Contributions to the morphology and development of the female urogenital organs in the marsupialia / by Jas. P. Hill.

[*From the Proceedings of the Linnean Society of New South Wales, 1899, Part 1, March 29th.*]

CONTRIBUTIONS TO THE MORPHOLOGY AND DEVELOPMENT OF THE FEMALE UROGENITAL ORGANS IN THE MARSUPIALIA.

I. On the Female Urogenital Organs of Perameles, with an Account of the Phenomena of Parturition.

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(Plates i.-xii.)

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 in 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 urogenital 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 find only two references to the condition of the genital organs in *Perameles*. The first is a short account by Owen (**1**, p. 683) 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 Kan-

garoos. Each communicates with a vagina, expanding into a cæcum with semitransparent walls and greatly surpassing the uteri in size: the cæcum suddenly contract near the ora tincæ, 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 short paper by Alix (2) entitled "Sur les organes de la parturition chez les Marsupiaux" 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 d'autre part je n'ai pas trouvé de communication entre le vagin médian et le vestibule urogénital soit sur le Sarigue, soit sur le Péramèle," a statement which certainly shows 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* (3) 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 vaginæ (including the two lateral vaginal canals, with their cæca 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 consists in the fact that the lateral vaginal canals and the urethra lie imbedded throughout their entire extent in an elongated mass of connective tissue (Plate i., 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 fœtus. 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 cæca, 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 thick mass in which the urogenital sinus and cloaca are situated. At the anterior end of the strand the urethra, occupying its mid-ventral 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 cæca,—separated from each other by a common partition wall (Plate i., fig. 1, *vag.c.*), and lying immediately dorsal of the bladder, between it and the uteri. The posterior ends of the latter, as well as the median vaginæ, lie imbedded dorsally in the connective tissue at the anterior end of the strand. In Plate i., 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 cæca (*vag.c.*). Each of the latter is seen to contract posteriorly and to pass back as the lateral vaginal canal (*l.vag.c.*) in the urogenital strand (*u.s.*). Dorsally to the vaginal cæca 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 vaginæ 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. At this level it is reflected from the uteri as a free peritoneal fold or duplication, which passes forwards about as far as the level of the anterior ends of the uteri, and whose free and lunated margin at that level lies in contact with the ventral aspect of the rectum. This fold separates the uteri from the rectum and forms the roof of a fair-sized 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 morphologically dorsal (mesially directed) surface of the broad ligament along a line parallel with and just ventral to the ureter, which runs backwards in the latter, and is continued forwards on each side of the rectum as a fold, continuous laterally with the reflection of the broad ligament, and carrying in its substance the ureter and the ovarian artery and vein.

The *broad ligament* is reflected from the lateral side of each uterus, and contains between its two layers the Fallopian tubes, ovaries and uteri. Dorsally to each uterus it forms a definite ovario-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 (**4**) has termed this the "Ligamentum uterorum superius," without apparently appreciating its real nature.

The broad ligament after being joined by the above-mentioned free fold forming the roof of the dorsal uterine fossa, passes almost vertically upwards to become continuous dorsally with the parietal peritoneum. A duplication of it, however, forming the *utero-pelvic fold* of the broad ligament (Plate i., fig. 1, *ut.p.f.*) passes outwards and slightly forwards to join the parietal peritoneum dorso-laterally. The posterior free margin of this utero-pelvic fold is traversed 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 origin 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 outwards, 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 2·3 cm., 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 Surgeons' Museum (**5**), 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." 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 cæcum, to be continued as a peritoneal fold reflected from each side of the urogenital strand to the pelvic wall. This urogenital fold extends back, of course, only as far the posterior end of the pouch of Douglas.

The bladder is connected with the ventral abdominal wall by a median fold, which extends almost up to its apex. Brass (**4**)

terms this the "Ligamentum vesicæ medium." From each side of the bladder there passes down a low ridge-like fold representing the obliterated hypogastric artery, much more strongly developed in *Macropus*, which proximally conveys the vesical artery and vein from the urogenital fold to the bladder.

Vessels.

The vesical arteries arise together with the internal iliacs from the aorta. They (fig. 1, *ves.v.*) pass in the lateral urogenital fold of peritoneum to divide into branches supplying the bladder, the lateral aspects of the uteri and vaginal cæca and the urogenital strand. The vesical 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 i., 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 about 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 (either 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 even 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 (6, p. 418) that "die Anlage des Eierstockbandes mit dem runden Gebärmutterbande einen proximal-distalwärts sich erstreckenden continuierlichen Strang bildet."

Fallopian Tubes.

Each is a greatly convoluted thin tube measuring as much as 4 cm. in length, and sharply marked off from the uterus. 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 i., fig. 1, *ut.* and *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 vaginæ) 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 cæca, the organs are examined from the ventral aspect. They lie dorsal to the posterior portions of the vaginal cæca and are connected posteriorly with the latter by a low median peritoneal fold. Viewed from the dorsal aspect (Plate i., fig. 1) the uteri are seen throughout 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 cæca 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 cæca 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 this region the hinder sections of the uterine necks, together with the median vaginal cul-de-sacs, come to lie 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 cæca, 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 ii., fig. 3, *ut.n.*, *vag.c.*, *bl.*).

In a previous paper (3, p. 389) 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 (1), and Brass (4) 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*, *Dasyurus*, *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 esentially a circular one is a point of some little interest and has not, so far as I am aware, been emphasised. Sobotta (7) has shown that the proper fundamental musculature of the uterus is the circular layer which primitively forms the muscular investment of Müller'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.

Vaginæ.

Vaginal cæca.—Posteriorly, as has been described above, the vaginal cæca 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 i., figs. 1 and 2, *vag.c.*). The cæca 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 cæca are lined by a layer of columnar epithelium which has usually a ridged appearance in surface view (fig. 2, *vag.c.*).

The vaginal cæca 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 cæca were greatly dilated and filled by a clear viscid semifluid 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 (*cf.* 8, p. 312). Usually the cæca contain only the hard, opaque material which is essentially similar to the "inspissated secretion commonly present both in the cul-de-sac and the lateral vaginal canals" of Macropus according to Owen (8) and noted by various observers from Home (14) onwards. According to Owen (9) these masses "most resemble those coagulated masses that are found in the vesiculæ seminales and sometimes in the urethra of the Agouti, Capromys, Guinea-pig and others of the Rodent order." Without doubt these hard masses are derived from the same source, viz., from the secretion accompanying the spermatozoa.

In certain species of Kangaroo Rats of the genus *Potorous* there are present, as described by Owen (9) and Brass (4), forward

expansions of the vaginæ which form a large diverticulum situated between the bladder and the uteri, like the vaginal cæca of *Perameles*, and no doubt identical in function with the latter.

In *Macropus major*, Stirling (**10**) 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 at the breeding season 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 cæca 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 *Chæropus 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.

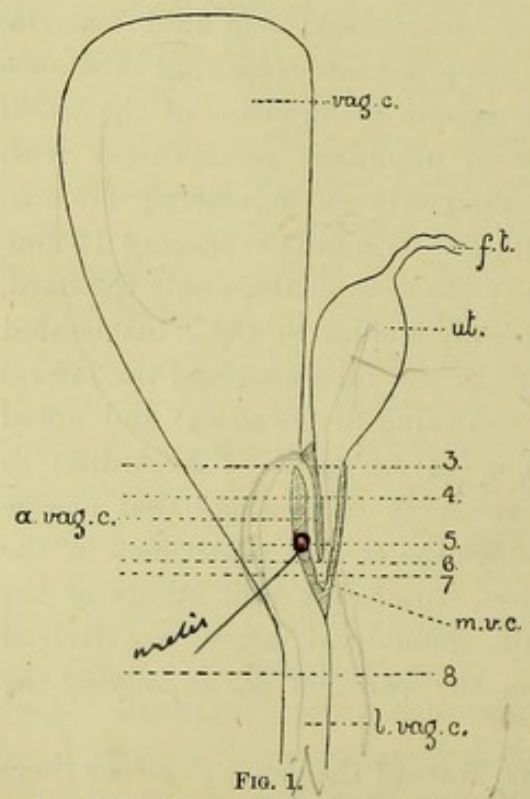

Fig. 1.

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 ii.-iv.

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 cæcum. 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 cæca (*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 of the lateral canal of one side into the cæcum, while the canal of the other side is seen in section in the common partition wall between the cæca. 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 cæca, which is at this level thicker than anteriorly. In other words, the vaginal cæca as they decrease in size at the same time bend slightly outwards. The uterine necks (*ut.n.*) are also smaller and now very distinctly invested by the surrounding connective tissue. In fig. 5, thirty-nine sections behind fig. 4, the vaginal cæca 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 former. 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.* and *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 and 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 i., 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 median vaginæ have been removed. Each uterine neck (*ut.n.*) is seen to open by a scarcely projecting and ill-defined os into the corresponding vaginal cul-de-sac (*m.v.c.*). At the anterior 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 cæcum 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 approach posteriorly to within a comparatively short distance from the opening of the lateral vaginæ into the urogenital sinus, in *Perameles* the cul-de-sacs are small structures which terminate at a relatively very great distance from that sinus.

Ureters, Urogenital Sinus, &c.

Ureters.—The ureters enter the anterior end of the urogenital strand between the posterior portion of the uterine necks and the lateral vaginal canals (Plate iii., fig. 5, *ur.*) and pass forwards (fig. 4, *ur.*) to open into the bladder shortly above its base and close to its dorso-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 vaginæ to the urogenital sinus) is between 3 and 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. Lying peripherally in the connective tissue and surrounding the three ducts is a very thin layer of involuntary muscle. I would direct special attention to the narrow strand of connective tissue separating the lateral vaginal canals, for it is here that the cleft-like pseudo-vaginal passage (3, p. 452) is found to occur after parturition has been effected, 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). The strand in question, as was above mentioned, is directly continuous with the deeper-staining mass of connective tissue situated around and just posterior to the ends of the median vaginal cul-de-sacs.

The lateral vaginal canals present a uniform structure throughout their course. They are lined by a mucous membrane consisting of dense connective tissue, clothed by a layer of columnar epithelium. External to the mucous membrane is a layer of non-striate muscle 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 and narrow chamber with a length of 4-7 mm., having as Owen pointed out (1, p. 683) "the least extent in this genus of Marsupialia." It

opens on the ventral wall of the cloaca by a small aperture (Plate i., 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, just within the margin of the opening of the sinus, 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 1 mm. in greatest breadth. It is attached over its whole extent, though exceptionally its apex may be free and slightly bifid. It is stated by Owen and Brass that where the glans penis is bifurcate in the male, in the female the clitoris is likewise bifid, but this statement does not hold for *Perameles*.

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 latter to enter the clitoris proper. The lumina of these canals may be continuous or interrupted, or the ducts 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 v., fig. 9, *m.s.*) each half containing one of the canals 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 (8, p. 312) "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."

