intra-uterine life. Selenka regards the enlargement of these cells as associated with their functional activity in transmitting the secretion of the uterine glands into the yolk sac but here again I am inclined to look upon the hypertrophy as a sign of degeneration.
The entoderm of the bilaminar omphalopleure is a very much thinner layer than the ectoderm, and consists of flattened, attenuated cells. (Plate II fig. 8.)

In concluding the description of this stage I may remark that since the completion of my previous paper on the Placentation of Perameles. I have discovered that the Native Cat, Dasyurus viverrinus , is also provided with a placental connection of a somewhat complex nature and probably of yolk-sac origin but whether or not there is also present an allantoic placental connection I am unable to state. My series of stages is as yet very incomplete and does not permit me to enter into details but this much is certain:- over certain portions of the inner surface of the uterus there is present a syncytial layer formed by the fusion of the ectoderm of the bilaminar omphalopleure with the uterine epithelium, the nuclei of which form nests of the syncytium of Perameles and this conjoint layer is vascularised by maternal capillaries. But whereas in Perameles the syncytium clothing the inner surface of the uterus is entirely of maternal origin being derived from the uterine epithelium, in Dasyurus it is partly of foetal origin (foetal ectoderm) and partly of maternal origin (uterine epithelium).
The foetal membranes are left behind in the uterus after parturition and as in Perameles the foetal and maternal portions of the placenta are absorbed in situ through the agency of maternal leucocytes. In other words the placenta of Dasyurus like that of Perameles is contra-deciduate in character. We have then in any discussion bearing on the general question of the significance of the occurrence of an allantoic placenta in Perameles to face the fact that a placenta of the contra-deciduate type has been found to

(1) Selenka. Studien über Entwickelungsgeschichte der Thiere IV (1 & 2) Das Opossum (virginiana). p.137 & 138.
Didelphys

exist in two distinct genera of Polyprotodont Marsupials and that the uterine epithelium in both forms undergoes an essentially similar transformation into a syncytium vascularised by maternal capillaries.

APPENDIX.

Organisation of Embryo. P.obesula. (Plate II. fig. 3.)

Measurements:- Greatest length, occiput to rounded hinder end of body 12.5 mm. Head Length 6.5 mm.
Form of body:- Head raised but not so much as in new-born and forming an acute angle with the trunk. Prominent snout. Slight neck protuberance. Lips fused laterally to form "Saugmund", the line of junction still recognisable. Mouth, lozenge-shaped. Tongue projects prominently from mouth and is grooved dorsally.
Eyes, distinct, roughly oval in shape and not covered by epitrichium. In front of cloacal opening is a small projecting "genital höcker."
Limbs:- Much as in new-born except that the claws are less developed. Fore-limb: flexed at elbow and palmar surface directed backwards. The 1st and 5th digits quite small tubercles, 2nd 3rd & 4th provided with short blunt recurved claws, the 3rd digit the largest.
Hind Limb: paddle-like with plantar surface directed mesially. Digits all indicated but not free from each other. The 4th the largest.

Notochord and Vertebral Column: Notochord intra-vertebrally constricted. Marked cartilaginous centra with transverse processes and neural arches, the latter not yet united above the spinal chord.

Nervous System: Marked fissura arcuata along mesial hemisphere wall. Budding from hypophysis anteriorly but not very marked.

Eye: Outer wall of optic cup about half pigmented. Ovalish lens cavity. Optic stalk solid in its middle portion. Eyelids not yet united.
Eye-muscles developing.

Ear: Semicircular canals formed. Cochlea bent. Periotic capsule partly pro-cartilage, partly cartilage. External auditory meatus plugged by epidermal cells.

Nose: Much as in new born. Choana formed. Turbinal projections arising and Jacobson's organ formed and its cartilage present.
Solid lachrymal ducts which reach the nasal epithelium.

Mouth: Palate formed and invests glottis posteriorly. Club-like tooth-germs but no enamel organs. Tongue, grooved and with distinct taste buds . Submaxillary salivary glands open into mouth.

Alimentary Canal &c:- Lateral thyroid anlagen on sides of trachea. Thymus anlagen approximated in their middle regions but free posteriorly. Extensive pancreas, its duct opening into bile-duct. Lungs with numerous simple alveoli. Cartilaginous rings round trachea. Diaphragm complete and muscle fibres developing in it. Intestinal loop no longer projects at navel.

Heart and Vessels: Ventricular septum not yet complete. Auricular septum complete and a foramen ovale present. Sinus venosus still extensive. Truncus aortae almost completely divided. Left ductus Botalli present. Single dorsal aorta. Renal portal circulation in connection with Wolffian bodies. Allantoic circulation greatly predominates over yolk-sac circulation.

Urogenital System: Mesonephros of large size. Peritoneal funnels of Mullerian ducts present. Commencing renal tubules. Ureters open into urogenital sinus mesially to Wolffian ducts. Genital-leisten prominent, sex ?.

Skin and Skeleton:- Thin nucleated epitrichial layer on epidermis. Hair anlagen well advanced on head. No ossification in cartilaginous skeleton. Premaxillary, maxillary and palatine ossifications. Rudimentary clavicle ossified. (1).

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(1). This is also present in the 8·75 mm. embryo of Stage D.

III. ON THE FOETAL MEMBRANES OF MACROPUS PARMA.

The following account of the foetal membranes of this small Wallaby is based on the examination of a single embryo from the left uterus, for which I am much indebted to Mr. J.J. Fletcher M.A., B.Sc.

Historical. (3)

In 1834, Owen (1) gave an account of the foetal membranes of an embryo of M. Major, 7 lines in greatest length, but no allantois was found in this embryo. In 1837, however the same author described (2) the existence of "a small allantois of a flattened pyriform figure" in an embryo of M. Major, 10 lines in length and pointed out that "the allantois depends freely from the end of the umbilical chord and has no connection at any part of its circumference with the adjoining membrane."
In 1881 Chapman also described (4) the foetal membranes of an embryo of M. Major, "six-eights of an inch in length from the mouth to the root of the tail." His account essentially confirms Owen's observations.
In 1884, Caldwell (5) in a paper on the arrangement of the foetal membranes in Marsupials first clearly pointed out that the embryo lay in the splanchnocoele surrounded by the invaginated upper portion of the yolk-sac wall. He described the general arrangement of the foetal membranes in Phascolarctus cinereus and showed that the allantois in this form fuses with the discoidal area of true chorion. He also referred to the membranes of M. ruficollis but in such a way as to lead the reader to suppose that in this form also, the allantois fuses with the chorion.
Semon (6) in 1894, described the foetal membranes of -

(1) Owen. "On the generation of Marsupial Animals &c. Phil.Trans. 1834.

(2) "On the existence of an allantois in a Foetal Kangaroo.P.Z.S. Pt. V 1837. p-82. see fig. in Comp.Anat.of Vertebr.Vol III fig.569 and Todd's Encyclopaedia of Anat.& Physiol.,Vol.III p.324 fig.141.

(3) Only the more important papers are here referred to.

(4) Chapman."On a Foetal Kangaroo & its Membranes Proc.Acad. Nat. Sc. Philadelphia,Pt.III 1881 p. 468.

(5) Caldwell. "On the arrangement of the Embryonic Membranes in Marsupial Animals. Q.J. M.S. Vol XXIV 1884.

(6) Semon. "Die Embryonalhullen der Monotremen and Marsupialier" Zool.Forschungsreisen in Australien und den Malayischen Archipel. Bd.II.

Phascolarctus cinereus, confirming Caldwell's discovery of the fusion of the allantois with the chorion as well as those of Aepyprymnus rufescens. In this latter form he insisted on the rudimentary character of the allantois and its non-fusion with the chorion and expressed the opinion that such a condition would be found to hold good for Macropods in general.
In 1895 I shortly stated (1) that such was certainly the case for four species of the genus viz. M. parma, M. ruficollis, M. robustus and M. Major.
The present communication deals with M. parma alone.

External characters of Embryo.

The embryo (at least so far as external characters go) appears to be at a somewhat earlier stage of development than the previously described embryo of P. obesula. Unfortunately the embryo is not sufficiently well preserved for sectionising. It has a greatest length of 10 mm: and a head length of about 6 mm. It is characterised as follows:- Head bent almost parallel with trunk. Prominent neck protuberance. Lips not fused. Eye rounded. Lachrymal groove present. Rounded external nares. Snout little prominent. Wide external auditory meatus with triangular ear pinna. Fore-limb: not flexed, digits all present and with claw anlagen, palmar surface directed mesially. Hind-limb: paddle-like, digits not indicated, plantar surface directed mesially.

Foetal Membranes.

The foetal membranes in M. parma have the same general arrangement as in Aepyprymnus rufescens as described by Semon (2) i.e. the embryo enclosed in its amnion lies in the extra-enbryonic splanchnocoele surrounded by the upper part of the yolk-sac- the yolk-sac splanchnopleure - which is invaginated into the cavity of the latter. The splanchnocoele is closed externally by a discoidal area of chorion round the margin of which the yolk-sac splanchnopleure becomes continuous with the vascular omphalopleure. The allantois is a comparatively small short-stalked vesicle which never reaches and fuses with the chorion but lies permanently buried in the splanchnocoele.
The entire globular embryonic formation of this stage of M. parma has a diameter of 15 mm.
In Plate IV. fig 1. the cavity of the yolk-sac has been opened by the removal of the greater part of the bilaminar omphalopleure, exposing the embryo in its amnion, closely surrounded by the invaginated yolk splanchnopleure (y.spl.) together with the inner surface of the vascular area(vasc omph).

(1) Hill- "Prelim. Note on the Occurrence of a Placental Connection in Perameles obesula and on the Foetal Membranes of certain Macropods. P.L.S. N.S.W. Vol X.(2nd ser) pt.4 1895.

(2)Loc citp. 25.

The discoidal area of chorion, concealed in the figure by the embryo, is readily distinguishable externally from the vascular omphalopleure by its more transparent and smoother appearance. Compared with the extent of the chorionic area in Perameles and in Phascolarctus where according to Caldwell the chorion has a diameter of 12 mm, the area is here a small one, measuring in greatest diameter 4.5 mm. The surface of the vascular area (vascular omphalopleure) presents a roughened reticulate appearance in correspondence with the ridged surface of the uterine mucosa. It is distinguished from the bilaminar omphalopleure by its denser and darker appearance. The latter (Plate IV.fig.1.bil.omph) occupies rather less than half the surface of the entire embryonic formation. Its surface is also irregularly ridged. The vitelline artery leaving the yolk-stalk on the left side of the embryo courses in the yolk splanchnopleure backwards over the dorsal surface of the embryo to reach the junction of the latter membrane with the vascular omphalopleure (Plate IV. fig 1. vit.a). Here it passes over into the latter, does not at once divide as in Perameles but runs on for a distance of about 4 mm. before dividing into its two branches which form the sinus terminalis (s.t.). The Sinus is completed by a narrow anastomosis as in Perameles. It measures in diameter 14 mm by 12. mm. The vascular area has a greatest width of 8 mm. opposite the point of bifurcation of the vitelline artery and a least width of 4 mm. at that point. It is thus evident from these measurements that in mere surface extent the vascular area of this Macropod embryo very considerably exceeds that of the Perameles embryo described in the preceding pages. And not only is the area greater in extent but its capillary system is also much more richly developed than in that form, in correlation with its high functional importance in the nutrition of the embryo. From the sinus there pass off into the vascular area numerous branches (1) which divide up into much finer branches to form a rich capillary system from which the factors of the vitelline veins take their origin. The numerous fine long wavy branches of the vitelline artery which run in the yolk-splanchnopleure are especially well developed,(Plate IV. fig. 1. a.v.). Above, these branches come off directly from the vitelline artery while below they arise from an independently arising branch of the artery which runs parallel with the same. The blood circulating in these vessels must as in Perameles pass over into the vascular area at the junction of the yolk-splanchnopleure with the vascular omphalopleure. After the vitelline artery has passed over into the vascular omphalopleure it still continues to give off small branches from both sides almost up to its point of bifurcation. The vitelline veins (Plate IV. fig. 1.,vit.V),show the usual relations and include between them a very large area of yolk-sac splanchnopleure altogether devoid of vessels. The anterior vein is formed by the union in the yolk splanchnopleure of a larger anterior and a small posterior factor

(1) In the figure these branches have been represented too short.

which pass over from the vascular area. There each is formed by the union of lesser factors coming from the capillary net of the same. Similarly the posterior vein is formed by the union of two factors, a smaller anterior and a much larger posterior factor, returning the blood from the posterior portion of the vascular area. The anterior vein passes back in the splanchnopleure over the head of the embryo behind the eye, while the posterior one passes in transversely on a level with the snout. The two unite at the yolk-stalk to form the single vitelline vein.

The allantois is a small globular thin walled vesicle provided with a very short stalk and measuring in diameter 5·5 mm. It is situated mainly on the embryo's right side, lying between the snout and the rounded hinder end of the body. In the figure (Plate IV fig. 1. all.) it is seen through the yolk splanchnopleure in contact with which it lies. Its vessels are poorly developed. As Owen long ago pointed out for M. major and as Semon has recently described for Aepyprymnus , so here the allantois is a quite rudimentary structure which lies remote from the chorionic area and never comes into contact, much less fusion, with the same. Such a specialised condition of the allantois is probably general for the entire family of the Macropodidae. That it also exists outside the limits of that family we know from the observations of Osborn(1) and Selenka (2) on Didelphys and probably the condition is also general for the family,Phalangeridae - it certainly holds for Petaurus sciureus according to Semon and from my own observations I can add for Trichosurus vulpecula

But whether or not the condition turns out to be the general one for Marsupials, it is admitted on all hands to be an essentially modified one.

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(1) Osborn. "Observations upon the Foetal Membranes of the Opossum and other Marsupials Q.J.M.S. XXIII 1883.
" "The Foetal Membranes of Marsupials &c Jour.of Morph.Vol 1. 1888.

(2) Loc. cit. "Das Opossum".

EXPLANATION OF PLATES. I-IV.

All sections drawn were outlined by means of Zeiss's camera lucida.

List of Common Reference Letters, Plates 1 - IV.

Amn. Amnion.
a.v. Branches of Vitelline artery. - all. a. Allantoic artery. - all.c. Allantoic cavity. - all.cl. Allantoic canal. - all.cap. Allantoic capillary. - all. coe.w. Coelomic wall of allantoic vesicle - all.ent. Allantoic entoderm - all.mes. Allanto-chorionic mesenchyme. - all.v. Allantoic vein. -
bil. omph. Bilaminar omphalopleure.
Ch. Chorion. - ch.ect. Chorionic ectoderm. - coe.Coelom.
ect. Ectoderm. - ent. Entoderm. - ex. syn. Syncytium beyond allantoic placental area.
mes. mesoderm of proamniotic remnant.
pl. a. Allantoic placental area. - pl. syn. Allantoic placental syncytium.
sp. space in syncytium (lymph space?) s.t. Sinus terminalis.- Syn.c. Capillary of Syncytium.
u.s. Umbilical stalk.
vasc.omph Vascular omphalopleure. - vit.a. Vitelline artery. - vit. v. Vitelline vein. -
y. spl. Yolk-sac splanchnopleure.

Fig. 1. Right uterus, P.obesula with ventral half of wall removed and portions of the foetal membranes reflected to expose the embryo.

X nearly 7.

Fig. 2. The same, after removal of the embryo. $\frac{3}{4}$

X 6 10.

Fig. 3. Embryo. P.obesula. $\frac{7}{25}$

X 6

Fig. 4. Trans. section through umbilical stalk.

X 90.

Fig. 5. Trans. section through proamniotic remnant.

X 90.

Fig. 6. Section through the margin of the allantoic placental area.

X 120.

Fig 7. Section through allantoic placental area, showing the relation of the foetal and maternal capillaries.

X 380.

Fig.8. Section through the sinus terminalis and the adjacent portions of the vascular and bilaminar omphalopleure.

X 150.

Plate IV

Fig.I9. Uterine embryo of M. parma, in its foetal membranes, seen after removal of the greater portion of the bilaminar omphalopleure. $\frac{1}{2}$

X 7

Plates V - X. Genital Organs of Perameles.

Contributions to the Morphology and Development of the Urogenital Organs in the Marsupialia.

I. On the Urogenital Organs of Perameles together with an account of the phenomena of Parturition.

Introduction.

The present paper, forming the first of a series of papers I hope to contribute on the above subject, deals with the anatomy of the female urogenital organs of the genus Perameles. These present features of exceptional interest and importance, not only structurally but also in relation to the act of parturition and form a most excellent starting point from which to discuss the comparative morphology of the uro-genital organs in the Marsupialia. In this present paper, however, I do not purpose entering into an extended discussion of this subject but content myself with giving a fairly extended account of the adult structural condition of the organs, together with an account of the main phenomena connected with the act of parturition. The material at my disposal has consisted of a large number of sets of the female genital organs of either P. nasuta or P. obesula. Doubtless a careful comparison of the genital organs of these two species would reveal the presence of minute differences between them but such, if present, may from the point of view of this research, be disregarded. In the literature of the subject, I can only find two references to the condition of the genital organs in Perameles. The first is a short account by Owen (1) of the organs in P. obesula. His account is as follows:- "In Perameles obesula the uteri are wider in proportion to their length than in the Kangaroos. Each communicates with a vagina, expanding into a caecum with semitransparent walls and greatly surpassing the uteri in size: the caeca suddenly contract near the ora tincae, to form long and slender vaginal canals which converge but terminate separately near the vulva.
The urethra is of corresponding length and tenuity; its orifice is near those of the vagina, the urogenital passage having the least extent in this genus of Marsupialia."
It may be noted that in this account no mention is made of a median vaginal apparatus. The second reference is contained in a paper by Alix entitled "Sur les organes de la parturition chez les Marsupiaux"(1) and published in 1879. After remarking that he had several times confirmed his previous observation of the open condition of the median vaginal apparatus in Halmaturus bennettii he goes on to say "mais de l'autre part je n'ai pas trouve de

(1) Owen, Comp. Anat. & Phys. of Vertebr. Vol III p.683.
(1) Bulletin Societe Zoologique de France, 1879 p. 118. quoted by Lister & Fletcher, P.Z.S. 1881 p.982.

communication entre le vagin median et le vestibule urogenital soit sur le Sarigne, soit sur le Perameles," a statement which certainly shews that Alix had recognised the presence of a median vagina in Perameles.. At the time of writing an account of the process of parturition in my paper on the placentation of Perameles (2) I overlooked the above statement of Alix and misinterpreted the median vaginal canals as posterior prolongations of the uteri, an error which I trust will be sufficiently corrected in the present communication.

General account of the Genital Organs.

In Perameles the female genital organs consist of the following parts,- two ovaries, two oviducts, two uteri, two vaginae, (including the two lateral vaginal canals, with their caeca and a median vaginal apparatus,) a urogenital sinus containing the clitoris and opening into the cloaca. The most distinctive feature of the urogenital organs of this form lies in the fact that the lateral vaginal canals and the urethra lie embedded throughout their entire extent in an elongated mass of connective tissue (Plate V. fig, 1 u. s.) to which I gave in a previous paper the name of urino-or better uro-genital strand and which is developmentally none other than the persistent genital cord of the foetus. Owing to the very considerable length of the urogenital strand the various structures connected with its anterior end, viz, the bladder, the uteri and their appendages, and the vaginal caeca are situated in the abdominal cavity well in front of the anterior end of the pubic symphysis. The strand itself is the only portion of the urogenital organs which lies in the proper pelvic cavity. At its posterior end at the hinder margin of the pubic symphysis, the strand becomes continuous with the rounded thickmass in which the urogenital sinus and cloaca are situated. At the anterior end of the strand the urethra, occupying its midventral line expands into the bladder, while the lateral vaginal canals occupying the dorso-lateral regions of the strand are produced forwards into two large thin walled outgrowths, the vaginal caeca, separated from each other by a common partition wall (Plate V. fig.1 vag.c.) and lying immediately dorsad of the bladder, between it and the uteri. The posterior ends of the latter as well as the median vaginae lie imbedded, dorsally, in the connective tissue at the anterior end of the strand. In Plate V. fig, 1. the urogenital organs are represented as viewed from the dorsal aspect. The apex of the bladder (bl.) is just visible below the enormous bilobed vaginal caeca (vag.c). Each of the latter is seen to contract posteriorly and to pass back as the lateral vaginal canal (lat. vag. c.) in the urogenital strand (u.s.). ~~dorsally~~

(2) Q.J.M. S. Vol. 40. 1898

Dorsally

to the vaginal caeca, the two uteri (ut) lie side by side. Their contracted posterior ends,-uterine necks- (ut. n.), pass back to become imbedded together with the median vagina in the connective tissue of the anterior end of the urogenital strand. In the figure the rectum (rect.) and the cloaca (cl.) are shown opened up, exposing the opening of the urogenital sinus (o.u.s) into the latter.

Peritoneal relations of the Urogenital organs.

When the peritoneum covering the ventral face of the rectum is traced back, it is found to leave the surface of the latter and to be reflected forwards on to the dorsal surface of the urogenital strand, just posterior to the anterior end of the pubic symphysis. The peritoneal pocket thus formed, corresponds to the recto-uterine cul-de-sac or pouch of Douglas of human anatomists. The reflected peritoneum continues forwards on the dorsal surface of the urogenital strand up to about the middle of the uterine necks where it joins the peritoneum covering the dorsal surfaces of the two uteri. The double peritoneal layer thus formed is reflected forwards as a free fold with a concave anterior margin which lies in contact with the ventral face of the rectum, about on a level with the anterior ends of the uteri. This fold separates the uteri from the rectum and forms the roof of a fairsized pouch which we may term the dorsal uterine fossa. In fig 1. the fold has been removed in order to better expose the uterine necks. Into the fossa open the apertures of the peritoneal pouches enclosing the ovaries and fimbriated openings of the Fallopian tubes. Laterally the fold becomes continuous with the dorsal (mesially directed) surface of the broad ligament along a line parallel with and just below the ureter, which runs back in the latter, while anterolaterally it passes forwards on each side of the rectum as a fold which is continuous laterally with the reflection of the broad ligament and which carries the ureter and the ovarian artery and vein.

The broad ligament, reflected from the lateral side of each uterus and containing between its two layers the Fallopian tubes, ovaries and uteri, forms dorsal to each uterus a definite peritoneal pouch in which are situated the corresponding ovary and the fimbriated opening of the Fallopian tube. Each ovarian pouch opens into the dorsal uterine fossa by a wide postero -mesially directed opening. In Perameles and Marsupials generally, the Fallopian tube does not occupy the anterior free margin of the broad ligament but is situated some distance behind that margin as e.g. is the case in the Rabbit amongst higher Mammals. These portions of the broad ligaments situated anteriorly to the Fallopian tubes are confluent in the mid-line between the anterior free portions of the uteri and form a

fold connecting them together. Brass (1) has termed this the Ligamentum uterorum superius, without apparently appreciating its real nature.
The broad ligament after being joined by the fold forming the the roof of the dorsal uterine fossa, passes almost vertically upwards to become continuous with the dorsal peritoneum. A portion of it however forming the utero-pelvic fold of the broad ligament (Plate V. fig. 1. ut.p.f.). passes outwards and slightly forwards to join the general peritoneum dorso-laterally. The posterior free margin of the utero-pelvic fold is formed by a well-defined thick band of a white colour - the round ligament of the uterus. (fig.1 rd. lig.) This contains smooth muscle fibres and fibrous tissue and takes its origen from the lateral aspect of the anterior end of each uterus, shortly behind the junction of the Fallopian tube with the latter. It runs obliquely forwards and on reaching the body wall, bends back towards the region of the epigastric artery where it is apparently lost. The round ligament may reach a length in Perameles of 2·3cm. and a breadth of 1·5 mm. In Macropus I find the round ligament is proportionately much smaller and much less conspicuous than it is in Perameles. So far as I am aware the round ligament of the uterus has not previously been described in any Marsupial. In the descriptive Catalogue of the Royal College of Surgeon's Museum, under the description of preparation, 2740, (female organs of Kangaroo, M. major), occurs the following statement, (p. 156), "the round or ovarian ligament may be seen extending from the ovary to the side of the uterus upon which it is lost".(2) But the true round ligament extends from the uterus, not from the ovary, and both in Perameles and in M. major is quite distinct from the proper ovarian ligament, even though situated almost directly under the latter.
Posteriorly, the broad ligament extends back on each side over the base of the vaginal caecum to become continuous with the peritoneal fold reflected from each side of the urogenital strand. This urogenital fold extends back of course only as far as the posterior end of the pouch of Douglas. It passes up on each side of the rectum to join the dorsal peritoneum. The bladder is connected with the ventral abdominal wall by a median fold which extends almost up to its apex. Brass terms this the Ligamentum vesicae medium. From each side of the bladder there passes down a low ridge-like fold, much more strongly developed in Macropus, which conveys the vesicle artery and vein from the urogenital fold to the bladder.

(1) Brass- Beiträge Zur Kenntniss des weiblichen Urogenital Systems der Marsupialen. Inaug. Diss. Leipzig 1880.
(2) Desc, & Ill. Cat. of the Phys. Series of Comp.Anat. cont. in the Museum of the R.C.of S. in London.
Vol IV. Organs of Generation, London 1838.

Vessels.

The vesicle arteries arise together with the internal iliacs from the aorta. They pass up in the urogenital fold to divide into branches supplying the bladder, the lateral aspects of the uteri and vaginal caeca and the urogenital strand. The vesicle veins join the iliac veins just before they unite to form the Inferior Vena Cava.
The Spermatic (ovarian) arteries arise separately from the dorsal aorta, the right in front of the left. They pass back to supply the ovaries, Fallopian tubes and anterior ends of the uteri.

Ovaries.

The ovaries (Plate V. fig. 1. ov.) are usually compressed oval bodies, with except in young females grooved and tuberculated surfaces. The graafian follicles are small and do not project prominently, while the corpora lutea, when present, form prominent swellings 2·5 to 3 mm. in diameter. The ovaries have a maximum length of about 6 mm and a breadth of 3·5 mm. As before mentioned they lie enclosed together with the fimbriated openings of the Fallopian tubes in peritoneal pouches formed by the broad ligaments. The pouches lie dorsal to the uteri and open posteriorly by wide apertures into the dorsal uterine fossa. In the natural position of the parts, the ovary is situated in its peritoneal pouch about opposite the mid-region of the body of the uterus+just above the dorso-lateral surface of the same or quite external to it) and almost immediately above the round ligament. Its long axis may be directed either transversely, longitudinally or obliquely, the direction of the axes of the ovaries(varying on the two sides of the same individual. Each ovary has a broad usually oblique attachment to a thickened area of the broad ligament just above the round ligament and projects into the peritoneal pouch dorso-laterally. It is attached to the uterus by a short posterior ovarian ligament which joins the uterus in close proximity to the point of origin of the round ligament from the same. From the anterior point of attachment of the ovary there passes off a delicate short ligament which enters the round ligament and represents the anterior ovarian ligament. This close association of the ovarian ligaments with the round ligament is interesting in view of the statement of Mihalkovics (1) that "die Anlage des Eierstockbandes mit dem runden Gebarmutterbande einen proximal-distalwärts sich erstreck-enden continuierlichen Strang bildet." ~~The fimbriated opening~~

(1) Mihalkovics. Entwickl.d. Harn u. Geschlechtsapparates d. Amnioten." Intern. Monatsch. f. Anat n. Physiol. Bd. 2 1885, p. 418.

Fallopian Tubes.

Each is a greatly convoluted thin tube measuring as much as 4 cm. in length, and sharply marked off from the uteri. The greater part of the tube lies in the antero-dorsal wall of the peritoneal pouch, above the anterior end of each uterus. Its peritoneal opening, connected with the anterior end of the ovary by the infundibulo-ovarian fimbria, is markedly fimbriated and during life closely invests the ovary from above.

Uteri.

The uteri of Perameles are somewhat club-shaped in form, very much broader and thicker in front than behind and also very much longer than wide, (Plate V. fig 1. ut & ut. n.). Each consists of a swollen anterior portion forming what we may, for convenience of description, term the "body" of the uterus i.e. the portion in which the young undergo their development and of a much narrower posterior portion not sharply marked off from the former, which may be termed the "neck" and which opens posteriorly into one of the median vaginal cul-de-sacs. In the organs represented in fig. 1. the body of the uterus had a length of 9 mm and a breadth of 5·5 mm, while the uterine necks (including the median vaginae measured 11 mm. in length and 3·5 mm. in conjoint breadth.

The two bodies of the uteri lie with their mesial surfaces in close apposition, surrounded by a common peritoneal layer, except anteriorly where they are separate over a short part of their extent and connected by the common median portion of the ligamenta lata (the ligamentum uterorum superius of Brass. The "bodies" alone of the uteri are visible when, after pulling aside the vaginal caeca, the organs are examined from the ventral aspect. They lie dorsal to the posterior portions of the vaginal caeca and are connected posteriorly with the latter by a low median peritoneal fold. Viewed from the dorsal aspect (Plate V. fig.1.) the uteri are seen through out their extent. In fig.1, it will be noticed that the groove between the bodies of the uteri fades away at the commencement of the contracted necks, which except for a faint median line appear to form externally a single tube about half the thickness of one of the uteri. The cavities of the uterine necks are separated from each other posteriorly by a common partition wall and each opens into a very short median vaginal cul-de-sac. The two cul-de-sacs also separated by a common partition wall, externally appear to form the direct continuation of the uterine necks and are not in any way outwardly marked off from the latter. They form the extreme posterior end of the portion marked ut.n. in fig.1. While the bodies of the uteri are only connected with the vaginal caeca by a low median fold, the uterine necks become closely united over

their entire breadth with the dorsal surface of the latter. Posteriorly however the caeca rapidly decrease in size to pass directly over into the lateral vaginal canals, while the latter at the same time take a very slight outward bend with the result that in the region, the hinder sections of the uterine necks together with the median vaginal cul-de-sacs come to be imbedded in the connective tissue enclosed between the upper ends of the lateral vaginal canals. About on a level with the union of the uterine necks with the dorsal surface of the caeca, the fundus of the bladder likewise becomes united with their ventral surface so that all three parts are here united into a single mass (Plate V. fig 3. ut. n., vag.c., bl.,).

In a previous paper (1) I gave a short account of the histology of the normal uterus and need only add here a few remarks on the uterine musculature. This is essentially composed of circularly running non-striate fibres. Along the attachment of the ligamentum latum, oblique strands of fibres are found extending in from the musculature of the ligament, while in the connecting bridge between the bodies of the uteri similar oblique strands pass between the circular muscle layers. In both places together with these oblique strands, there occur irregularly distributed bundles of longitudinal fibres but these do not extend round the dorsal and ventral surfaces of the uteri to form a continuous layer of longitudinal muscles.

Both Owen (2) and Brass (3) who describes the histology of the uterus of Phascolomys wombat, agree in stating that the musculature of the uterus consist of an outer longitudinal and an inner circular layer of fibres. In representatives of the following genera, Petrogale, Acrobates, Petaurus, Sminthopsis, Peragale, Dasywins, Macropus, Myrmecobius, Tarsipes and Phascolomys, I find, however, that the uterine musculature has the same simple character as in Perameles, in all these forms the musculature is essentially a circular one. Even in Phascolomys where the bundles of longitudinal fibres are strongly developed on the lateral and mesial surfaces of the uteri, they do not form a continuous layer all round the uterus.