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 trabeculæ. 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 large specimens 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 sponge-like 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 common 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 Müllerian 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 22 mm. 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.*, and 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 cæca, 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 imbedded 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 cæcum. 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 v., fig. 10, *m.v.c.* and *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 median vagina,—formed, as we have seen, by the union posteriorly of the two vaginal cul-de-sacs. Fig. 11, Plate vi., 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 loses 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.* and *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 former, 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 urogenital 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 extravasted 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 born 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 (pp. 431-2), but without figures. For com-

pleteness I here reproduce the main points in my previous description in explanation of figs. 13, 14 and 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; 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 urogenital 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 xii., 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 without 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 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 corpuscles 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 portions 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 urogenital sinus.

vii. *P. nasuta*, with an early blastocyst in one of the uteri. (Stage A of 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 blastodermic 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 urogenital 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 her, 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 urogenital 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 longitudinally, 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 a few millimètres in length, 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 3-4 cms. in length—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 specialised wall" (3, 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 merely a solution of continuity 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 throughout 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 loses its continuity with the lumen of the latter 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 vaginæ, 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" (3, 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 fœtus 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 separateness 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 congested condition during the act of parturition. In my previous paper (3) I instituted a comparison between the median pseudo-vaginal passage in *Perameles* and the epithelially lined median vaginal

passage in the Wallaroo (*M. robustus*), by way of which, as Stirling (**10**) has shown, the young Wallaroo reaches the exterior. In that comparison, misled by my misinterpretation of the median vaginæ as posterior prolongations of the uteri, I stated that the former passage had "no connection whatever" with the lateral vaginal canals, an erroneous statement which I trust the present paper sufficiently 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 themselves arise developmentally as posteriorly directed cæcal diverticula, one from each Müllerian duct at the junction of its uterine and vaginal segments.

Now in young fœtal 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 the genital cord up to within a comparatively short distance from the anterior end of the sinus urogenitalis, 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, and even then the fusion is only partial, are entirely imbedded in the tissue of the genital cord and terminate far remote from the urogenital 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 canals.

It is thus evident that the median vaginal apparatus remains, as compared with that of Macropods, in an extremely primitive condition, at a stage of development which is early passed through in the fœtal Macropod.

In view of the fact that both in *Perameles* and in certain Macropods [*cf.* especially Stirling (**10**)], the young reach the exterior by way of a direct median passage, involving in both cases the median vaginal apparatus, the question next arises, may not the mode of 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 there 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, from Home (**14**), who first described the condition, onwards [I need here only cite the careful work of Lister and Fletcher (**11**), and Fletcher (**12** and **13**), 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 *Macropodidæ*, 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 in Macropods been found to communicate with the urogenital sinus in virgin animals, namely, "by Lister in *H. ualabatus* and Brass in *H. bennettii*" (Fletcher, **13**, Part ii. p. 9), but such cases are to be regarded as very rare and exceptional variations.

In virgins, normally, as Fletcher's investigations (**13**) show, the median vagina ends blindly in the connective tissue between the posterior ends of the lateral vaginal canals and in comparatively close proximity to the urogenital sinus. Figures such as the classical figure of Owen of the genital organs of a pregnant *M. major* (**9**, Plate vi., fig. 7), and certain of those of Brass (**4**, notably fig. 2, Taf. ii., representing the vaginæ of a young *Trichosurus*, fig. i., Taf. iv. representing the genital organs of *Phascolomys*, and fig. i. Taf. iv. those of *M. major*), are, as Fletcher has already pointed out (**13**, Part i. p. 658), 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 vaginæ and urethra lie imbedded. This tissue, with its enclosed canals, lateral and median vaginæ 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 (**13**, Part ii. 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 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 this actually is the case; but more usually it would seem to be formed late in life, probably during pregnancy or at parturition." Brass (**4**, p. 27) also remarks : "es ist wohl die Ansicht ausgesprochen worden, dass dieser Durchbruch des Blindsackes gegen den Sin. urog. hin zur zeit der Schwangerschaft stattfände, um den Embryonen einen bequemeren Weg nach aussen zu verschaffen."

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, from the study of the condition in *Perameles*, that the formation of the direct passage involves

solely the median vaginal apparatus and the connective tissue tract leading backwards therefrom, the completion of the passage by a definite independent involution of the urogenital sinus appears to me inexplicable. However, leaving this point aside, since it is only offered by Fletcher as a tentative suggestion based on appearances seen in only two specimens, we come to his important conclusion, founded on the examination of the genital organs of eighty females, that the direct opening in Macropods is "more usually . . . formed late in life, probably during pregnancy or at parturition," a conclusion identical with that arrived at, in my previous paper (3), for *Perameles*. In the present paper I have expressed the opinion that the pseudo-vaginal passage in *Perameles* is actually formed at the time of parturition, and I think that the facts herein set forth justify us in concluding that, as in *Perameles* so also in Macropods, the median passage is completed during parturition by actual rupture by the embryo of the tissue intervening between the posterior end of the median vagina and the sinus urogenitalis. But in those Macropods with a direct opening, owing to the close approximation of the median vagina to the urogenital sinus, the cleft in the connective tissue or pseudo-vaginal passage is either extremely short or, indeed, hardly present where the two cavities are only separated in the virgin by a thin septum. The consequence of this is that the ruptured epithelium of the median vagina and that of the urogenital sinus are able, in the healing process, to extend completely along the very short pseudo-vaginal passage and to become directly continuous with each other. Once formed, the opening of the median vagina into the sinus, in these Macropods, thus becomes a permanent one, while in *Perameles*, as has already been pointed out, owing to the great length of the pseudo-vaginal passage, the edges of the opening into the sinus can only unite with each other, and as a consequence the opening is obliterated and has to be temporarily reformed at each succeeding act of parturition.

Now there are forms even amongst Macropods, *e.g.*, *M. major*, in which, as Fletcher points out (13, Part ii. p. 10), "unless very exceptionally there is no direct communication even after young

have been produced," in spite of the fact that the median vagina is well developed and extends down to within a short distance from the sinus. The distance, however, between the posterior end of the median vaginal cul-de-sac and the sinus urogenitalis, appears to be greater in virgins of *M. major* than in the virgins of species which later possess the direct post-partum communication. Fletcher says in his description of virginal genital organs of *M. major*, "from three specimens sections which were cut differ from those considered above, chiefly in the fact that the cul-de-sac came to an end sooner, and always before the urogenital canal appeared in section" (13, Part ii. p. 9). If, then, a pseudo-vaginal passage were developed in *M. major* during parturition, it would be of greater length than in those forms with a persistent direct opening, and the question thus arises whether, in view of the closure of the direct opening in *Perameles* after each parturition in association with a long pseudo-vaginal passage, a similar explanation may not account for the apparently anomalous condition in *M. major* and other forms in which the direct opening appears to be absent?

At all events the fact of the closure of the direct opening into the urogenital sinus 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 direct median passage.

Finally, as regards parturition, it seems to me that the foregoing discussion 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 shown 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 to-day the earliest stage in the evolution of that direct median passage which reaches its highest development in the specialised

Macropodidæ. 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*, however, 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 Macropodidæ. That it also exists outside the limits of this family, I can affirm for *Tarsipes rostratus*, and Alix (2) states that "sur un Phascolome wombat le vagin médian communiquait avec le vestibule urogénital par un petit pertuis bien distinct." Although I find that this is not the case in *Phascolomys mitchelli*, yet I would not on that account 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 forms, 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 for the birth of the young. That this median passage has not been twice independently acquired within the Marsupial class I am convinced, and its existence in *Perameles* in a condition so obviously unspecialised and in association with such a persistently embryonic condition of the genital organs, tends to suggest that its acquisition is of ancient date, and at the same time leads us to ask whether the acquirement of the median passage in the first instance may not be the direct outcome of some such peculiar disposition of the Müllerian ducts in the genital cord as occurs in the adult *Perameles* and in the pouch young of other Marsupials, a disposition without doubt to be associated with the mesial position of the ureters?

The very fact of the constant occurrence in *Perameles* 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 the loss of more or less blood at each act of parturition, shows that with all its apparent defects it has proved of such direct advantage as to have led to its adoption in preference to the route offered by the lateral vaginal canals. What this advantage is, is not far to seek when we contrast the two routes. By way of the median passage, the young reach the exterior by the shortest possible path; they simply pass back in a straight line, while to reach the exterior through the lateral vaginæ they must first pass back into one of the median vaginæ, then directly forwards through the anterior portion of one of the lateral canals into the corresponding vaginal cæcum and hence back again through the posterior portion of the lateral canal to the urogenital sinus. Parturition then through this latter path must, we can easily imagine, have been not only a slow and laborious process, but one difficult of successful accomplishment and even fraught with danger to the lives of the young, cumbered as they are with attached allantoic stalks At all events, the acquirement of an entirely new passage is quite sufficient to show that the old route proved in some way to be unsatisfactory.

Now the origin of this new and direct passage in the first instance presupposes, it seems to me, the existence of the median vaginal cul-de-sacs. These may have originally arisen as outbulgings mechanically produced by the young to facilitate their passage from the contracted neck of the uterus into the lateral vaginal canal, here bent outwards and forwards in association with the mesial position of the ureter. Whether or not this be the true explanation of the origin of the vaginal cul-de-sacs, if we grant their existence, then it seems probable that the median passage was discovered 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 correlation with the reten-

tion by the genital organs as a whole of a persistently embryonic condition; while the 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.

Conscious as I am that the last word has not yet been said on the evolution of the median passage in Marsupials, and that many points still stand in need of explanation, I put forward these few remarks and suggestions on the parturition phenomena in general and on the origin of the direct passage, in no dogmatic spirit, but in the hope that they may be the means of eventually leading us to a better understanding of this, certainly one of the most remarkable of all the adaptive modifications exhibited by the Marsupialia.

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. It will here suffice to briefly direct attention to the more noteworthy features in which the organs of *Perameles* depart from the more usual Marsupial condition, and thereafter to shortly inquire what light the study of their development throws on the question of the primitiveness or otherwise of the urogenital organs in this genus of Marsupials.

If we contrast the urogenital organs of *Perameles* with those of other Marsupials, *e.g.*, *Macropus*, the following features stand out as worthy of remark :—

(1.) The absence of any sharply marked separation between the uterine and vaginal segments of the organs, the uterus being directly continued into the median vaginal cul-de-sac and its os being extremely ill-defined.

(2.) The small size and distinctness in the virgin, of the median vaginal cul-de-sacs, their termination at a relatively great distance from the urogenital sinus and their complete investment by the connective tissue of the urogenital strand.

(3.) The fact that the lateral vaginal canals (except their forward expansions—the vaginal cæca), are imbedded throughout their entire extent, together with the urethra, in an elongated mass of connective tissue—the urogenital strand.

(4.) The extremely short sinus urogenitalis, and the existence of a very distinct cloaca.

As regards (1) and (4) these features constitute, I think, obvious marks of lowly organisation, while as regards (3), I have already pointed out in the preceding pages that the median vaginal apparatus in *Perameles* remains at a stage which is early passed through in the fœtal Macropod, and which is without doubt extremely primitive. As concerns (3), the adult structural relations of the urogenital strand led me to believe that it represented the genital cord of the fœtus, and serial sections of a small pouch-young at once convinced me of the rightness of this belief. The urogenital strand of the adult is simply nothing else than the persistent genital cord, from the tissue of which the posterior ends of the uterine segments of the Müllerian ducts and the entire vaginal segments of the same never become free, except in so far as the forwardly projecting vaginal cæca may be said to have become free from the original tissue of the cord.

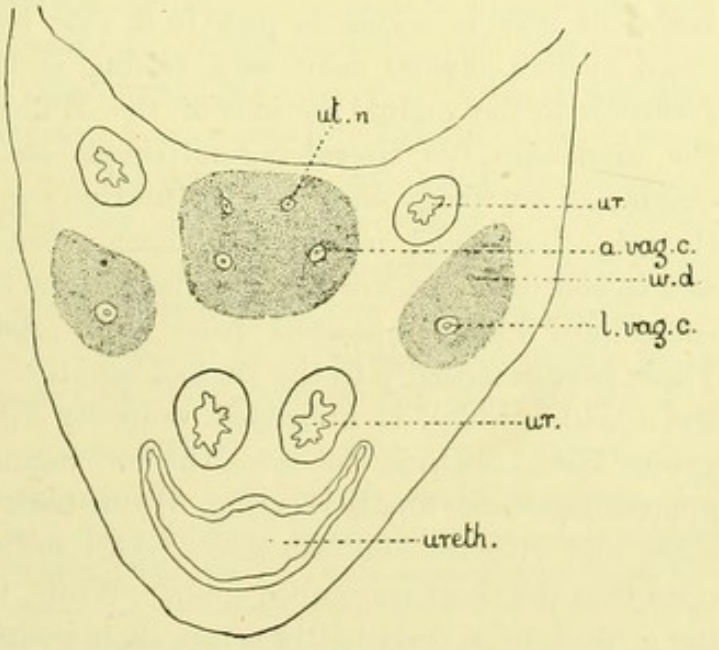

Fig. 2.

Text-figures 2 and 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 and 8, Plates iii.-iv., representing sections 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 a condition which can only be described as persistently embryonic.

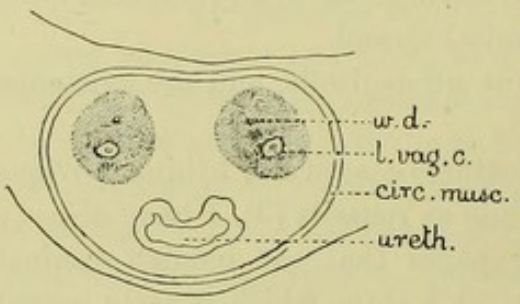

FIG. 3.

Now, in young fœtal Macropods, the genital ducts have essentially the same disposition as in the fœtal and adult *Perameles*, *i.e.*, the posterior portions of the uterine and the entire vaginal segments of the Müllerian duct and the urethra lie imbedded in a common mass of mesodermic tissue – the genital cord. In both, the uterine segments pass back side by side to open into small median vaginal cul-de-sacs, arising at the junction of the former with the vaginal sections of the Müllerian ducts. From the cul-de-sacs, the lateral vaginal canals continue 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. These pass in mesially to the vaginal canals to reach the base of the bladder, which is imbedded ventrally in the tissue of the genital cord. Behind this level, the two vaginal canals gradually approximate and finally (text-fig. 3) run back parallel with each other and with the Wolffian ducts (*w.d.*) and urethra (*ureth.*) to open into the short urogenital sinus. While, then, in *Perameles*, the genital ducts persistently retain their position in the genital cord, in Macropods they later become more or less free from the tissue of that cord.

I would lay special emphasis on the fact that the anteriorly directed vaginal portions of the Müllerian ducts remain permanently imbedded in the tissue of the genital cord, a structural condition never before described for any Marsupial, and confined, so far 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 vaginal canals become entirely free from the genital cord, but in many forms, *e.g.*, Macropods, their 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 briefly set forth, in my opinion, show conclusively that the condition of the genital organs in Macropods—undoubtedly one of the most specialised families of living Marsupials—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. Indeed, the urogenital organs of the Peramelidæ appear, so far as I am able to judge, to have retained a more archaic condition than those of any other hitherto described Australian Marsupial,* a conclusion which I believe gives very material support to that view which regards the existence of an allantoic placenta in the genus *Perameles* as an extremely primitive feature in its organisation.

The present work and that to be detailed in succeeding parts of this series of papers has been carried out with the aid of a

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*The condition of the genital organs in the Didelphyidæ requires re-examination. In the figures both of Owen (9) and Brass (4) the tissue of the genital cord, which ought developmentally to be found extending between the small median vaginal cul-de-sacs and the sinus urogenitalis, is not shown, hence it is impossible to determine with certainty the relation of the lateral vaginal canals to that tissue, though the bent character of the canals suggests that they are free from it over the greater part of their extent as in Macropods.

grant from the Royal Society, the liberality of whose Committee I desire here to gratefully acknowledge. I am much indebted to my friends, Prof. J. T. Wilson and Mr. J. J. Fletcher, for kind advice, and I further desire to express my thanks to Mr. R. Grant, late of the Physiological Department, for invaluable help in the preparation of the photo-micrographs illustrating this paper and for much assistance in other ways.

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1.—Owen, R. Comp. Anat. and Phys. of Vertebrates. Vol. iii. p. 683.

2.—Alix, P. H. E. "Sur les organes de la parturition chez les Marsupiaux." Bull. Soc. Zool. France, 1879. p. 118.

3.—Hill, J. P. "The Placentation of Perameles. (Contributions to the Embryology of the Marsupialia, I.)". Q.J.M.S. Vol. 40. 1897.

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5.—Desc. and 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.

6.—Mihalkovics, G. von.—"Entwickl. d. Harn- u. Geschlechtsapparates d. Amnioten." Intern. Monatsch. f. Anat. u. Physiol. Bd. ii. 1885.

7.—Sobotta, J. "Beitr. zur vergl. Anat. u. Entwick. d. Uterusmuskulatur." Archiv f. mikr. Anat. Bd. 38. 1891.

8.—Owen, R. Article 'Marsupialia.' Todd's Cycl. of Anat. and Phys. Vol. iii. 1841.

9.——— "On the Generation of the Marsupial Animals, with a Description of the Impregnated Uterus of the Kangaroo." Phil. Trans. 1834.

10.—Stirling, E. C. "On some Points in the Anatomy of the Female Organs of Generation of the Kangaroo, &c." P.Z.S. 1889.

11.—Lister, J. J., and Fletcher, J. J. "On the Condition of the Median Portion of the Vaginal Apparatus in the Macropodidæ." P.Z.S. 1881.

12.—Fletcher, J. J. "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.

13.—Fletcher, J. J. "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.

14.—Home, E. "Some Observations of the Mode of Generation of the Kanguroo, with a particular Description of the Organs themselves." Phil. Trans. 1795.

EXPLANATION OF PLATES.

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 o urogenital sinus. *op.* Opening of anterior portion of lateral vaginal canal into vaginal cæcum. *ov.* Ovary. *pv. p.* Pseudo-vaginal passage. *rect.* Rectum. *u.s.* Urogenital strand. *ur* Ureter. *ureth.* Urethra. *ut.* Body of uterus. *ut.p.f.* Utero-pelvic fold of broad ligament. *ut.n.* Uterine neck. *vag.c.* Vaginal cæca. *ves.v.* Vesical artery and vein.

N.B.—With the exception of figs. 1 and 2, the figures are reproductions from photo-micrographs of transverse sections.

Plate i.

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

Fig. 2.—Urogenital organs of *P. obesula*. Dissection from dorsal aspect. *x*. Commencement of anterior forwardly directed portion of lateral vaginal canal. (× 1).

Figs. 3-8, Plates ii.-iv.—Trans. sections through the genital organs of virgin *P. nasuta*. For approximate positions of sections, see text-fig. 1, p. 52, and for description, see text, p. 53.

Fig. 9, Plate v.—Trans. section through 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.*)

Fig. 10, Plate v., and Figs. 11-12, Plate vi.—Trans. sections through median vaginal apparatus of *P. obesula* with two 17·5 mm. young.

Fig. 13, Plate vii., Figs. 14-15, Plate viii.—Trans. sections of *P. obesula* with two 22 mm. young. In 13, the section passes through the anterior portion of the common median vagina (*c.m.v.*); in 14, through the anterior region of the pseudo-vaginal passage, blocked up by three allantoic stalks (*all.s.*) ; and in 15, through the mid-region of the urogenital strand, with the cleft-like pseudo-vaginal passage (*pv.p*) containing detritus.

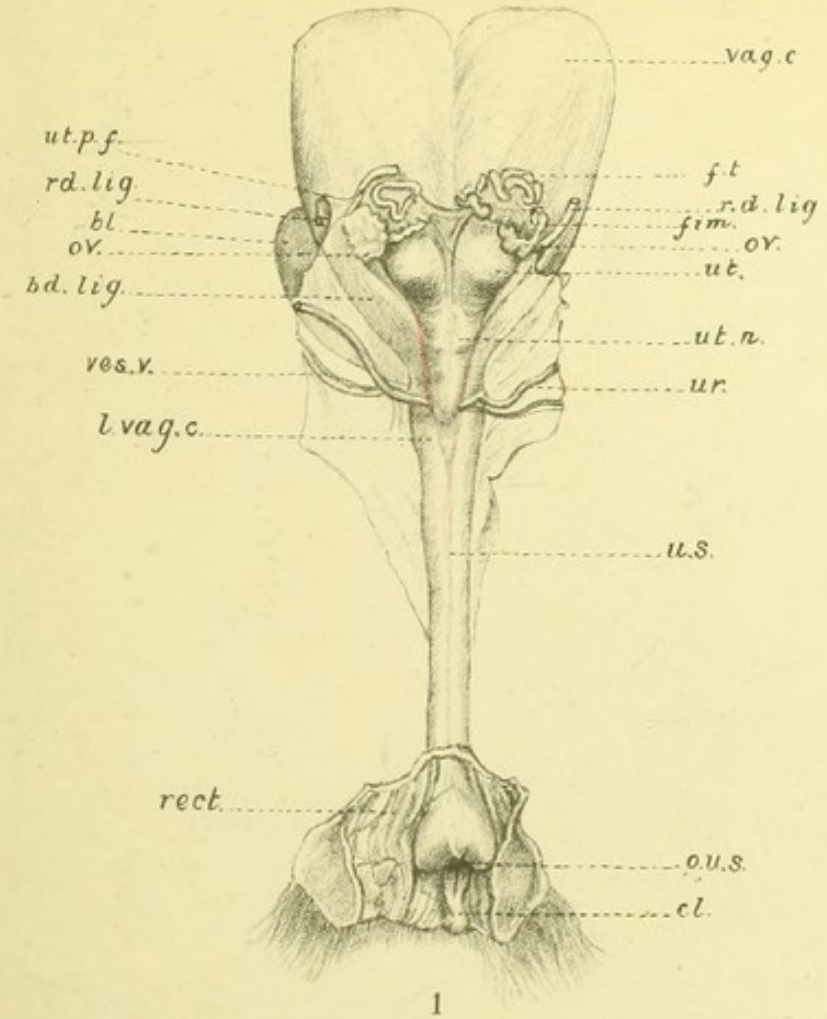
Fig. 16, Plate xii.—Trans. section. Just behind the posterior end of the common median vagina. *P. obesula* with four 3·7 cm. young.

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

Fig. 18, Plate viii., and Figs. 19 and 20, Plate ix.—Trans. sections, *P. nasuta* (?) bred, showing in 18, the common median vagina (*c.m.v.*) in 19, a well marked example of a fibrosed allantoic stalk (*all.s.*) in the pseudo-vaginal passage, and in 20, the cleft-like passage containing remnants of stalks.

Fig. 21, Plate x.—Trans. section through the urogenital strand of *P. obesula* with blastodermic vesicle in uterus.