This fact, that the musculature of the uterus in Marsupials is essentially a circular one, is a point of some little interest and has not so far as I am aware been emphasised. Sobotta (4) has shown that the proper fundamental muscula-

(1) Loc. Cit. p. 389.
(2) Owen. Comp.Anat. of Vert. Vol III p. 683.
(3) Brass - Loc. Cit. p. 28.
(4) Sobotta - Beitr. Zur Vergl. Anat. u. Entwick. d. Uterus muskulatur. Archin. f. Mikr. Anat. Bd 38 1891.

ture of the uterus is the circular layer which primitively forms the muscular investment of Muller's duct, the layer of longitudinal muscles and the intermediate layer carrying blood vessels are only differentiated later and reach a very varying degree of development in different mammals. Where then as in Marsupials we find continuous longitudinal and intermediate layers absent and the uterine musculature essentially composed of circularly running fibres, we can only regard the condition as a primitive one and as a mark of lowly organisation.

Vaginae.

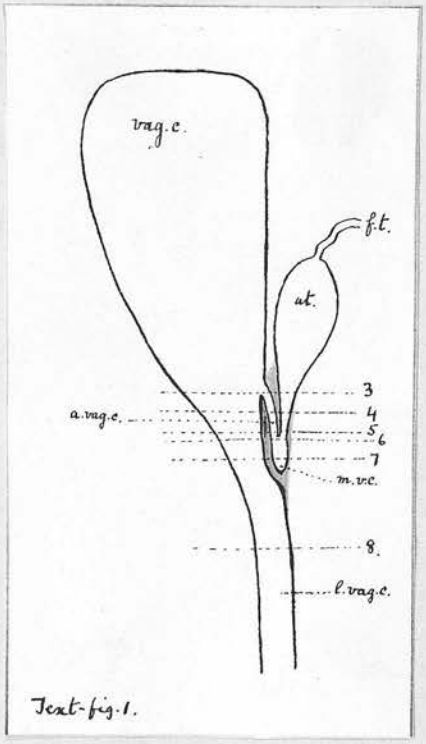
Vaginal caeca:- Posteriorly as has been described above, the vaginal caeca are closely united to the uterine necks above and to the fundus of the bladder below, but anteriorly they become quite free and form a large bilobed sac (up to 4·5 cm. in length) with thin semi-transparent walls lying between the uteri above and the bladder below and greatly exceeding either in size (Plate V, figs 1 & 2 vag. c). The caeca are separated from each other by a common median partition wall and each is directly continuous behind with the corresponding lateral vaginal canal of which it simply forms a forward expansion. The caeca are lined by a layer of columnar epithelium which has usually a ridged appearance in surface view (fig 2. vag. c.).
The vaginal caeca function as receptacula seminis. Of this I have been able to satisfy myself through the capture of a female specimen of P. obesula, apparently just after an act of coitus. The uteri were slightly enlarged and congested, while the caeca were greatly dilated and filled by a clear viscid semi-fluid material together with masses of hard, opaque, caseous-looking substance of an albuminous nature. Microscopic examination of the viscid material revealed the presence of abundant spermatozoa with somewhat oblong heads, pointed anteriorly and measuring ·005 mm in length by ·002 mm in breadth and with tails averaging ·15 mm in length. (1) Normally the caeca contain only the hard opaque material which is essentially similar to the "inspissated secretion commonly present both in the culde-sac and the lateral vaginal canals" of Macropus according to Owen (2) and noted by various observers from Home onwards. According to Owen (3) these masses "most resemble those coagulated masses that are found in the vesiculae seminales and sometimes in the urethra of the Agouti, Capromys, Guinea-pig and others of the Rodent order." Without

(1) cf. Owen. article Marsupialia Todd's Encyclop. p.312.
(2) Article, Marsupialia p. 319.
(3) On the gen^{n} of Marsupial Animals. Phil. Trans. 1834 p. 357.

doubt, these hard masses are derived from the same source viz, from the secretion accompanying the spermatozoa. In Macropus Major, Stirling (4) has shown that the lateral vaginal canals and the median vaginal canal act the part of seminal receptacles and I also find that in Trichosurus and Phascolarctus, the median vagina becomes much enlarged and is utilised for a similar purpose. In other cases where as in Perameles the median vaginal apparatus remains of small size, receptacula have been developed as forward outbulgings of the lateral vaginal canals. In Peragale lagotis, vaginal caeca similar to those of Perameles occur, only they remain separate from each other and such Prof. W.B. Spencer informs me (in litt.) also occur in Choeropus castanotis.

Median vaginal cul-de-sacs and associated parts:-

Here I propose to describe the condition and general relations of the median vagina in a young virgin female of Perameles, reserving the details of the changes consequent on parturition for a later section.



Text-fig. 1.

The accompanying Text-fig.1. is a diagrammatic lateral view of the anterior portion of the urogenital organs. The lines indicate the approximate positions of the sections through the genital organs of a virgin shown in figs 3-8, Plates V and VI.

From the diagram, it will be seen that the uterine neck continues back to open into a short terminal median vaginal cul-de-sac (m.v.c). From the anterior end of this, there arises ventrally a fine canal which passes forwards in the connective tissue ventral to the uterine neck to open into the vaginal caecum. This fine canal, which throughout its entire extent, is imbedded in connective tissue, represents the morphologically anterior portion of the lateral vaginal canal. We may now look at the structural relations of these various parts as seen in figs. 3-8.

In fig. 3, the uterine necks (ut.n) separated by a common partition wall, the vaginal caeca (vag.c.) also separated by a common wall and the bladder (bl.) are already united into a single mass. The section passes through the opening (op.) of the anterior portion

(4) Stirling. "On some points in the Anatomy of the Female organs of Generation of the Kangaroo &c. P.Z.S. 1889. p. 437.

of the lateral canal of one side into the caecum, while the canal of the other side is seen in section in the common partition wall between the caeca. Fig. 4, thirty seven sections behind fig. 3, shows the two canals (a. vag. c.) running back in the connective tissue of the wall between the vaginal caeca, which is at this level thicker than anteriorly. In other words, the vaginal caeca as they decrease in size, at the same time bend slightly outwards. The uterine necks (ut.n.) are also smaller and very distinctly invested by the surrounding connective tissue. In fig. 5, thirty nine sections behind fig. 4, the vaginal caeca have passed over into the lateral vaginal canals (l. vag.c.), while the bladder has also passed over into the urethra (ureth.). The lateral vaginal canals are widely separated from each other and passing in between them and the central mass of connective tissue are the ureters (ur.). The central mass of connective tissue encloses the uterine necks (ut.n.) and the anterior portions of the lateral canals (a. vag.c) now somewhat larger and situated directly below the cavities of the necks. Fig. 6, thirty eight sections behind fig. 5, shows the opening of the uterine neck of one side into the continuation of the canal which we must now term the median vaginal cul-de-sac (m.v.c.). On the other side the two are still separate (ut.n. & a. vag. c.). Fig. 7, twenty one sections behind fig. 6, shows the two median vaginal cul-de-sacs, (m.v.c.) lying in the connective tissue between the lateral vaginal canals (l. vag.c.) and above the urethra (ureth.) They are separated by a common partition wall and each is surrounded by a delicate layer of circular non-striate muscle fibres. Posteriorly, the vaginal cul-de-sacs gradually become smaller and finally end blindly and without opening into each other, twenty sections behind fig. 7. The cul-de-sacs end in a small cone-shaped mass of dense, deeply staining connective tissue seen in figs. 1 & 2, just behind the posterior end of the cul-de-sacs. This tissue is directly continuous with the thin strand (c.t.) lying between the lateral vaginal canals in fig. 8.

In fig. 2 (Plate V), representing a dissection from the dorsal aspect of the anterior portion of the genital organs of a multipara, certain of the above described features are shown. The uteri have been opened up along their dorsal mid-lines and the dorsal walls of the vaginal cul-de-sacs have been removed. (1) Each uterine neck is seen to open (ut.n.) by a scarcely projecting and ill-defined os into the corresponding vaginal cul-de-sac (m.v.c.). At the anterior

(1) In the figure, the partition wall between the cul-de-sacs has been drawn as if it completely separated the cul-de-sacs. In reality as in all females which have borne young (v.p.) the cul-de-sacs open into each other posteriorly.

ventral end of the left cul-de-sac is seen a deep depression (x) marking the point of origin of the anterior portion of the lateral canal. The course of the latter forwards in the connective tissue below the uterine neck is not visible externally, but the dorsal wall of the left vaginal caecum has been removed to show its crescentic opening (op.) on the common partition wall.
It is thus evident that Perameles possesses a median vaginal apparatus which in the virgin consists like that of e.g. Dasyurus and Phascolarctus, of two separate cul-de-sacs. But whereas in these two forms the cul-de-sacs are of some size and extend posteriorly to within a comparatively short distance from the opening of the lateral vaginae into the urogenital sinus, in Perameles the cul-de-sacs are small structures which terminate at a relatively very great distance from that sinus.
The ureters enter the anterior end of the urogenital strand between the posterior portion of the uterine necks and the lateral vaginal canals (Plate VI fig. 5. ur.) and pass forwards (fig. 4, ur.) to open into the bladder shortly above its base and close to its ventro-mesial line.

Urogenital Strand:- This, as already defined, is the name given to the elongated mass of connective tissue containing imbedded in it, the lateral vaginal canals throughout their entire extent, the urethra and anteriorly the uterine necks and median vaginal cul-de-sacs. In large specimens it may reach a length of as much as 6 cm and a breadth of 6 mm. Its average length (from the posterior end of the median vaginae to the urogenital sinus) is between 3 & 4 cms. with a breadth of 4-5 mm.
Fig. 8 represents a transverse section through the mid-region of the urogenital strand of the virgin above referred to. The median ventral portion of the strand is occupied by the urethra (ureth.), while the lateral vaginal canals (l.vag.c.) pass along in it dorso-laterally. The three ducts lie imbedded in the connective tissue of the strand and strands of the same separate them from each other. I would direct special attention to the narrow strand separating the lateral vaginal canals. It is in this strand that the cleft-like pseudo-vaginal passage (1) is formed later for the exit of the young during parturition but in this strand in the virgin, indeed prior to the first parturition "there is no trace of a median vaginal passage or any epithelial or other track which might indicate the site of a future passage of any kind whatever." (loc. cit. p.429.). This strand as was above mentioned is directly continuous with the deeper staining mass of connective tissue situated around & just posterior to the ends of the median vaginal cul-de-sacs.

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(1) Hill - The Placentation of Perameles - Q.J.M.S. Vol. 40 p 425.

The lateral vaginal canals present a uniform structure throughout their course. They are lined by mucous menbrane consisting of dense connective tissue and clothed by a layer of columnar epithelium. External to the mucous membrane is a layer of non-striate musole of no great thickness The mucosa is thrown into distinct longitudinal ridges. At its posterior end the urogenital strand becomes continuous with the rounded mass in which the urogenital sinus and cloaca are situated.

Urogenital Sinus:- The urogenital Sinus is a short narrow chamber with a length of 4 to 7 mm, having as Owen pointed out "the least extent in this genus of Marsupialia"(1) It opens on the ventral wall of the cloacaby a small aperture (Plate V, fig. 1. o.u.s.) situated from 3·5 to 5 mm. within the margin of the cloacal opening. Its lining is thrown into longitudinal ridges. The vaginal canals open together into its anterior end dorsally, while a short distance posteriorly the urethra opens on its floor under a slight median papilla. Also situated on the floor of the sinus some distance behind the urethral opening is the small clitoris. It lies in a distinct longitudinal depression on the floor of the sinus, just within the margin of the opening of the latter and is bounded by lateral preputial folds which may be continued beyond the margin of the opening. In form, the clitoris is bluntly cone-shaped and measures from 1·5 to 2 mm. in length by about 1mm.. in greatest breadth. It is attached over its whole extent though exceptionally its apex may be free and slightly bifid.
I am unable to discover any reference in the literature to the minute structure of the clitoris in Marsupials; the following facts may therefore be of interest. Shortly in front of the clitoris, two ducts leave the floor of the urogenital sinus and run back in the ventral wall of the sinus to enter the clitoris proper. The lumina of these canals may be continuous or interrupted or the duct may even be entirely solid in different females. They run back enclosed below by a horse-shoe shaped band of erectile tissue. Posteriorly, towards its apex, the clitoris is divided into two halves by a median septum (Plate VII, fig. 9, m.s.), each half containing a canal below which is a horse-shoe shaped mass of erectile tissue (e.t). Eventually the canals open on the surface of the organ shortly behind its apex (fig.9 c.d.). In view of the above, it is interesting to note that according to Owen (2) "in the Perameles lagotis not only is the glans [penis] bifurcate but each division is perforated and the urethral canal is divided by a vertical septum for about half an inch before it reaches the forked glans."

(1) Owen Comp. Anat. of Vert. Vol III p. 683.

(2) Owen. Article Marsupialia - Todd's Encyclop. Vol III p. 312.

There open into the dorsal corners of the urogenital sinus, slightly behind the opening of the urethra the ducts of two large branching alveolar glands with muscular and fibrous trabeculae. The glands somewhat resemble the human prostate gland and are not sharply marked off from each other. They lie partly imbedded in the voluntary musculature investing the posterior end of the urogenital strand, ventro-laterally to the urethra.

Cloaca:- The Cloaca is a fairly large chamber having in a large specimen a maximum depth of 9 mm. In some cases, it is distinctly marked off from the rectum by the fact that the ridges of the latter terminate abruptly at the point of junction of the two, but in other cases the limit is not so well defined. The lining of the cloaca may be comparatively smooth or in other cases thrown into ridges. In its wall is the large cloacal sphincter muscle. Imbedded ventro-laterally in the latter are two large oval, so called, anal glands. A fine duct passes from the posterior end of each gland to open into the cloaca by a small aperture on its ventral wall some distance within the margin of the opening. Each gland is invested by a layer of non-striate muscle fibres and in section presents a spongelike appearance, consisting of a large central lumen from which come off numerous glandular alveoli. There also occur in the walls of the cloaca numbers of branched tubular glands.

PARTURITION.

In my previous paper on the Placentation of Perameles, I described the condition of the genital organs in an immediately post-partum stage of P. nasuta and showed conclusively that the young reached the exterior by way of a median cleft-like passage - which I termed the median pseudo-vaginal passage- situated in the connective tissue between the lateral vaginal canals. At the time of writing the above paper, however, I misinterpreted what is herein described as the median vagina as "a posterior common portion of the two uteri (common uterine canal)" and hence came to the erroneous conclusion that the median pseudo-vaginal passage "has no connection whatever with the lateral canals" and regarded the apparently anomalous mode of birth in Perameles as seeming "to be without parallel in the whole mammalian class." As regards the first point. I shall show in the present account that in reality the pseudo-vaginal passage leads away from the posterior ends of the united median vaginal cul-de-sacs which themselves arise as outgrowths of the Mullerian ducts at the junction of their uterine and vaginal sections, while as regards the second, I hope to bring forward sufficient evidence to show that the mode of birth in Perameles must be almost exactly paralleled by the parturition phenomena seen in those Marsupials which like Perameles give birth to the young through a direct median passage.

If for the expression "common uterine canal" the reader substitute "common median vagina" the main facts in my previous short account of the parturition phenomena remain substantially correct.

The following account is based on the examination in serial sections of the female urogenital organs of nine specimens of Perameles, some of which were shortly described in my previous paper.

The specimens include the following:-

I. P.nasuta with two new-born young.
(Stage E of previous paper)
II. P.obesula with two. 17.5 mm. young in pouch.
III. P.obesula with two, 22mm, young in pouch.
(Stage F. of previous paper).
IV. P. obesula with four 3.7 cm. young.
V. P. obesula with several 4 cm. young.
VI. P. nasuta (?), bred.
VII. P.nasuta with early blastocyst in uterus
(Stage A. of previous paper)
VIII. P. obesula with blastodermic vesicle in uterus.
(Stage B. of previous paper)
IX. P.obesula with two, 12.5 mm. young in uteri.

Description of Specimens, I - IX.