Fig. 22, Plate xii.—Trans. section, urogenital strand of *P. obesula* with two 12·5mm. young in uteri, showing the vascular character of the connective tissue (*c.t.*) between the lateral vaginal canals.



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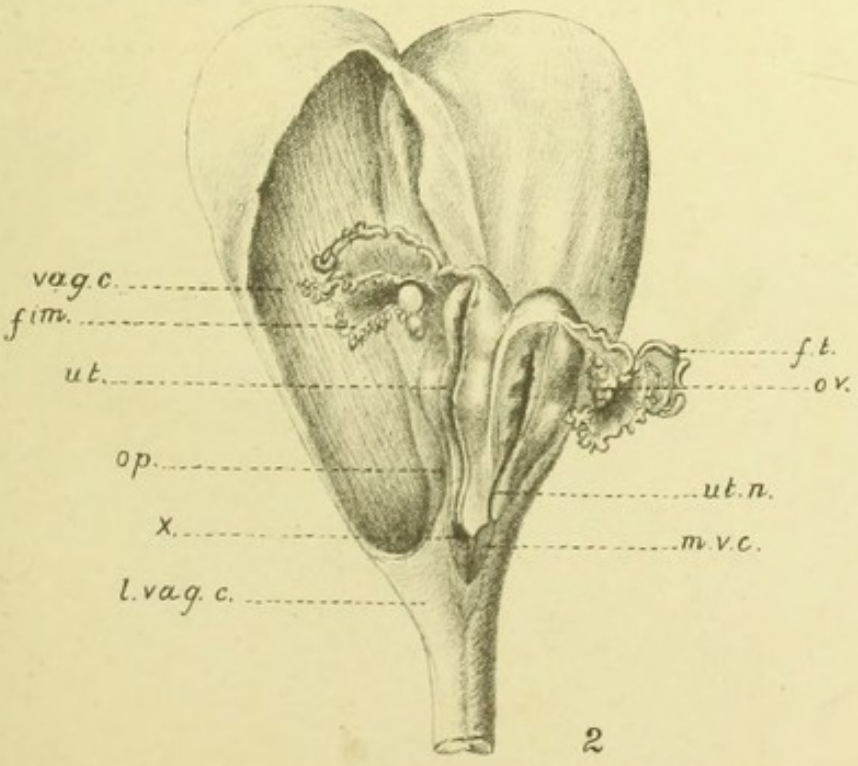

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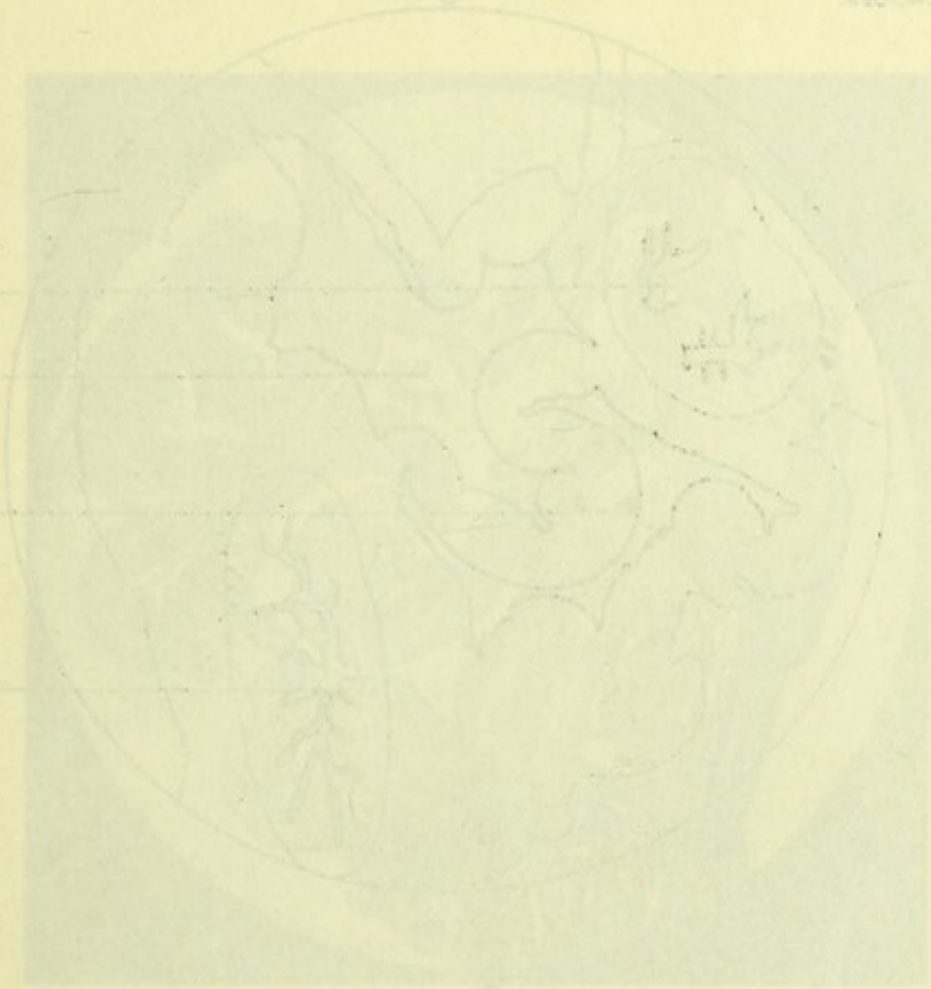
PERAMELES OBESULA.



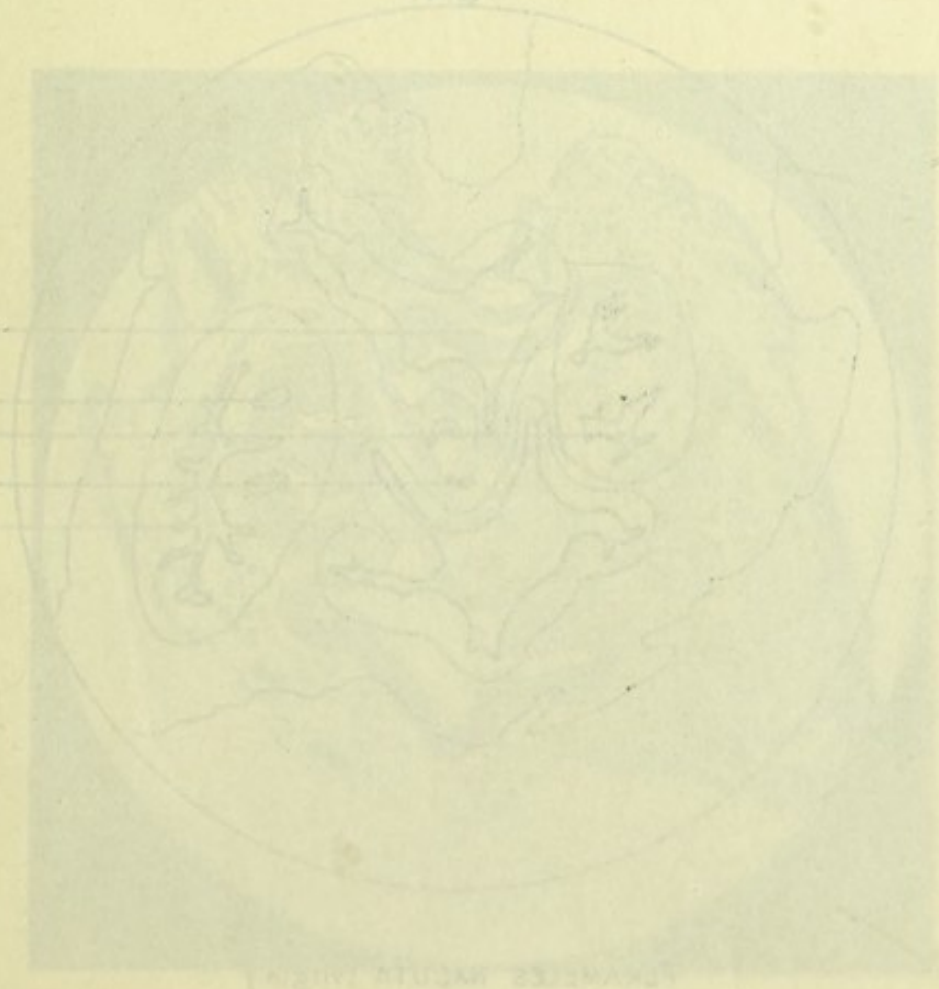
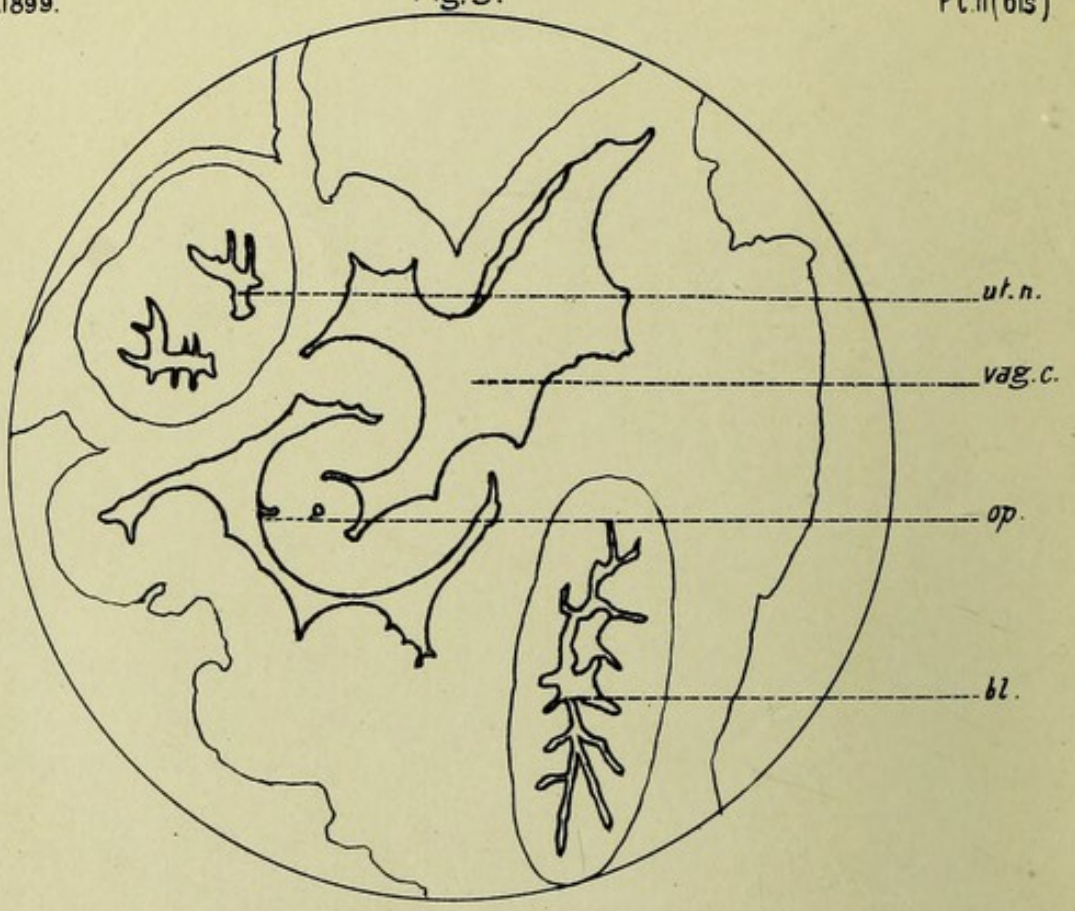


Fig. 3.