I. P. nasuta with two new-born young (G. L. 14 mm.).

The genital organs of this specimen were described in my previous paper (p. 425 et seq. & Fig. 25. Plate 32.) The allantoic stalks, one from each uterus, were shown to extend down from the placental areas, not into the lateral vaginal canals but into a cleft-like passage, - the median pseudo-vaginal passage - for a distance of about 3 cm. The allantoic stalks were already in process of histological degeneration, the cells appearing mostly as clear spaces with nuclei staining deeply and homogeneously and often irregular in shape. A section through the urogenital strand is figured on Plate 33. fig 35. and shows the two degenerating allantoic stalks in position in the cleft-like passage in the connective tissue between the lateral vaginal canals. The walls of the pseudo-vaginal passage "are entirely formed by the connective tissue core of the strand and they exhibit no histological differentiation into coats muscular or other" (p. 427). Masses of coagulated blood were present in the passage and extravasated blood was also abundantly present in the surrounding connective tissue, the whole appearance of the passage and its surroundings strongly suggesting that an extensive rupture of the connective tissue and its contained vessels had taken place along the line of passage of the embryo i.e. the pseudo-vaginal passage.

II. P.obesula with two, 17.5 mm. young in pouch.

Sections through the uterus show that the mucosa has almost regained its normal condition. The uterine epithelium forms a complete layer of low cubical cells. The cavity of the uterus contains a cellular detritus containing leucocytes and red blood corpuscles. In sections through the mid-portion of one of the uteri, two allantoic stalks are present but disappear further back. They have evidently been broken across for they reappear, curiously enough, in the cavity of one of the vaginal caeca and from there pass down through the anterior forwardly directed portion of the lateral canal into the median vaginal canal. The neck portions of the uteri continue back as described for the virgin and open eventually into the median vaginal canals. Their lining is greatly folded and the lumen of each is largely occupied by a cellular detritus. As in the virgin, the posterior portions of the uterine necks and the median vaginæ lie embedded in the connective tissue between the slightly bent upper ends of the lateral vaginal canals. From the anterior ventral end of each median vaginal

canal there passes forwards in the connective tissue underlying the uterine necks, the duct-like anterior portion of the lateral canal to open into the corresponding vaginal caecum. The canals are now very much larger than in the virgin before described and in one of them pass down the ruptured allantoic stalks to enter the median vaginal canal of the same side.

The two median vaginal canals continue on for some distance as laterally compressed canals separated by a common partition wall, the one containing two allantoic stalks, and a cellular detritus, the other, the detritus alone (Plate VII fig 10. m.v.c., & all. s.).

Eventually through the disappearance of the middle portion of the common partition wall, the two canals open into each other. The dorsal and ventral portions of the common wall rapidly diminish in size posteriorly and finally disappear so that we have eventually in place of two separate canals, a single median canal, - the common median vagina, - formed as we have seen by the union posteriorly of the two vaginal cul-de-sacs. Fig. 11, Plate VII, represents a section through the common median vagina (c.m.v.) and in it are plainly visible the sections of the two allantoic stalks (all. s.) surrounded by detritus. Posterior to the level of this section the common median vagina rapidly diminishes in size, it looses its thin muscular layer and finally its epithelial lining disappears on its lower side, thus allowing the two allantoic stalks to come into contact with the surrounding connective tissue,(Fig.12 all.s. & c.m.v.) As the sections are traced back, the common median vagina disappears completely and the allantoic stalks are left stranded in what is simply a mere rounded space, - the pseudo-vaginal passage- in the deeply staining dense mass of connective tissue surrounding the posterior end of the common median vagina and situated between the lateral vaginal canals and above the urethra. The stalks extend back in the pseudo-vaginal passage, surrounded by dense connective tissue, over certainly one-third of the length of the uro-genital strand. Posteriorly they are looped upon themselves and some distance before they disappear come to lie quite free in a large cleft occupying almost the entire area between the urethra below and the lateral vaginal canals at the sides. They extend altogether through over six hundred sections of medium thickness, behind the posterior end of the common median vagina. The stalks measure in diameter .36 mm by .26 mm. They are greatly degenerate, presenting a reticulate appearance with deeply staining small fragmentary nuclei in the meshes. The positions of the allantoic vessels are just recognisable in some sections. The two stalks lie close together but not in contact since they are separated by a thin layer of connective tissue which also forms a common adventitious sheath around them. And not only are the stalks invested and separated by connective tissue but connective tissue corpuscles have now definitely invaded the degenerate tissue of the stalks. Posteriorly the stalks are found to

have been infiltrated by maternal blood but this is the only specimen in which I have found blood clots in such a position. The extravasated blood so abundantly present in and around the pseudo-vaginal passage of the previous specimen has now almost entirely disappeared.
Beyond the points of termination of the two stalks, the pseudo-vaginal passage can be traced on right up to near the point of opening of the lateral canals into the urogenital sinus. In the extreme posterior part of its course the passage is a much less definite one consisting merely of a series of irregular clefts. Serial sections passing through the junction of the urogenital strand with the sinus fail to reveal the presence of any interruption in the lining of the latter. I am therefore unable to state definitely the actual position of the aperture by means of which the young reach the urogenital sinus.
That the present female had borne young on at least one previous occasion the following facts almost certainly demonstrate. Towards the extreme posterior end of the common median vagina, just dorsal to the deeply staining mass of connective tissue enclosing the pseudo-vaginal passage with its two allantoic stalks, occurs a definite small triangular cleft. This can be traced posteriorly for a considerable distance when it enlarges and opens into the above described pseudo-vaginal passage containing the allantoic stalks. This cleft I regard as the pseudo-vaginal passage of a previous parturition and this view is strengthened by the occurrence just below it of fragments of allantoic stalks incorporated in the connective tissue. These remnants are recognisable by their staining lighter than the surrounding dense connective tissue, by their reticulate fibrous appearance and by the presence in them of small spindle-shaped nuclei showing in places a distinct tendency to concentric arrangement.
A less altered remnant of a stalk which is not yet so definitely incorporated in the surrounding tissue also occurs laterally to the pseudo-vaginal passage and may belong to a later parturition than the above described remnants. Both sets are traceable through a considerable number of sections. In the description of certain of the remaining specimens, similar persisting remnants of allantoic stalks will be shown to exist and in such a condition as to necessitate the reforming of the pseudo-vaginal passage over at least part of its extent, as has apparently been the case in the female under consideration.
The present specimen,then, shows us that after parturition is completed, the median vaginal cul-de-sacs open into each other posteriorly to form a short median epithelially lined canal - the common median vagina - from the end of which there leads away the non-epithelially lined cleft-like pseudo vaginal passage, in this stage definitely continuous with the common median vagina but with its opening into the urogenital sinus no longer recognisable.

III. P. obesula with two, 22 mm. young in pouch (Stage F. of previous paper.)

The genital organs of this specimen have already been described in my previous paper (p. 431-2) but without figures. For completeness I here reproduce the main points in my previous decription in explanation of figs. 13, 14, & 15. Fig. 13. represents a section through the common median vagina shortly after the point of union of the two canals. It contains here an irregular detritus but further back contains fragments of what are apparently greatly degenerated broken up portions of allantoic stalks. Its lumen becomes continuous ventrally with that of the pseudo-vaginal passage in which there almost immediately appear the sections of three allantoic stalks, a larger and more degenerate one measuring .4 mm by .3 mm in diameter and two smaller ones, each .2 mm in diameter, (fig. 14. all. s.). As the genital organs reached me with only two young, it may be that the larger stalk has persisted from a previous parturition. These three persistent stalks completely occupy the lumen of the passage (fig. 14.). They are closely surrounded by a loose connective tissue sheath derived from the surrounding tissue and strands of the same pass in between and separate the stalks. They are here in a more degenerate condition than in the preceding specimen and the larger one has undergone marked fibrous degeneration, and into all three connective tissue corpuscles have penetrated. Fig. 15. represents a section through the urogenital strand behind the terminations of the allantoic stalks and shows very clearly the cleft-like nature of the pseudo-vaginal passage, here containing a detritus of red blood corpuscles and cellular elements.
The uro-genital sinus and cloaca were not available for examination.

IV. P. obesula with four, 3.7 cm. young.

The two median vaginal canals each with a greatly folded lining, continue back and eventually open into each other to form the here extremely short common median vagina, which extends through only four sections as compared with one hundred and thirty one in specimen II.
There is now no trace of allantoic stalks in any part of the median vaginal apparatus. The lumen of the median vagina must now be described as ending blindly since the greatly degenerate and irregular remains of allantoic stalks which appear in the connective tissue forming its direct continuation can only be described as forming an integral part of the same, so closely are they interpenetrated and surrounded by it. (Plate VIII. fig. 16. all. s.). As sections

are traced posteriorly, the stalks become more distinct and easily recognisable, but vary greatly in size, in shape, and in character. Surrounded and invested as they are by connective tissue which is now definitely intergrown with the degenerate tissue of the stalks, they completely block the lumen of the pseudo-vaginal passage. The tissue of the stalks is now quite fibrosed and is invaded by large numbers of connective tissue corpuscles. These are often found aggregated into groups occupying what were originally the cavities of the allantoic vessels and with or without such groups as a centre, other corpuscles are found to have taken on a definite concentric arrangement.
Behind the terminations of the stalks the pseudo-vaginal passage can be traced back into the terminal part of the urogenital strand situated in the rounded mass enclosing the urogenital sinus and cloaca, but here it narrows and finally disappears some two hundred and fifty sections in front of the anterior end of the sinus. In these sections the connective tissue in the direct line of continuation of the passage is perfectly uniform in character and exhibits not the faintest indication of the previous existence in it of the cleft by way of which the young reached the exterior.

V. P. obesula with several 4 cm. young.

Only portions of the urogenital strand and the urogenital sinus were examined in this specimen.
Sections through the anterior portion of the urogenital strand reveal features very similar to those described for the preceding specimen. In fig 17. the greatly degenerate remnants of the allantoic stalks (all. s.) are seen to almost completely block up the pseudo-vaginal passage. They are closely surrounded and interpenetrated by connective tissue and in places appear to be directly invaded by ingrowths of the latter. Posteriorly the passage appears as a long narrow empty cleft. In this specimen the cleft can be traced back into the fold separating the openings of the lateral canals into the sinus but it fades away before reaching the lining of the latter. No trace of the opening into the sinus is perceptible.

VI. P. nasuta (?) No history but from the condition of the genital organs evidently a multipara.

As is usual in multiparous specimens the two median vaginal

canals unite posteriorly to form a short common canal (fig. 18 c.m.v.) which here ends somewhat abruptly. In the connective tissue just behind its posterior end appears the remnant of an allantoic stalk. Posteriorly the pseudo-vaginal passage becomes patent as a slit-like space, containing dorsally small discontinuous fragments of stalks. Still further back there appears in the ventral corner of the passage a portion of another allantoic stalk which presents in section the markedly fibrosed appearance shown in fig. 19. Plate IX. This stalk measures in diameter .18 mm by .12 mm and extends through about sixty sections. In this stalk the concentric arrangement of certain of the connective tissue fibres is well shown. It is probable that this fibrosed stalk belongs to a later parturition than the fragmentary and small remnants of stalks occupying the dorsal part of the passage. After the appearance of this stalk, the dorsal half of the passage becomes separated off from the ventral and ends blindly, while the latter continues on as a narrow slit in which other fragmentary remnants of stalks appear (fig. 20.)
In this specimen also, the pseudo-vaginal passage can be traced almost up to the point of opening of the lateral canals into the uro-genital sinus.

VII. P. nasuta with an early blastocyst in one of the uteri (Stage A. of my previous paper.)

This specimen had borne young on at least one previous occasion. The two median vaginal canals unite posteriorly to form a single median common canal in the usual fashion in multipara. In the connective tissue following on the posterior end of the median vagina are incorporated the fibrosed remnants of an allantoic stalk, which forms an integral part of the tissue, and is only distinguishable therefrom by its more homogenous appearance and its slightly deeper staining qualities. Behind this the pseudo-vaginal cleft appears and posteriorly there is present in it another portion of an allantoic stalk with very much the appearance of the stalks in specimen IV. It is invested by a delicate layer of the surrounding tissue so that the lumen of the passage is completely blocked. The matrix of the stalk is fibrosed and contains numerous connective tissue cells.

VIII. P. obesula with blasto-dermic vesicle in uterus. (Stage B. of previous paper)

This female proves to have been in her first pregnancy

The two median vaginal canals end blindly without opening into each other just as in the virgin previously described. Fig. 21. represents a section through the uro-genital strand of this specimen. Except in size it in no way differs from the section through that of the virgin shown in fig.8.

IX. P. obesula with two 12.5 mm. embryos in the uteri.

Like the preceding, this female is also in her first pregnancy and as in it the two median vaginal canals end blindly and separately. The lumina of the two cul-de-sacs are separated by the common wall with a least average thickness posteriorly of .37 mm. There is no sign of any thinning of the wall nor any indication suggesting the subsequent union of the two canals.
The only point of importance in connection with the uro-genital strand is the fact that the connective tissue lying between the lateral vaginal canals is now very vascular (fig. 22, c.t.), numerous large and small veins running mainly longitidinally being distributed through it.

General Remarks on Parturition.

If now we shortly summarise the facts concerning the parturition phenomena contained in the preceding pages, we reach the following conclusions. The young in Perameles reach the exterior by way of a direct median passage, constituted in front, by a comparatively short epithelially lined tube formed by the union of the posterior portions of the median vaginal canals - the common median vagina - and behind, by a relatively very long cleft-like space - the pseudo-vaginal passage -, lying in the connective tissue between the lateral vaginal canals and leading back from the posterior end of the former but unlike it, "wholly destitute of any epithelial lining or any other specified wall" (loc.cit.p.429). Although I have not been able to demonstrate the presence of an opening from the pseudo-vaginal passage into the urogenital sinus in any of the specimens examined, there is not the slightest doubt but that such an opening must exist before parturition can be completed. Once that process is over, the opening, which must simply be of the nature of a rupture or breaking through by the young of the epithelial lining of the sinus, apparently rapidly heals up and must be reformed anew at every act of parturition as a temporary opening place for the exit of the young. The closure of this opening after each act of parturition is, without doubt, simply a necessary result of the fact that the median pseudo-vaginal passage is entirely destitute of any epithelial lining with which the ruptured epithelium of the margin of the opening could become continuous. Its edges simply have to unite with each other with the consequent healing up, and obliteration of, the opening.

When the pseudo-vaginal passage is once formed it persists over at least the greater portion of the posterior part of its extent as an empty cleft-like space which no doubt serves for the transmission of the young of successive gestations. But anteriorly, immediately behind the posterior end of the common median vagina, the pseudo-vaginal passage more or less completely looses its continuity with the lumen of the median vagina after each parturition owing to its becoming blocked up by the persistent remains of allantoic stalks, surrounded and enveloped by connective tissue sheaths. It is thus evident that in this region the false passage must be reformed at each parturition and the same also holds true for the extreme posterior end of the passage over a greater or lesser extent.

The allantoic stalks left behind in the anterior portion of the median passage after each parturition, very soon completely disappear from the uteri and median vaginae but portions of them remain recognisable in the upper portion of the pseudo-vaginal passage for a relatively very long time. The fate of these stalks has been traced in the preceding pages. They have been shown to undergo histological degeneration and to become surrounded and invaded

by the adjacent connective tissue, a process resulting in their complete conversion into fibrosed masses and their final incorporation in the surrounding connective tissue. As regards the formation of the pseudo-vaginal portion of the median passage I pointed out in my previous paper that it is "formed either just before or at the first act of parturition" (p. 429). I am now inclined to believe that the latter period is the correct one and that the passage is simply formed by the embryo as it passes down, as a longitudinal cleft-like rupture of the very vascular connective tissue core of the urogenital strand. "That some such rupture does occur is evidenced not only by the appearance of the false passage, but also by the pretty extensive extravasations of blood found both in and surrounding the track followed by the foetus during its egress i.e. the median pseudo-vaginal passage" (p. 429), At all events, I am unable to conceive of the formation of such a cleft-like passage other than in association with the downward passage of the young during parturition. As to the formation of the common median vagina, the condition of the median vaginal cul-de-sacs in specimen IX suggests that the disappearance of their common partition wall posteriorly may likewise be due to the passage of the young into their narrow posterior ends, resulting in pressure on and subsequent rupture of, the common wall which is, no doubt, in a stretched and strongly congested condition during the act of parturition.

The very fact of the constant occurrence of this mode of birth by a direct median passage, even formed as it is, in by far the greater part of its extent by rupture of maternal tissue involving loss of blood at each act of parturition shows that with all its apparent defects it has proved of such direct advantage to the animal as to have led to its adoption in preference to the circuituous route offered by the lateral vaginal canals. For the latter route is circuituous indeed and it is difficult to imagine the young, cumbered as they are with attached allantoic stalks, reaching the exterior in safety, after passing first, back into one of the median vaginal canals, then directly forwards through the anterior forwardly running portion of the lateral canal into one of the vaginal caeca and hence back into the posterior portion of the lateral vaginal canal to the urogenital sinus. In contrast with this round-about route, the median route is straight and direct and herein apparently lies its advantage over the other.

In my previous paper, I instituted a comparison between the median pseudo-vaginal passage of Perameles and the epithelially lined median vaginal passage in the Wallaroo (*M. robustus*), and stated that the former passage had "no connection whatever" with the lateral vaginal canals, and erroneous statement which I trust the present paper sufficienty corrects. For it has been demonstrated that the median pseudo-vaginal passage is directly continuous at and for some time after,

parturition with the lumen of the median vagina, and that the latter is formed by the union posteriorly of the two median vaginal canals, which arise developmentally as posteriorly directed caecal diverticula, one from each Mullerian duct at the junction of its uterine and vaginal segments.

Now in young foetal Macropods and other Marsupials the median vaginal apparatus consists, as in virgin females of Perameles, of two separate cul-de-sacs lying imbedded in the tissue of the genital cord. But whereas, in Macropods the two cul-de-sacs extend back in the tissue of genital cord up to within a comparatively short distance from the anterior end of the sinus uro-genitalis and eventually coalesce to form a single blindly ending median vagina, whose posterior end alone remains imbedded in the tissue of the genital cord, in Perameles, the vaginal cul-de-sacs remain relatively extremely small, do not undergo fusion until the first parturition, are entirely imbedded in the tissue of the genital cord and terminate far remote from the uro-genital sinus.

In virgin females of Macropus, then, the median vaginal apparatus consists of a single long tube which ends blindly in the tissue between the posterior ends of the lateral vaginal canals, while in virgins of Perameles, the homologous apparatus consists of two separate cul-de-sacs which end blindly in the tissue between the anterior portions of the lateral vaginal canals. In either case the tissue in which the apparatus ends and in which in Perameles it is wholly imbedded, originally formed part of the genital cord.

The above comparison has been made in order to emphasize the extremely primitive condition of the median vaginal apparatus in Perameles. It remains in a persistently embryonic condition, at a stage which is early passed through in the foetal Macropod.

In view of the fact that both in Perameles and in certain Macropods the young reach the exterior by a direct passage involving in both cases the median vaginal apparatus, the question next arises, may not the formation of the direct passage in Perameles associated as it is with such an extremely primitive condition of the median vaginal apparatus, throw light on the parturition phenomena in those other Marsupials with a direct mode of birth and in particular may these not occur, in the parturition of Macropods, phenomena recalling the formation of the pseudo-vaginal passage in Perameles ?

Now it has been shown by numerous independent investigators (I need here only cite the careful work of Lister & Fletcher (1)

(1) Lister & Fletcher, "On the condition of the Median Portion of the Vaginal Apparatus in the Macropodidae". P.Z.S. 1881.

and Fletcher (2) whose papers contain in addition to their own extensive observations, valuable historical summaries of the earlier investigations in this field) that in many species of the family Macropodidae, a direct post-partum communication exists between the median vagina and the urogenital sinus, that therefore the young reach the exterior in those forms in which such an opening exists, by a direct median passage as in Perameles. Only in two cases has the median vagina been found to communicate with the urogenital sinus in virgins "namely by Lister in H.ualabatus & Brass in H. Bennettii" (Fletcher b. Part II. p. 9), but such cases are to be regarded simply as very exceptional variations. In virgins, normally, as has already been insisted on by Fletcher, the median vagina ends blindly in the connective tissue between the posterior ends of the lateral canals and in comparatively close proximity to the anterior end of the urogenital sinus. Figures such as the classical figure by Owen of the genital organs of a pregnant M.major and those of Brass (notably fig. 2.Taf I. 11. representing the vaginae of a young Trichosurus and fig. 1.Taf IV. representing the genital organs of Phascolomys) are, as Fletcher has already pointed out, entirely misleading, since they represent the median vagina as ending freely, and without any connection with the connective tissue in which the posterior ends of the lateral vaginal canals and the urethra lie imbedded. This connective tissue with its enclosed canals, lateral and median vaginae and urethra, represents the persistent posterior portion of the genital cord and just in this tissue from analogy with Perameles we should expect the formation of a pseudo-vaginal passage to take place, if such occurs in Macropods. Fletcher is the only observer who offers any observations on the mode of origin of the direct communication in these forms and summarises his results in the following paragraph (loc.cit.(b) Part 11. p. 10.):-

"In virgin animals of H.ruficollis, H.dorsalis, P.penicillata, O.robustus and O.rufus the direct communication did not exist, but in one specimen of P.p(enicillata) and one of H.ualabatus the direct communication was in process of formation but still incomplete; and these two specimens seem to show that the aperture of communication arises probably not by a mere rupture of the intervening portion of the wall of the urogenital canal, but by an involution of the latter canal growing backwards to meet the cavity of

(2) Fletcher "On the Existence after Parturition of a Direct Communication between the Median Vaginal cul-de-sac so called and the Urogenital Canal, in certain species of Kangaroos." P.L.S. N.S.W. Vol VI 1881.
(b) "On some Points in the Anatomy of the Urogenital Organs in Females of certain species of Kangaroos.
Part I. P.L.S. N.S.W. Vol VII, 1882. Part II, Ibid. Vol VIII, 1883.

the median portion of the vagina when the latter has reached its maximum backward extension. My own observations show that it is possible for the direct communication to exist in virgins, while those of other observers show that exceptionally this actually is the case; but more usually it would seem to be formed late in life probably during pregnancy or at parturition." Although I have no direct observations of my own to offer on the formation of this direct communication in these forms, yet in view of the occurrences in Perameles I feel unable to accept Fletcher's suggestion that the direct communication is ever completed independently of the median vagina, by an involution of the urogenital sinus. Convinced as I am that the formation of the direct passage primarily involves solely the median vaginal apparatus and the connective tissue following on its posterior end, the completion of the passage by a definite independent involution of the sinus urogenitalis appears to me inexplicable. However leaving this point aside, since it is only offered by Fletcher as a tentative suggestion based on conditions seen in two specimens, we come to his important conclusion based on the examination of the genital organs of some eighty females that the actual direct opening in Macropods is "more usually - - - - formed late in life probably during pregnancy or at parturition," a conclusion in striking agreement with that arrived at for Perameles. And I think that the facts set forth in the preceding pages of this paper justify us in that Macropods the median passage is completed during parturition by rupture of the tissue intervening between the posterior end of the median vagina and the urogenital sinus. But in those Macropods with a direct opening owing to the close approximation of the median vagina to the urogenital sinus, the cleft or pseudo-vaginal passage is either extremely short or indeed hardly present where the two cavities in the virgin are only separated by a thin septum, so that the ruptured epithelium of the sinus is able to extend completely over it and to become directly continuous with the epithelial lining of the median vagina. Once formed, the opening is a permanent one.

There are, however, even amongst Macropods forms e.g. M. Major in which as Fletcher points out (b. part II p.10) "unless very exceptionally there is no direct communication even after young have been produced" although the median vaginal canal is well developed and extends down to within a short distance from the sinus. In Perameles, it will be remembered, that no trace of the opening of the pseudo-vaginal passage into the sinus was perceptible in any of the specimens examined. The question thus arises whether a similar obliteration of the opening may not account for the absence of the direct opening in the forms in question ? At all events, the fact of the closure of the direct opening in Perameles shows us that the mere absence of such, is no certain and sufficient criterion on which to decide whether or not the young are born by a median passage. Finally as regards parturition, the foregoing discussion, it seems to me, sufficiently upholds the conclusion that

Perameles in respect to the phenomena connected with that process, in no way stands alone amongst Marsupials as an aberrant and specialised type but quite on the contrary exhibits more primitive features in the mode of birth of the young than are show by any other Marsupial hitherto described as possessing a direct median passage. That the direct passage in Perameles is in a much more primitive condition than that of Macropods will, I think, be admitted without question. Indeed the condition of the passage in Perameles can only, in my opinion, be regarded as the precursor of the Macropine one and as showing us in use today the earliest stage in the evolution of that direct median passage which reaches its highest development in the specialised Macropodidae. So far as our present knowledge extends Perameles is the only Polyprotodont genus in which a direct median passage has yet been found, the condition of the genital organs in a pouch young of Peragale lagotis suggests that such also occurs in this genus. Among Diprotodonts, the direct communication has been observed, according to Fletcher, in twelve species of the family Macropodidae. That it also exists outside the limits of this family I can affirm for Tarsipes rostratus and Alix (loc. cit.) states that "sur une Phascolome wombat le vagin médian communiquait avec la vestibule urogénital par une petit pertuis bien distinct." I find that this is not the case in Phascolomys mitchelli though on that account I would not venture to assert that the young are not born by a median passage. As regards other forms there are some e.g. Trichosurus vulpecula in which the young are almost certainly born through the lateral vaginal canals, here comparatively short and simple in their course, while with regard to the majority of Marsupials extended observations based on serial sections through the termination of the median vaginal apparatus are necessary before any definite statements can be made concerning them.

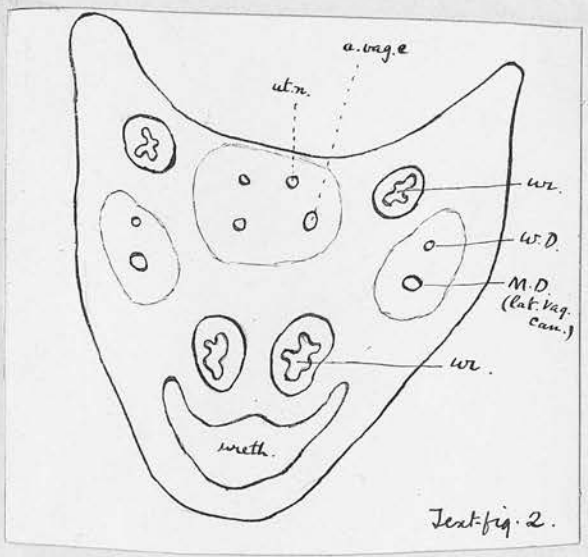
Such being the state of our knowledge, it would be hazardous to venture far into the uncertain field of speculation concerning the conditions which first led to the acquisition of the direct median passage. That this median passage has not been twice independently evolved within the limits of the Marsupial class I am convinced and its occurrence in Perameles in a condition so obviously unspecialised and in association with such an extremely primitive condition of the genital organs tends to suggest that its acquisition is of ancient date.

The origin of the passage in the first instance presupposes, it seems to me, the existance of the vaginal cul-de-sacs. These may have originally arisen simply as outbulgings mechanically produced by the young as they passed from the contracted os of the uterus into the lateral vaginal canal, at the time the Mullerian duct underwent differentiation into distinct uterine and vaginal segments. Whether or

not this be the true explanation of the formation of the vaginal cul-de-sacs, if we grant their existence, then it appears probable that the median passage arose in the first instance, through what we can only describe as an accident, which happening again and again, came eventually, owing to its value to be adopted as a normal occurrence. In the lowly Perameles, the old accidentally discovered passage has persisted probably unmodified, in association with the retention by the genital organs as a whole of a persistently embryonic state, while the more specialised Macropods have gone on to exhaust the possibilities implied in the possession of a median vaginal apparatus and have evolved a direct median passage eventually epithelially lined throughout its entire extent.

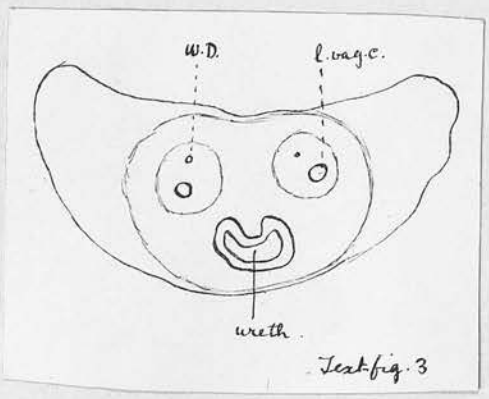
CONCLUDING REMARKS.

At the conclusion of the present series of papers, I hope, with a more complete knowledge of the development of the genital organs in Perameles, Macropus and Trichosurus, to be in a position to enter into a more extended discussion of the morphology of the genital organs of Perameles than is possible in the present communication. However, for the proper understanding of the adult condition of the organs, this much it is necessary to state; - the urogenital strand of the adult represents nothing else than the persistent genital cord of the pouch-young, from the tissue of which the portions of the Mullerian ducts forming the vaginae in the adult, never become free except in so far as the forwardly projecting vaginal caeca may be said to have become free from the original tissue of the cord.



Text-fig. 2.

Text-figs. 2 & 3 are outline drawings of sections through the genital cord of a pouch specimen of P. nasuta, 34 mm. in greatest length. Fig 2. represents a section through the anterior region of the cord a little behind the openings of the ureters into the fundus of the bladder, while fig. 3 represents a section through the cord at a somewhat lower level. They may be compared respectively, with figs. 5 & 8 Plate VI, through the corresponding regions of the genital organs in the adult, when it will at once be apparent that so far as concerns the general disposition and course of the genital ducts, these remain in what can only be described as a persistently embryonic condition.



Text-fig. 3

Now in young foetal Macropods, the genital ducts have es-

sentially the same disposition as in the foetal and adult Perameles, i.e. the uterine and vaginal segments of the Mullerian ducts lie imbedded together with the urethra in a common mass of mesodermic tissue, the genital cord. In both, the uterine segments of the ducts pass back side by side to open into small cul-de-sacs arising at their junction with the vaginal segments of the Mullerian ducts. From each cul-de-sac the lateral vaginal canal continues directly forwards and outwards ventral to the uterine segments of the ducts (Text fig 2, a. vag. c.), in order to sharply bend round anteriorly and to continue backwards. Just behind the bend the two lateral canals are widely separated from each other by the ureters which pass in mesially to them in order to reach the base of the bladder, united ventrally with the tissue of the genital cord. Behind this level, the two vaginal canals gradually approximate and finally run back parallel with each other and with the Wolffian ducts and urethra (Text fig. 3.) to open into the short urogenital sinus.

I would lay special emphasis on the fact that the anteriorly directed portions of the Mullerian ducts remain in the adult Perameles permanently imbedded in the connective tissue at the anterior end of the urogenital strand, a structural condition never before described for any Marsupial and confined so as our present knowledge goes to the two allied genera, Perameles, and Peragale, though there appears to be a close approximation to a similar condition in Myrmecobius fasciatus. In most other Marsupials, not only do these forwardly directed portions of the lateral canals become entirely free from the tissue of the genital cord but in many forms e.g. Macropods the backwardly directed portions also become free from the cord over the greater portion of their extent, only their terminal segments retaining their original position in that cord.

In concluding, for the present, this short discussion, I would remark that the facts here set forth, in my opinion, show conclusively that the condition of the genital organs in Macropods, - undoubtedly the most specialised of living Marsupials and whose exclusive study in the past has so largely served to distort our views on general questions of Marsupial morphology - can in no sense be regarded as primitive and that just in so far as the genital organs of Perameles depart from the prevalent Marsupial condition, they in the same degree realise the more primitive type, a conclusion which I believe gives very material support to that view which regards the existence of an allantoic placenta in the genus, as an extremely primitive feature in its organisation.