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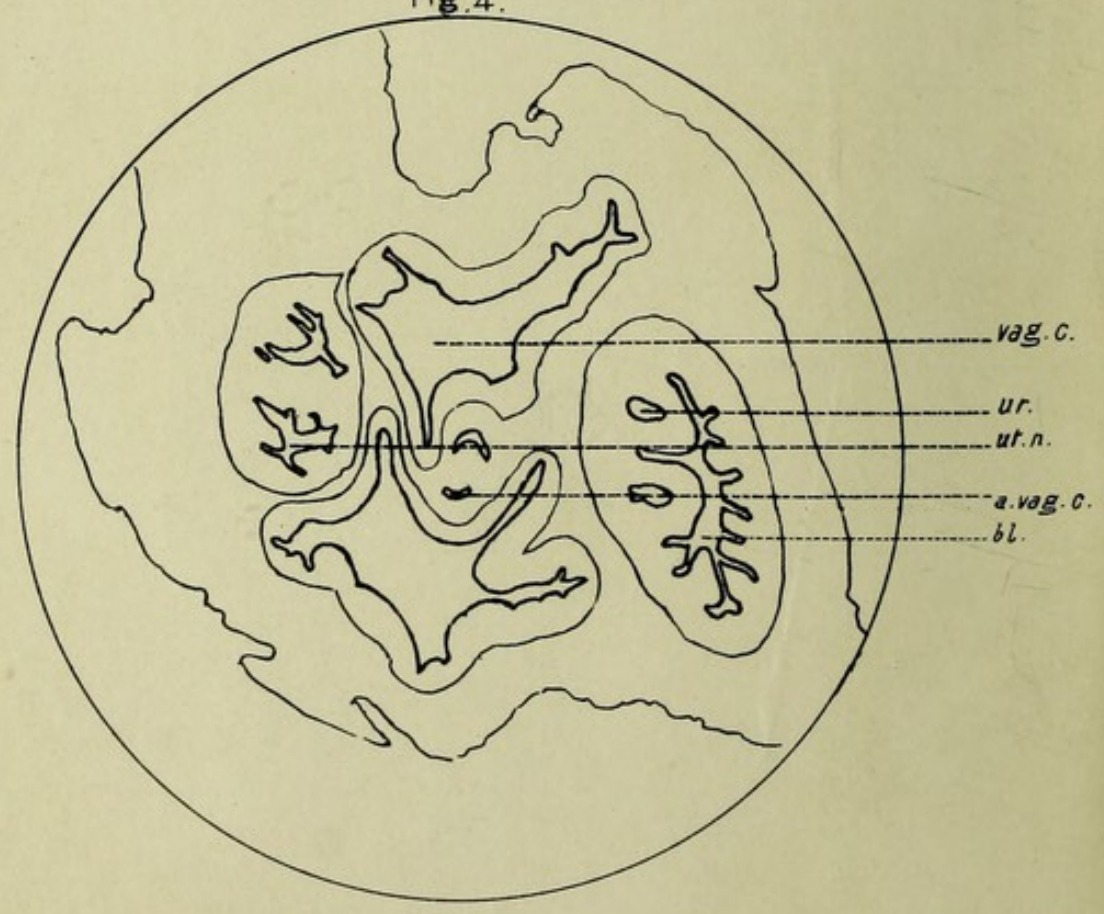
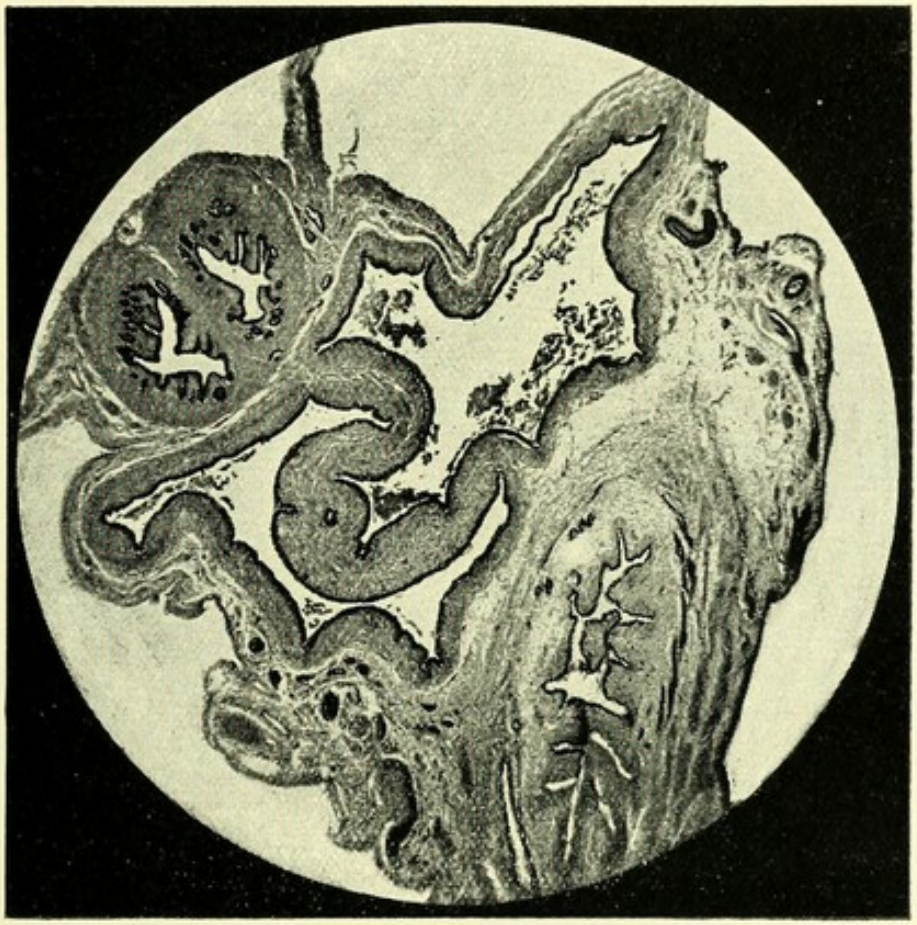
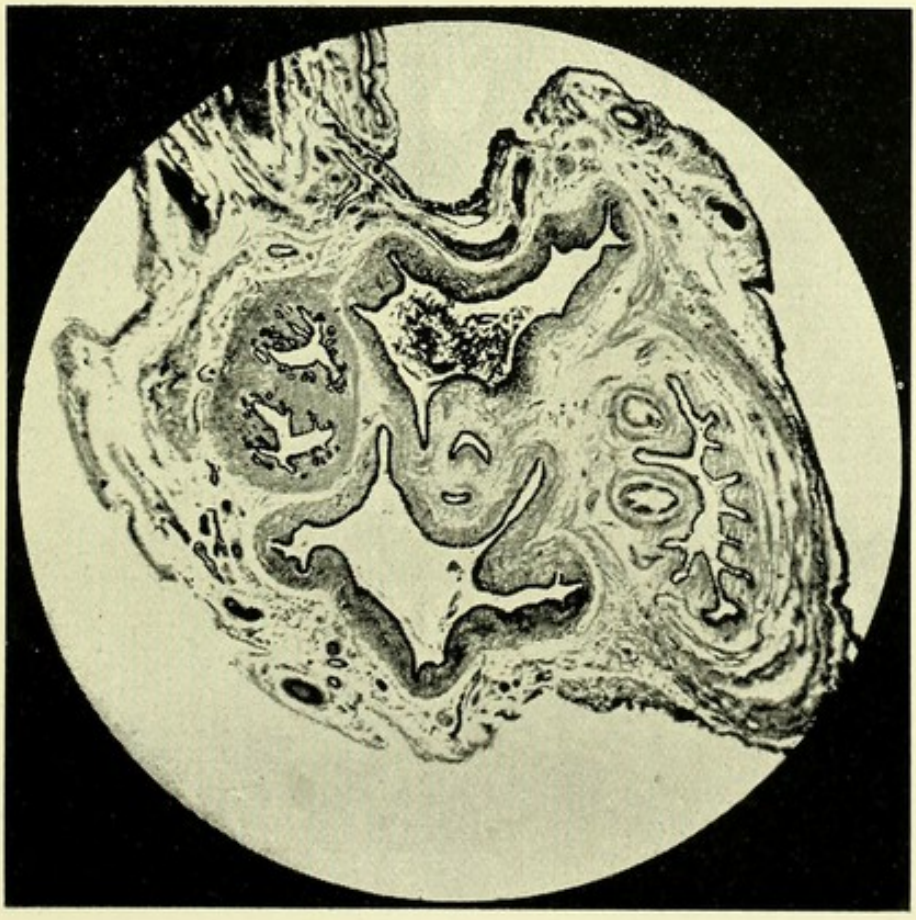


PERAMELES NASUTA (virgin)





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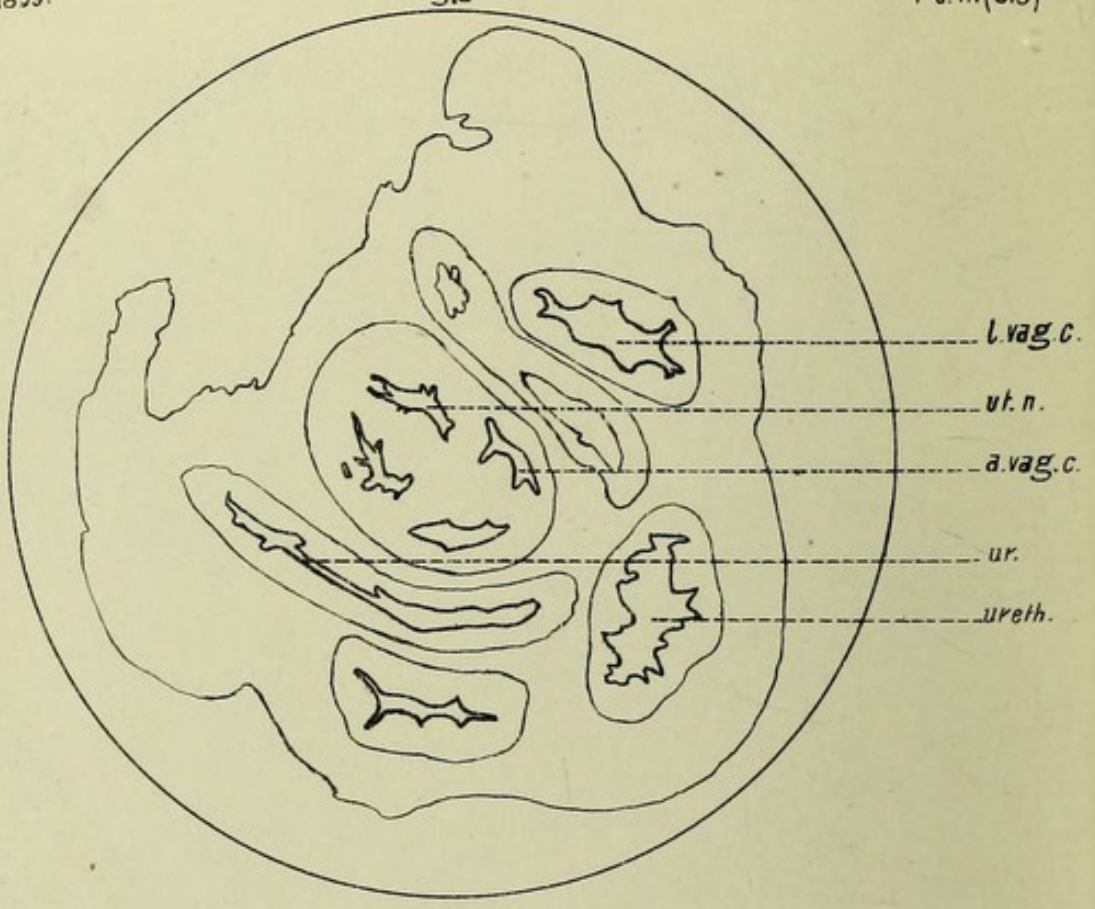