University of Sydney.

10. III. 99.

Plates V-X. Urogenital Organs of Perameles.

List of Common Reference Letters.

a. vag. c. Anterior forwardly directed portion of lateral vaginal canal.
Bl. Bladder. - Bd. lig. Broad ligament.
Cl. Cloaca. - c.m.v. Common median vagina. - c.t. Connective tissue between lateral vaginal canals.
fim. Fimbriated opening of Fallopian tube.- f.t. Fallopian tube.
l.vag.c. Lateral vaginal canal.
m.v.c. Median vaginal canal.
o.u.s. Opening of urogenital sinus. - op. Opening of anterior portion of lateral vaginal canal into vaginal caecum.- ov. Ovary.
pv. p. Pseudo-vaginal passage.
rect. Rectum.
u.s. Urogenital strand. - ur. Ureter. - ureth. Urethra.
ut. Body of uterus. - ut. p. l. Utero-pelvic fold of broad ligament. - ut. n. Uterine neck.
vag. c. Vaginal caeca. - ves. v. Vesicle artery & vein.

Except figs 1 & 2, the figures are Micro-photographs of transverse sections. I desire here to express my thanks to Mr. R. Grant, late of the Physiological Laboratory, for invaluable help in their preparation.

Plates V—X.

Fig. 1. Urogenital organs, P.obesula, seen from dorsal aspect. The cloaca has been opened to show the opening of the uro-genital sinus (o.u.s.) and the peritoneal pouches have been drawn forwards to expose the ovaries.
Nat. size.

Fig. 2. Urogenital organs. P. obesula.
Dissection from dorsal aspect.
X. Commencement of anterior forwardly directed portion of lateral vaginal canal.
Nat. size.

N.B. The common partition wall between the median vaginal

canals, should have been shown to gradually disappear posteriorly.

Figs 3 - 8. Trans. sections through genital organs, virgin P.nasuta. For description see text.

Fig. 9. Trans. section of the clitoris, showing the median septum (m.s.) the opening of the clitoris duct (c.d.) on one side and the erectile tissue (e.t.)

Figs. 10 - 12. Trans. sections, genital organs P.obesula with two 17.5 mm. young.

Figs. 13-15. Trans. sections. P. obesula with two, 22 mm. young.

Fig. 16. Trans. section, P.obesula with four 3.7 cm young, just behind the posterior end of the common median vagina.

Fig.17. Trans. section, P.obesula with 4 cm. young, showing the remnants of allantoic stalks filling up the pseudo-vaginal passage and surrounded by connective tissue.

Figs.18-20. Trans. sections, P.nasuta!, bred, showing in 18, the common median vagina, in 19. a well marked example of a fibrosed allantoic stalk in the pseudo-vaginal passage and in 20, the cleft-like passage with remnants of stalks.

Fig. 21. Trans. section thro' the urogenital strand. P.obesula with blastodermic vesicle.

Fig. 22. Trans. section urogenital strand, P.obesula with two 12.5 mm. young in uteri, showing the vascular character of the connective tissue between the lateral vaginal canals.

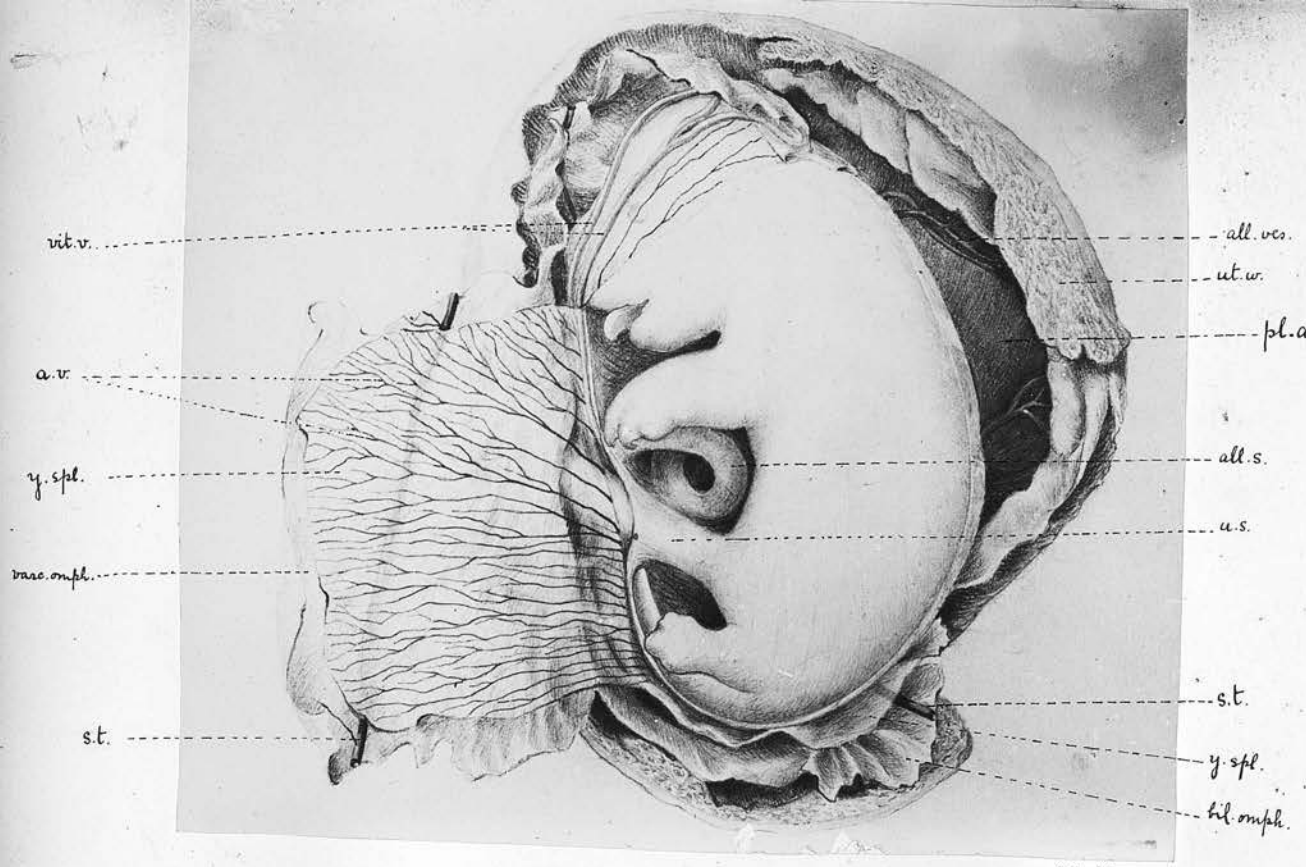

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Fig. 1.

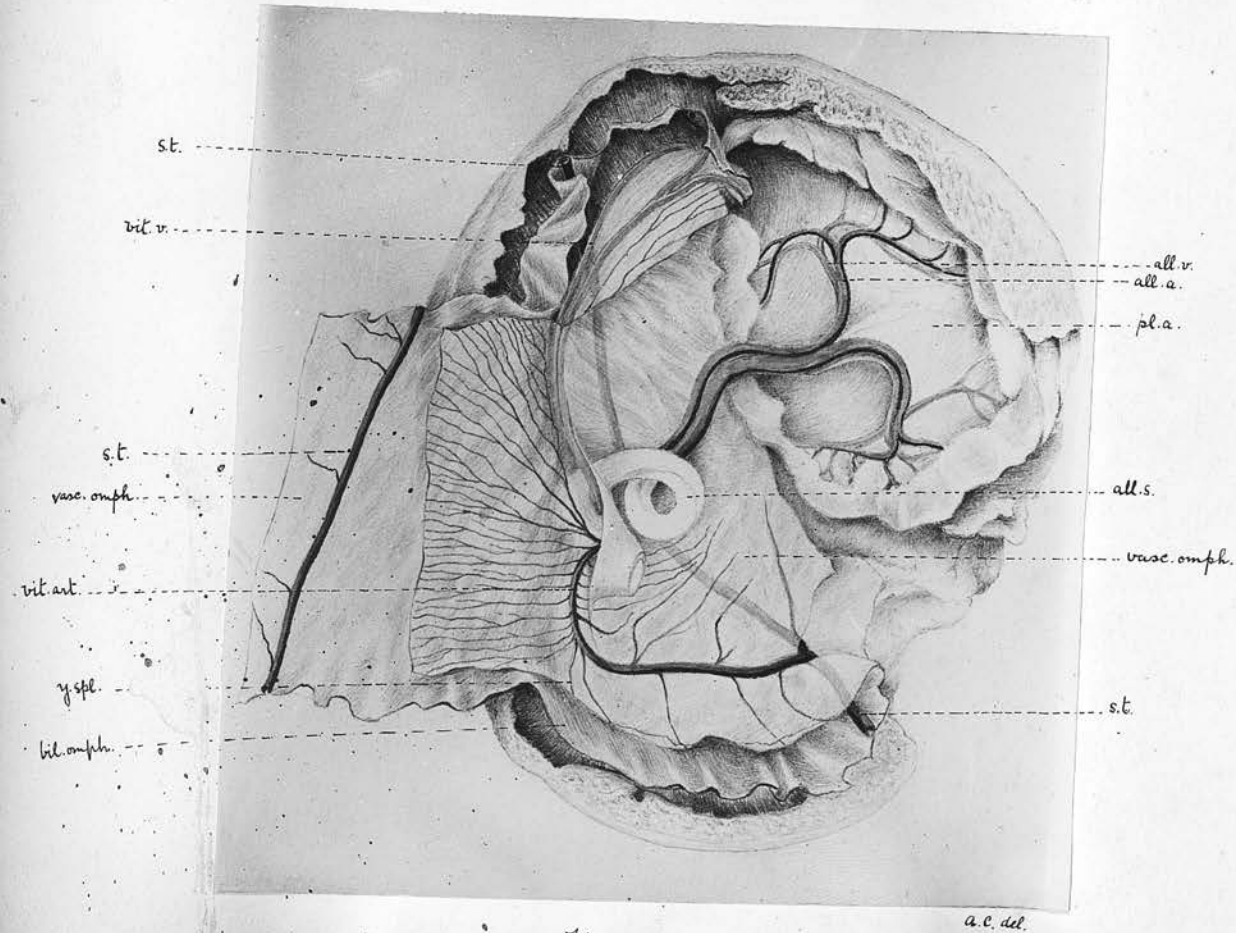
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Fig. 2.

A.C. del.

Fig. 3.

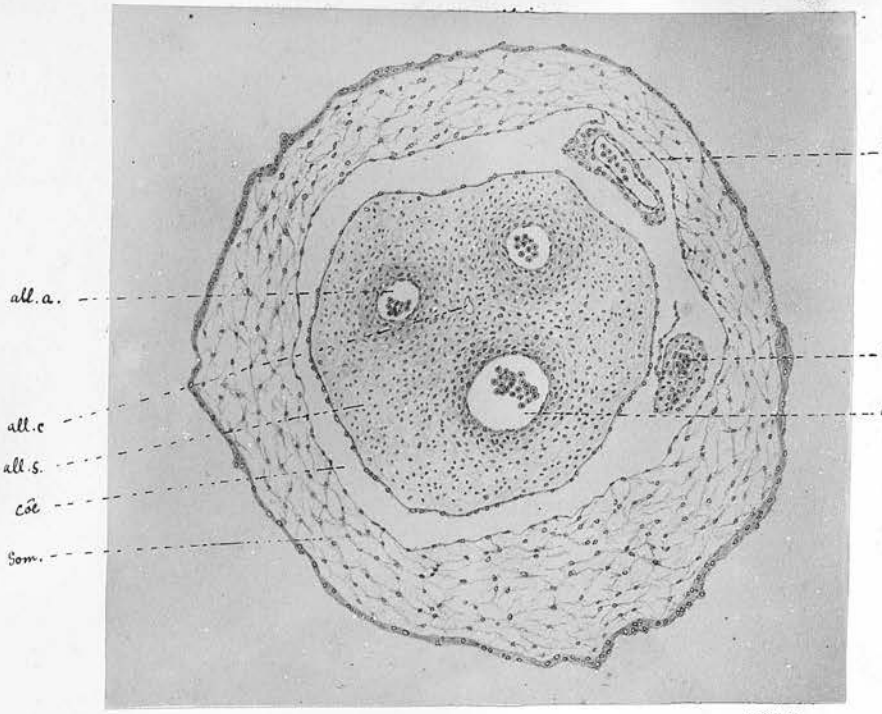

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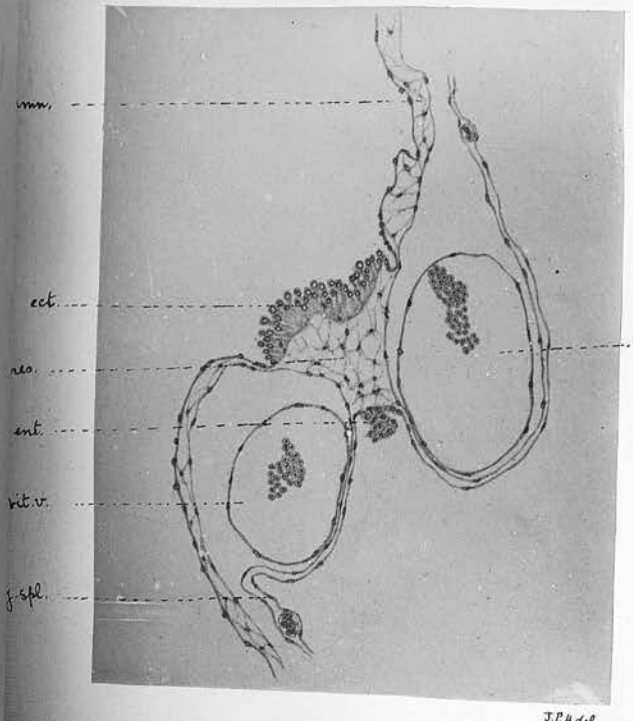
Fig. 4.