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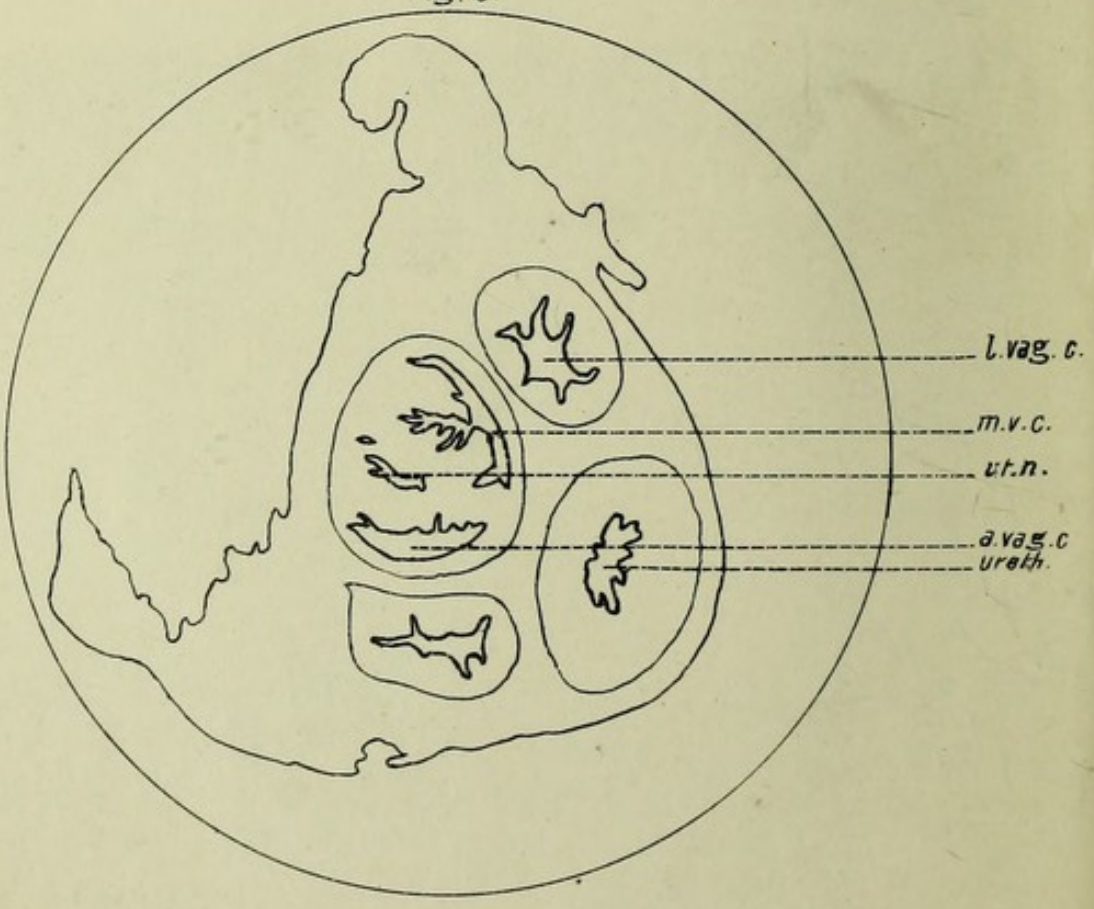
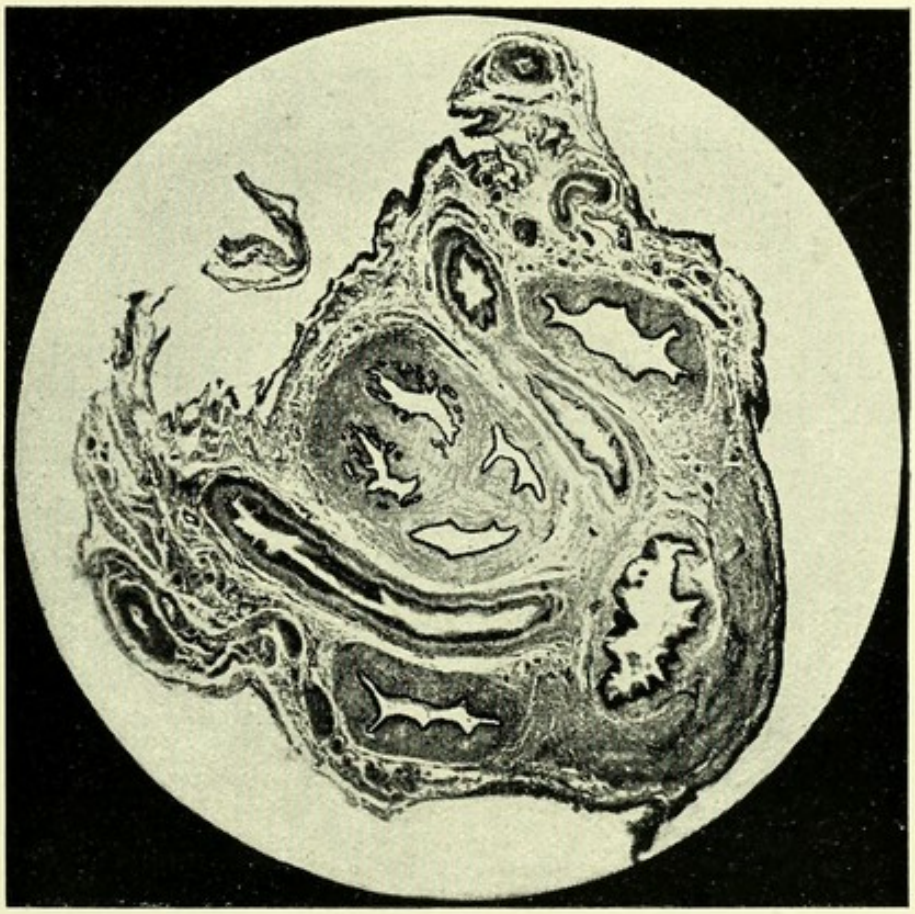
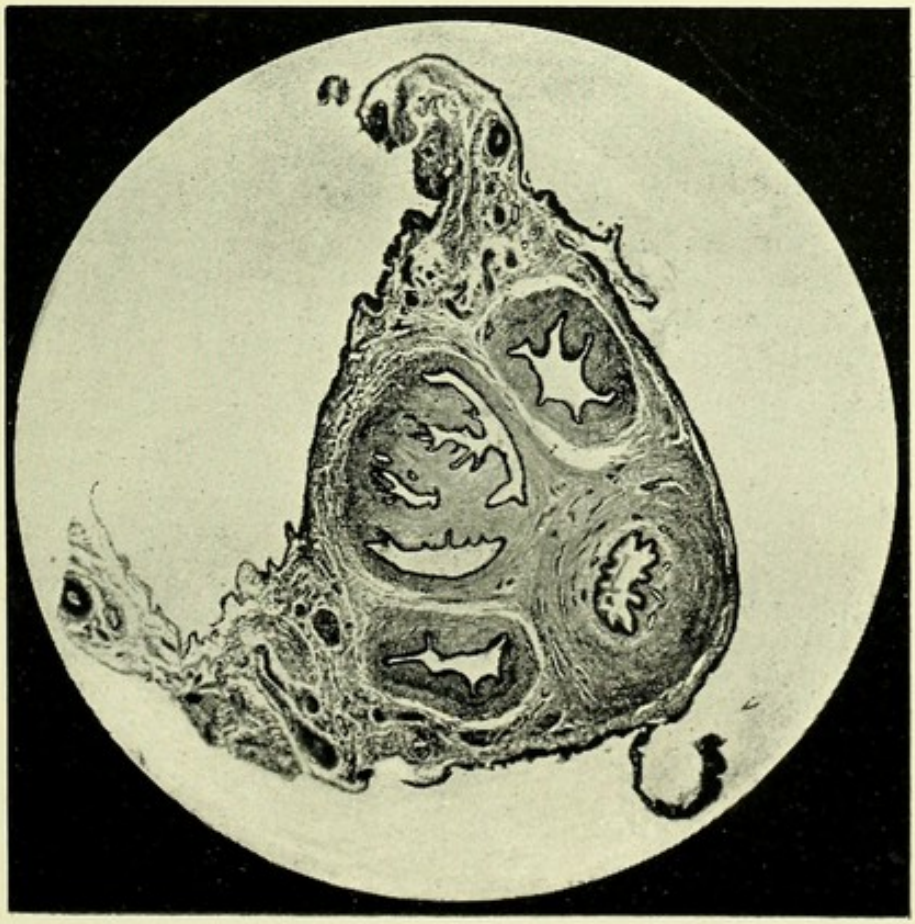


PERAMELES NASUTA (virgin.)





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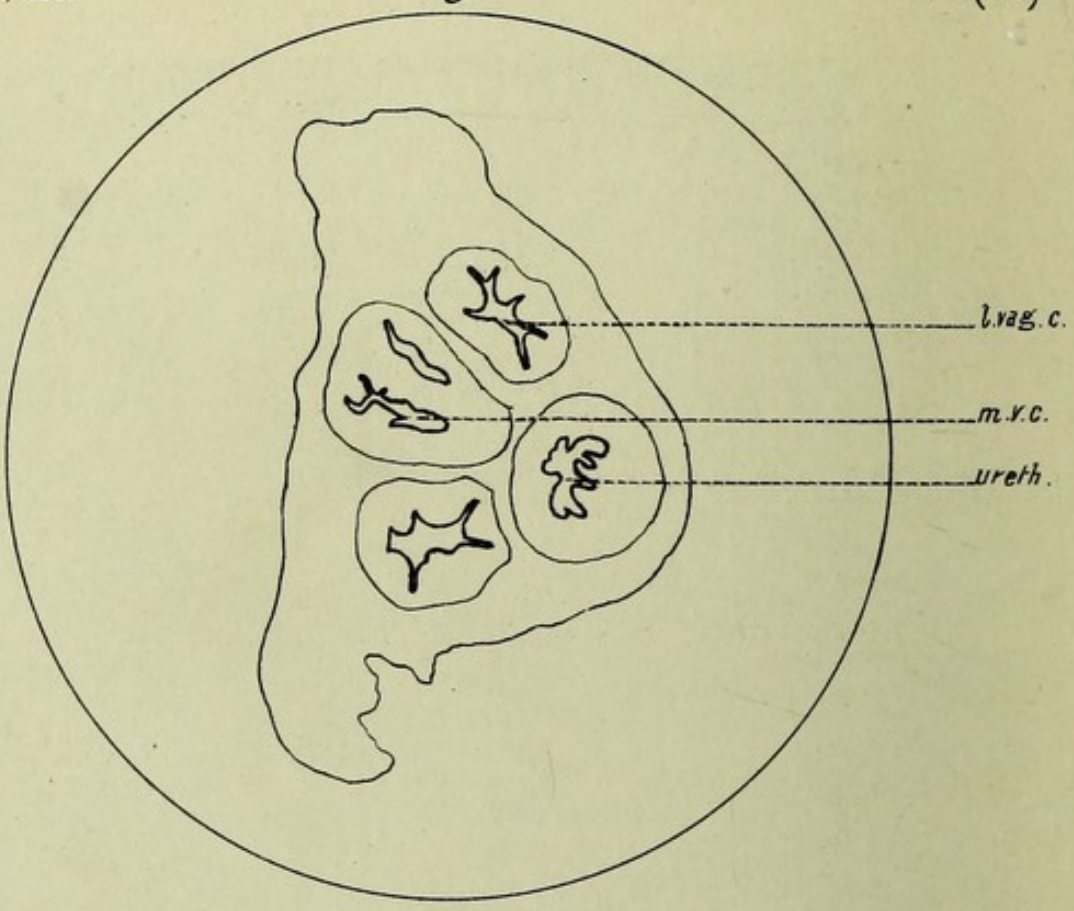