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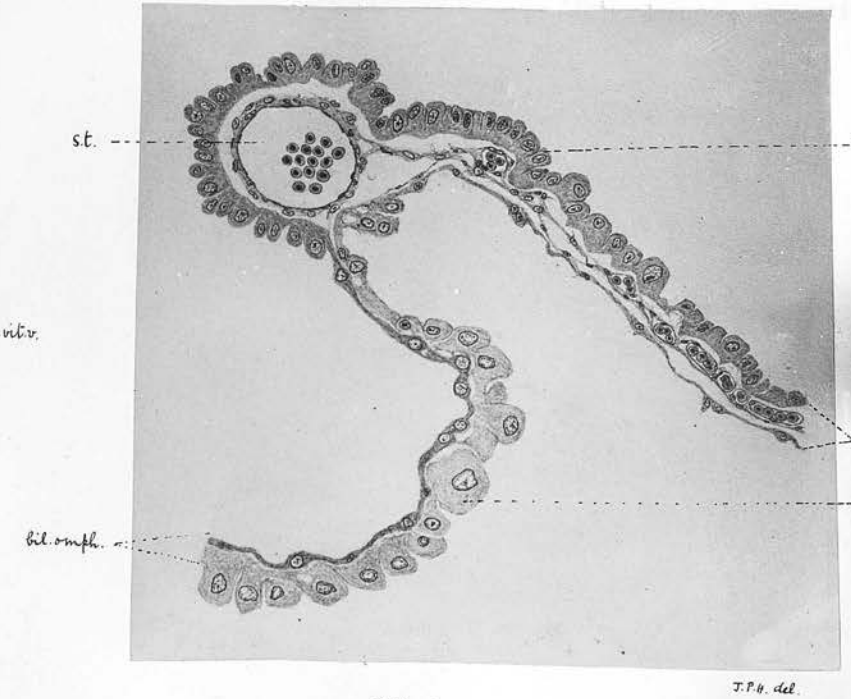

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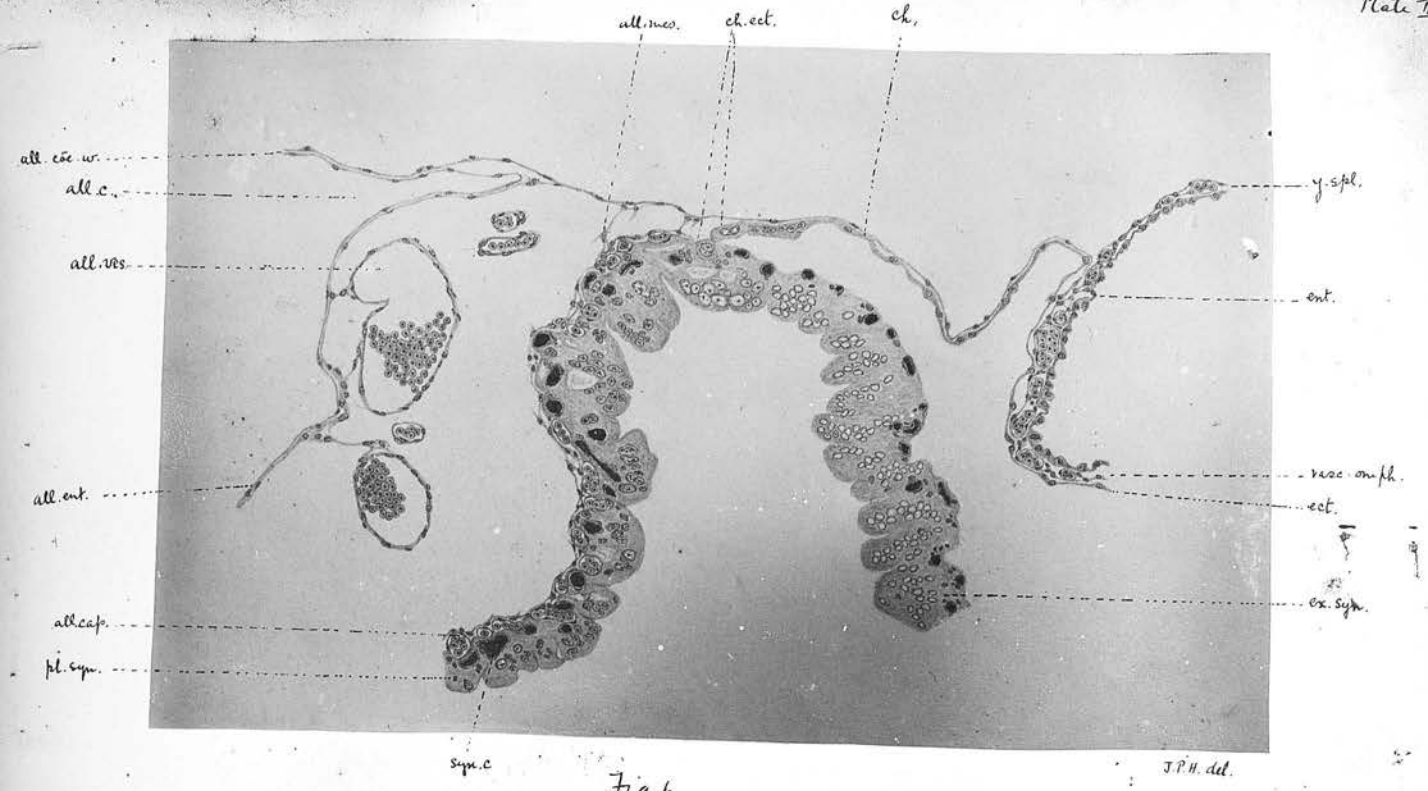
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Fig. 6.

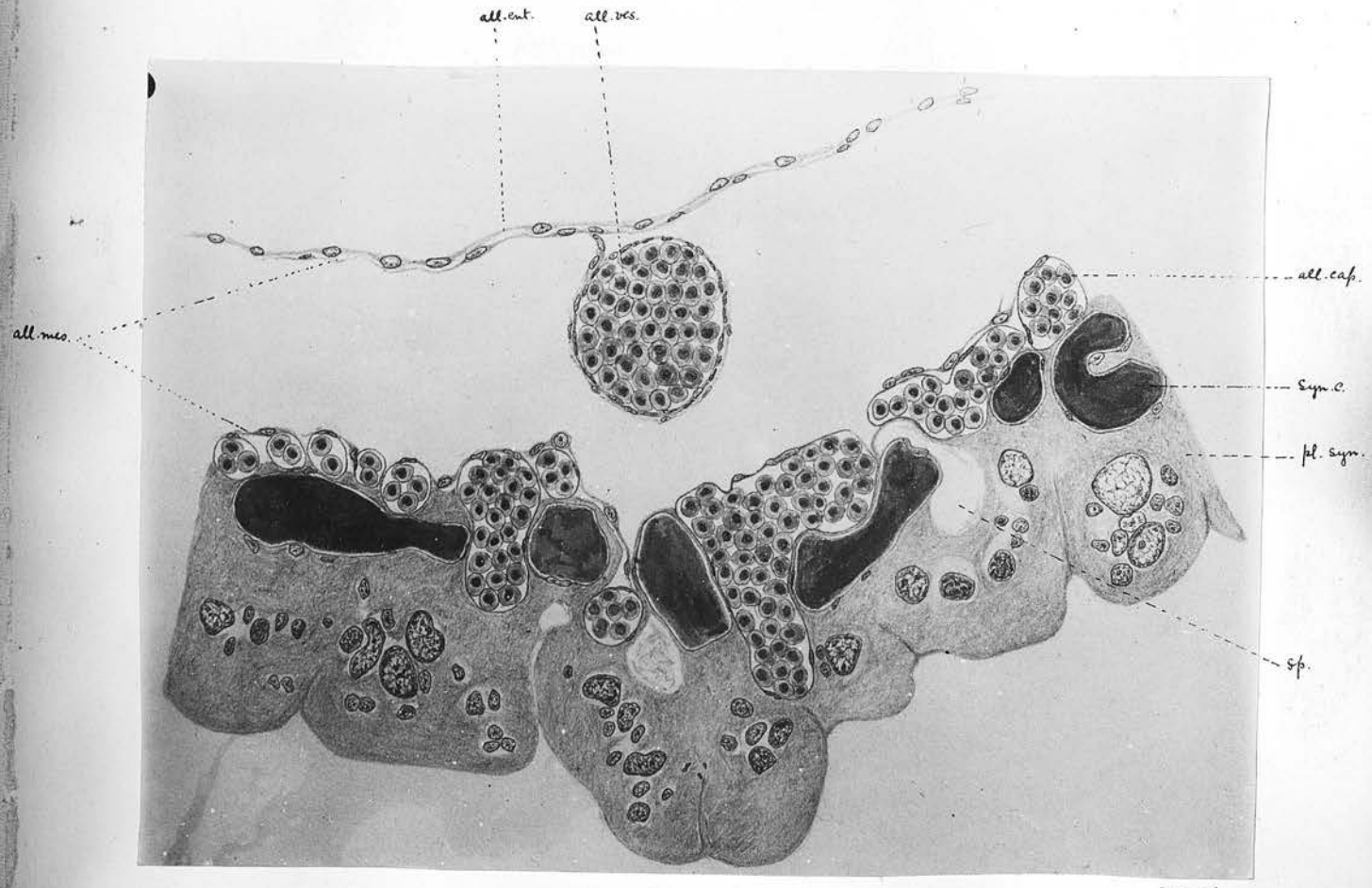
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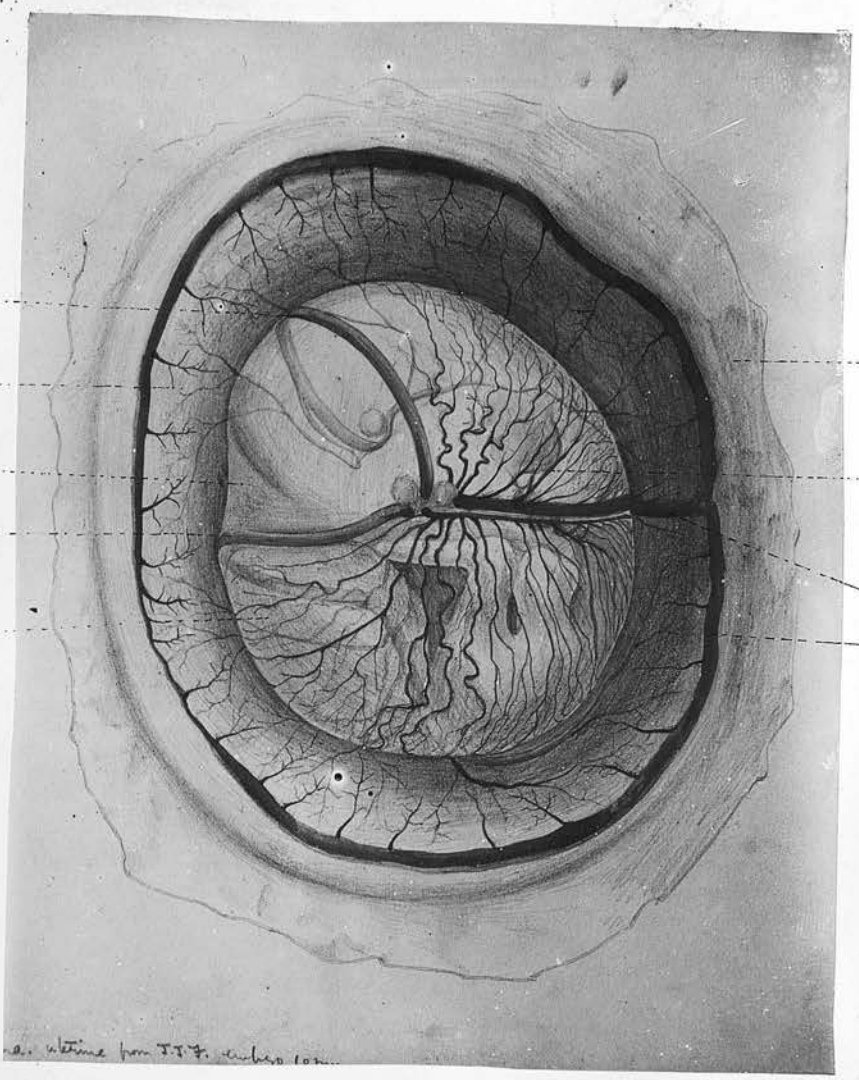
Fig. 7



a. uterine from T.T.F. embryo 10 m.

F.C.W. del.

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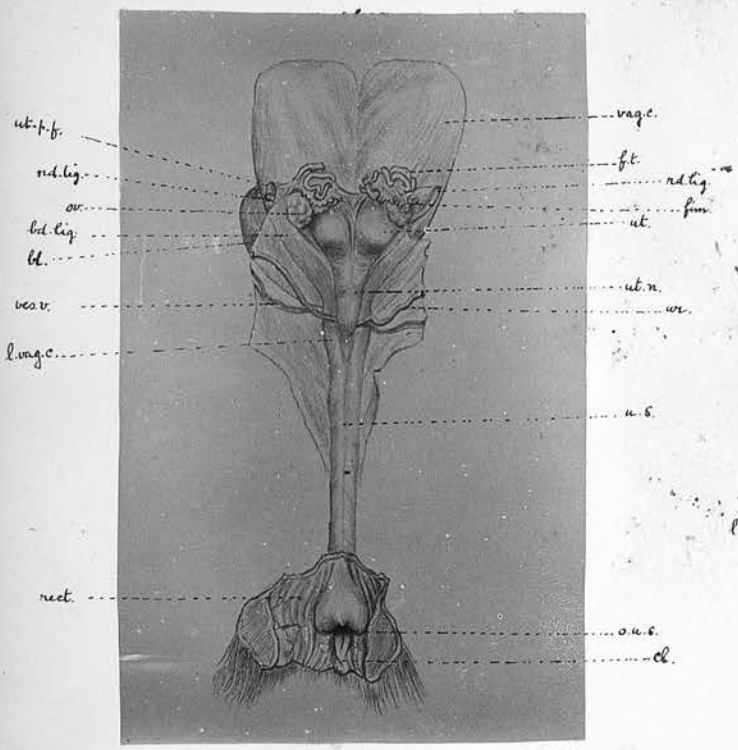

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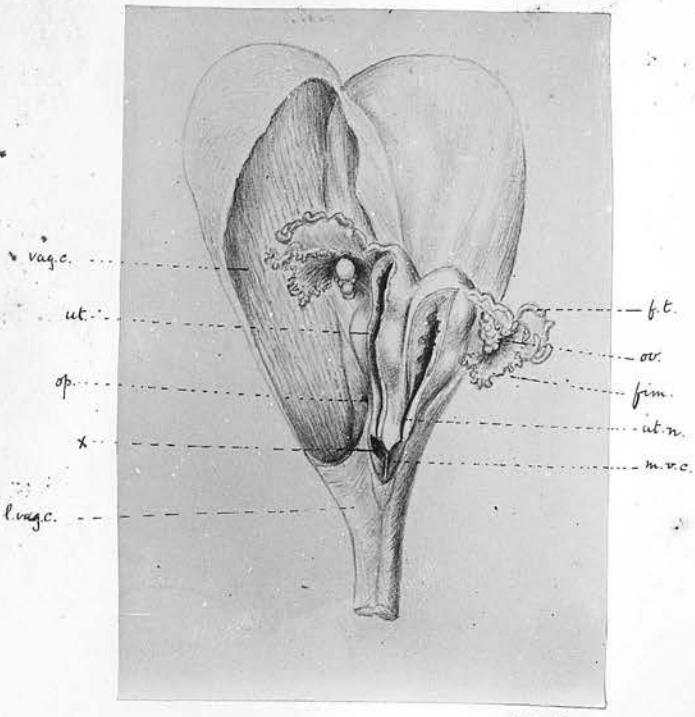