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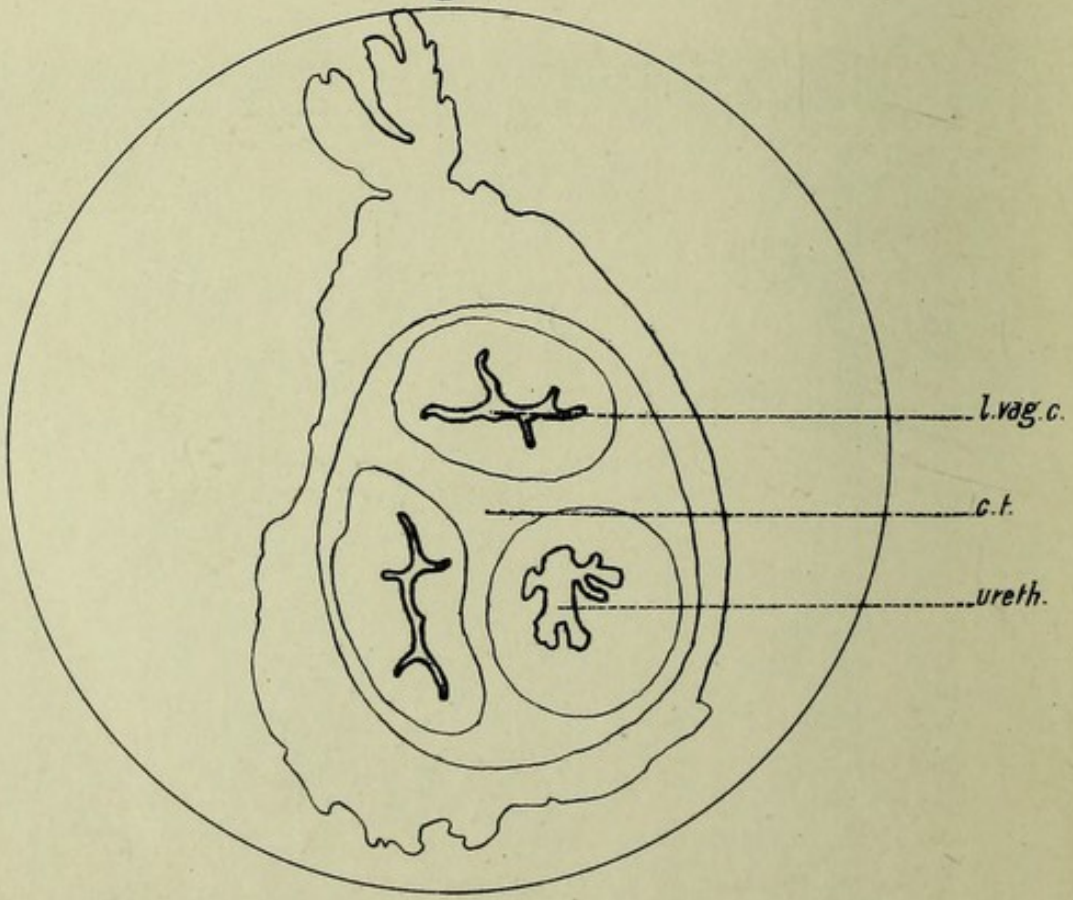
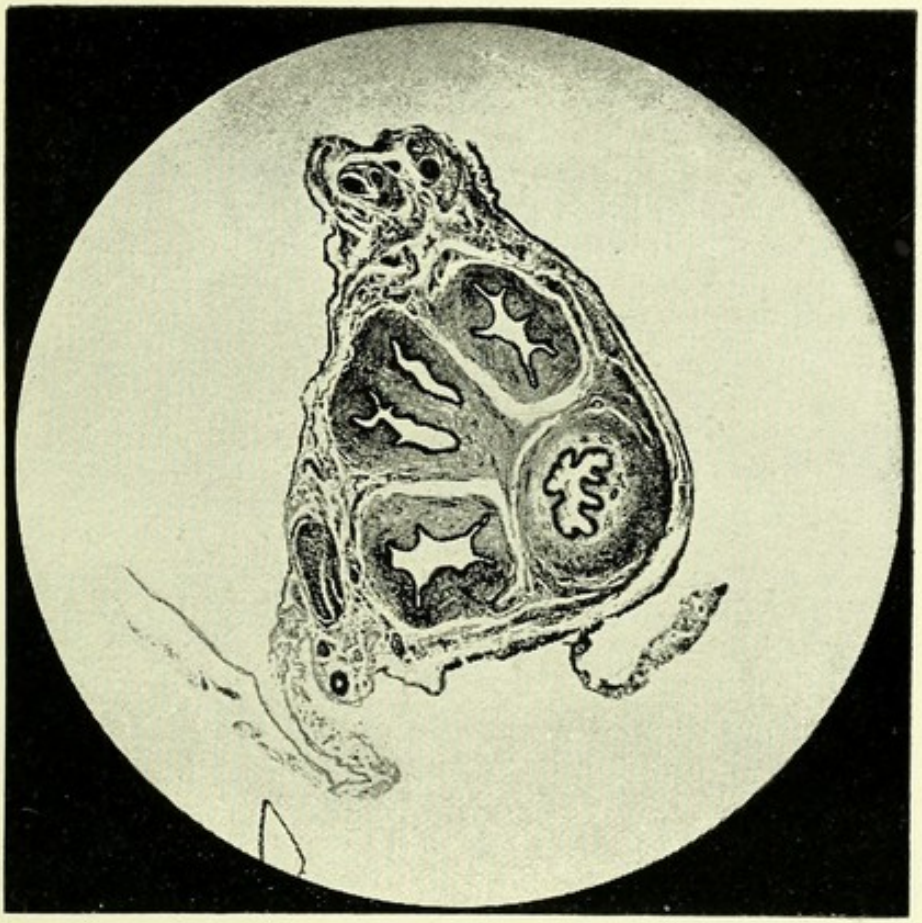
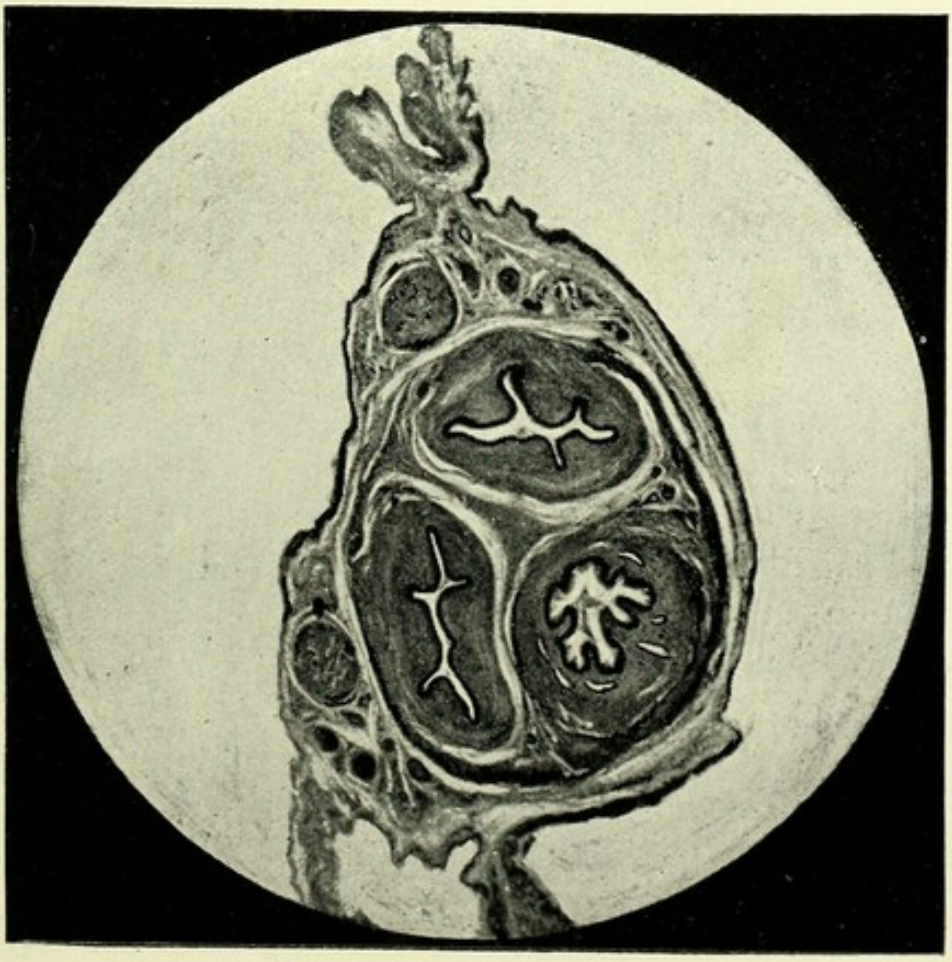
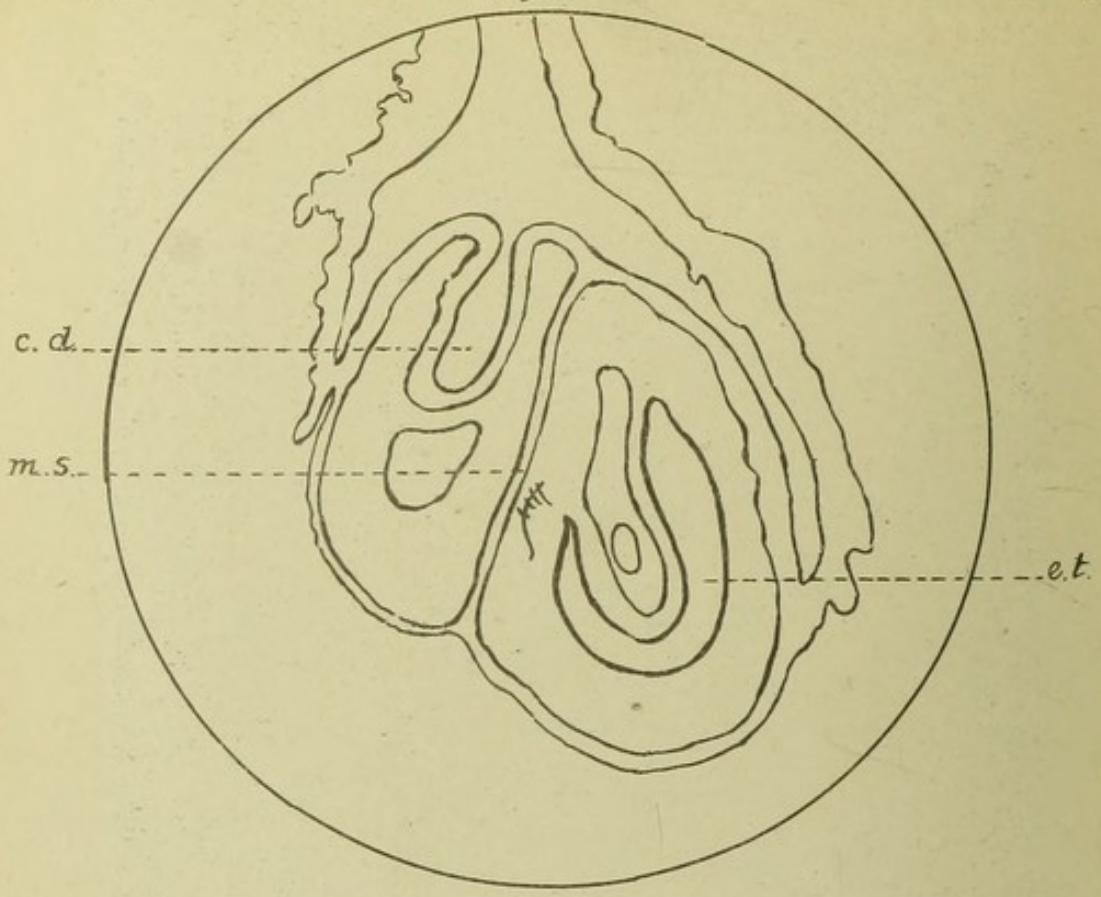