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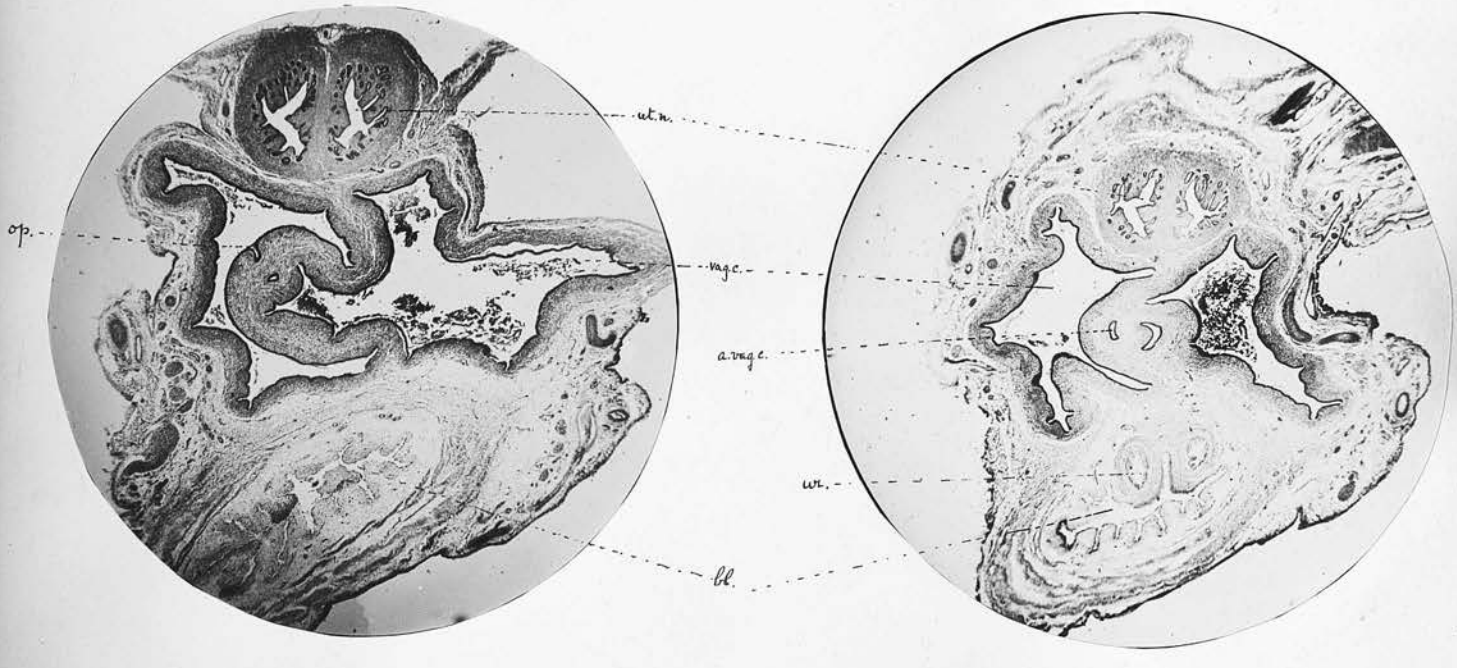
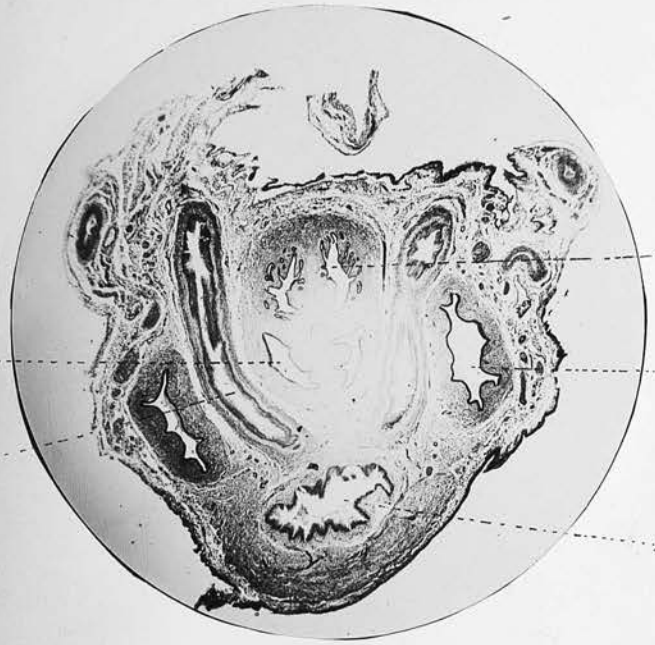


Fig. 3.

Fig. 4.

Figs 3 & 4 J.P.H. & R.G. photo.



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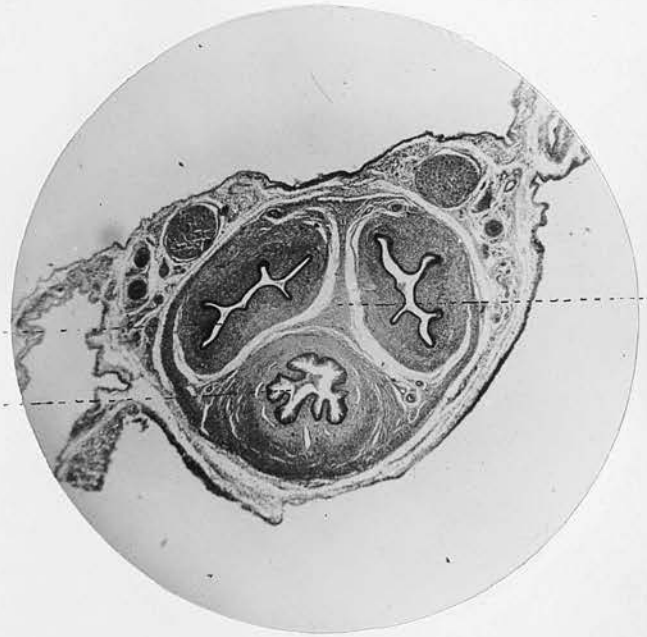

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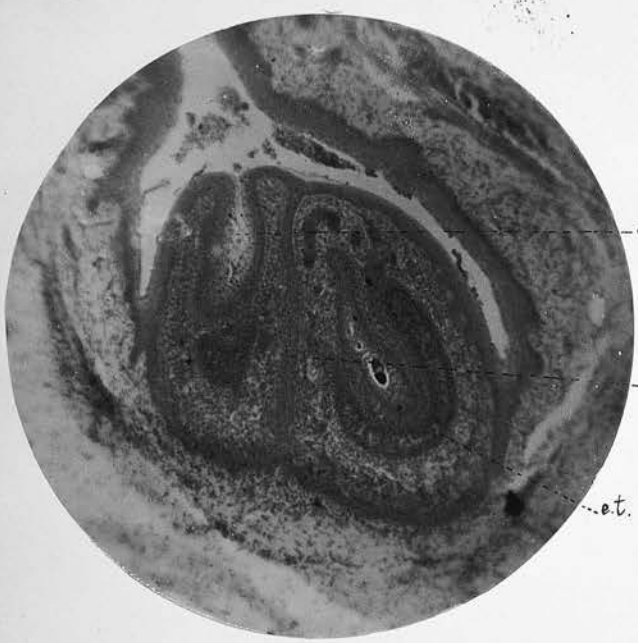
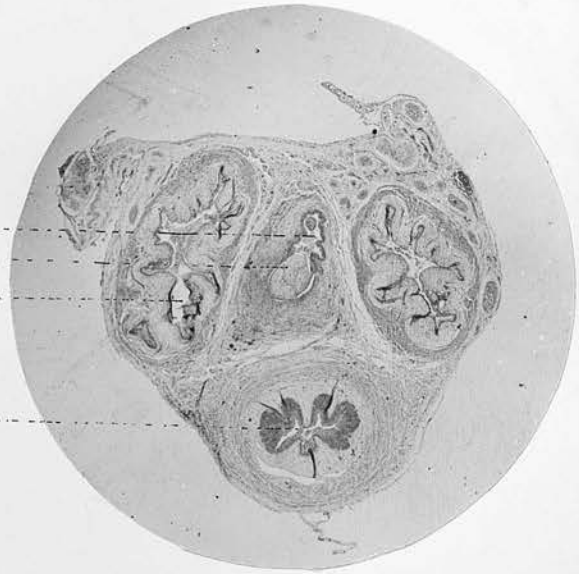


Fig. 9.

Fig. 10.

Fig. 11.



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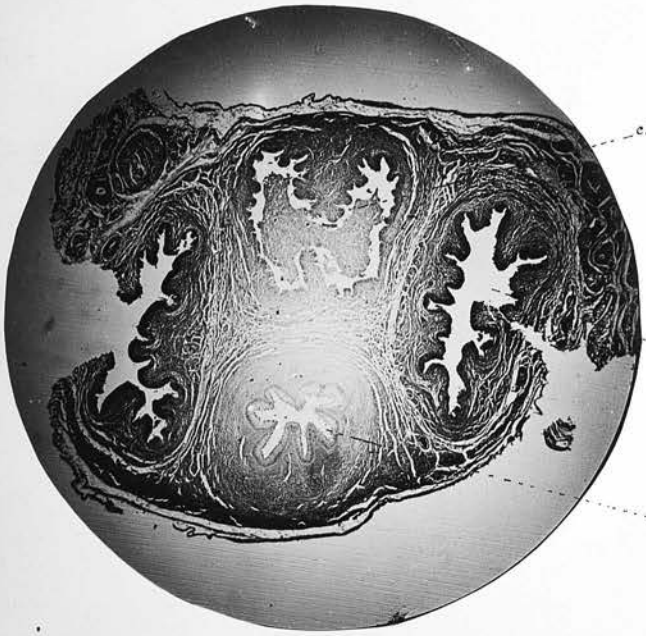

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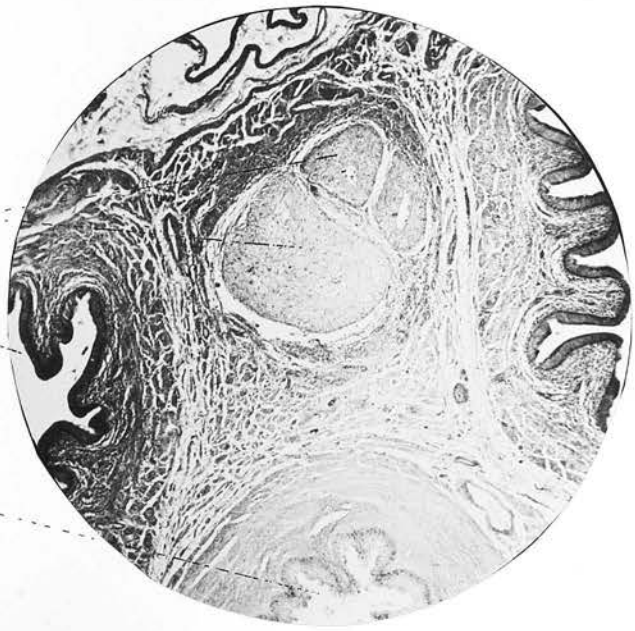

Fig. 14.

Fig. 15.

Fig. 16.

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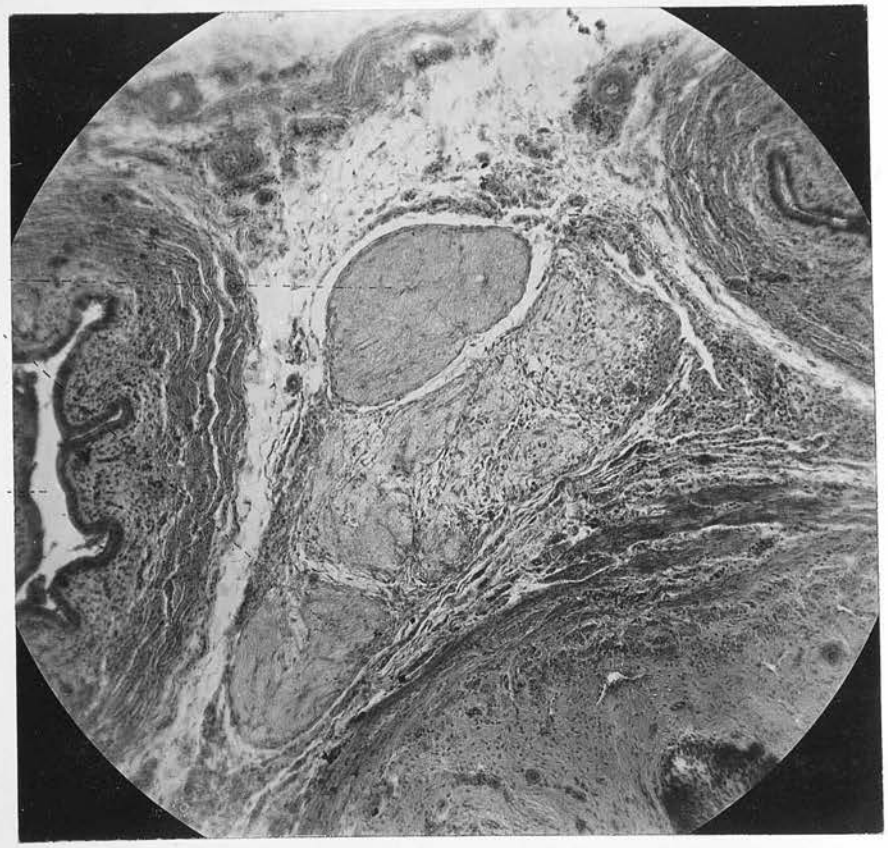

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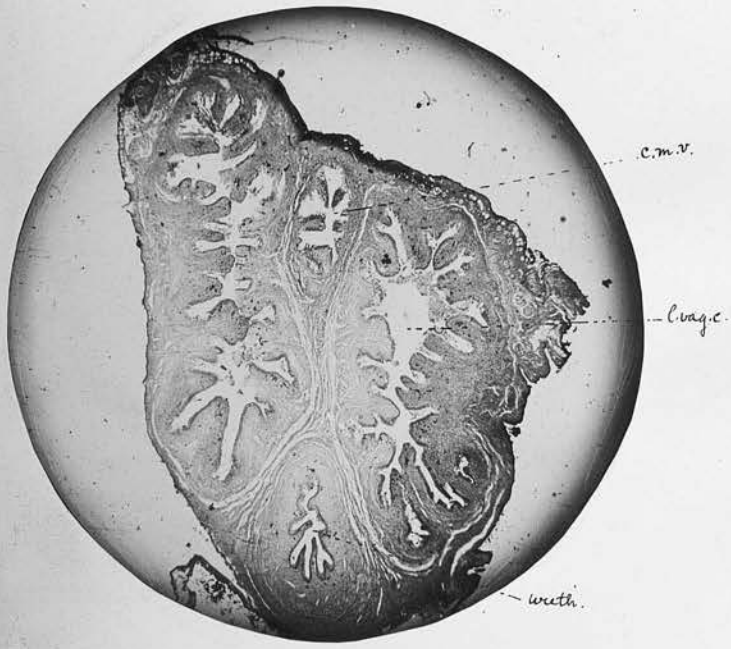

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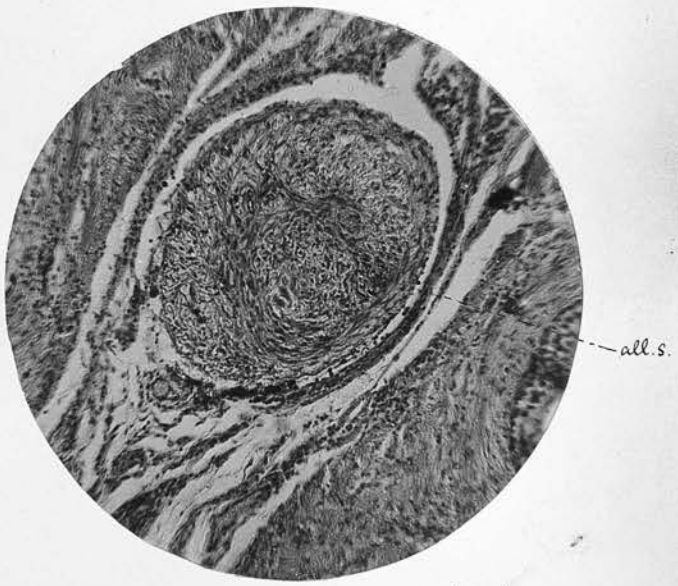

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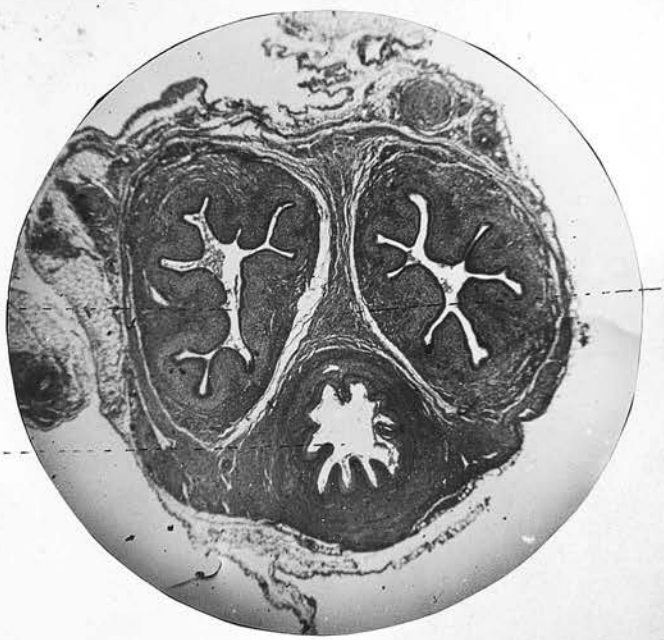

Fig. 21.

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