PERAMELES NASUTA.







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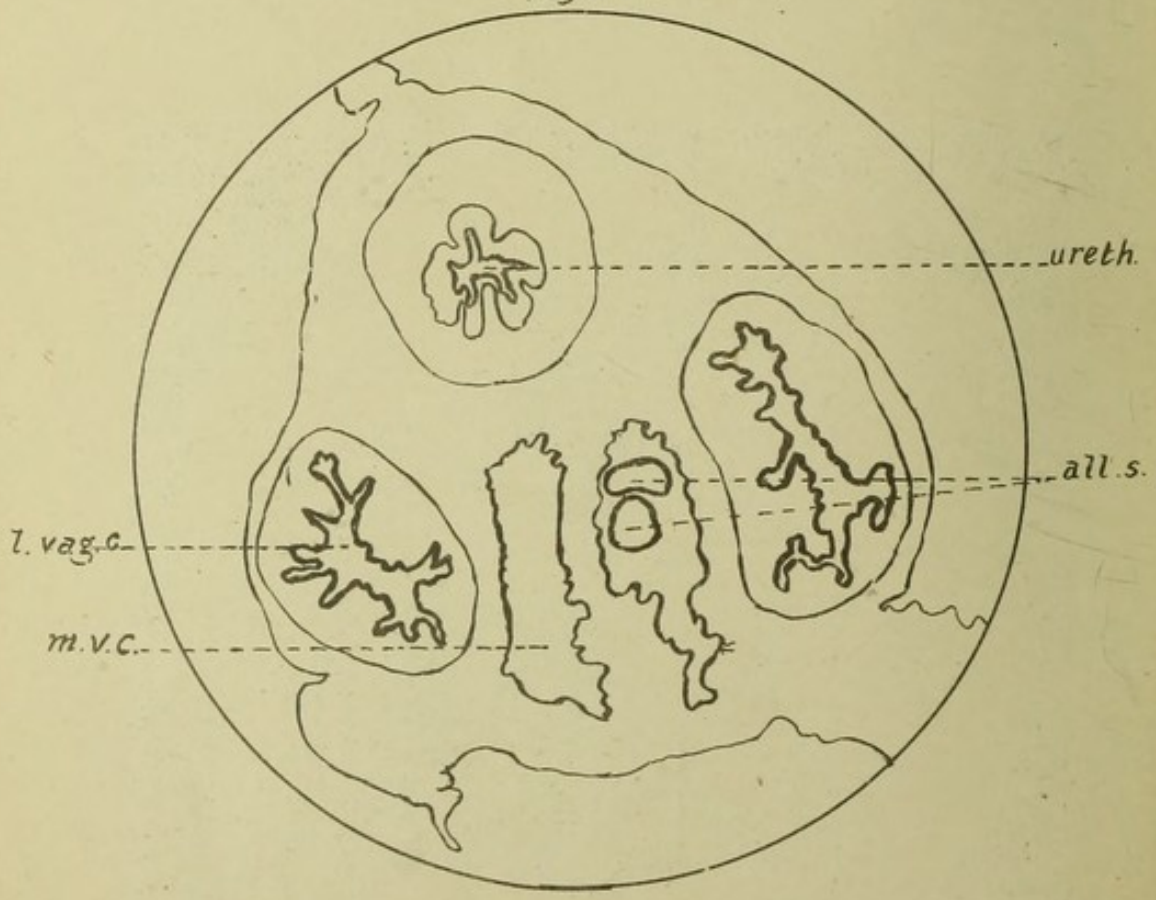

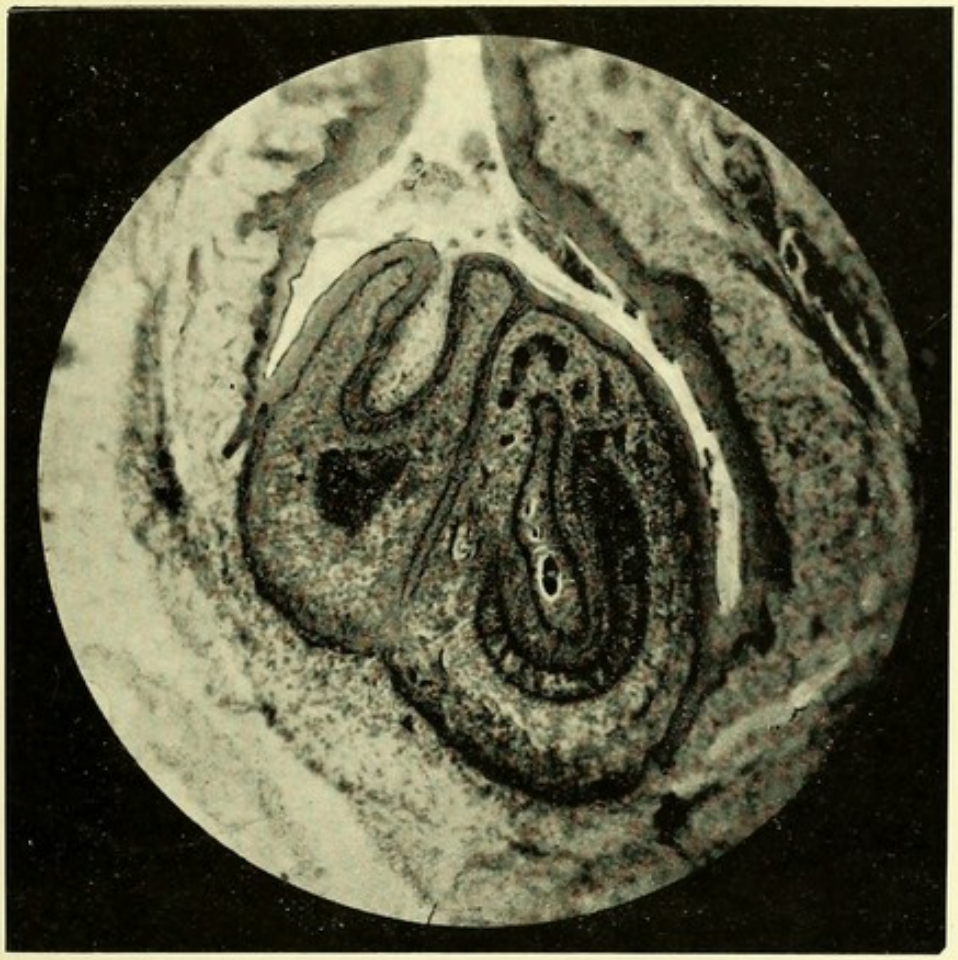

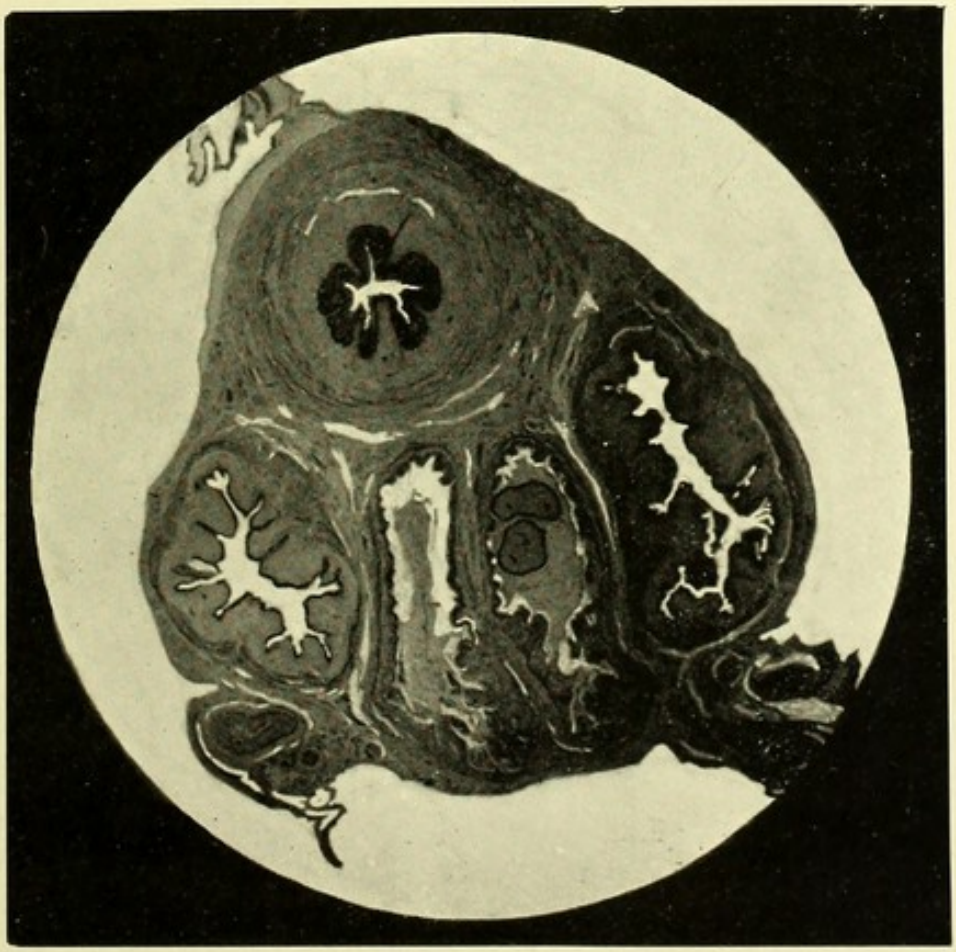

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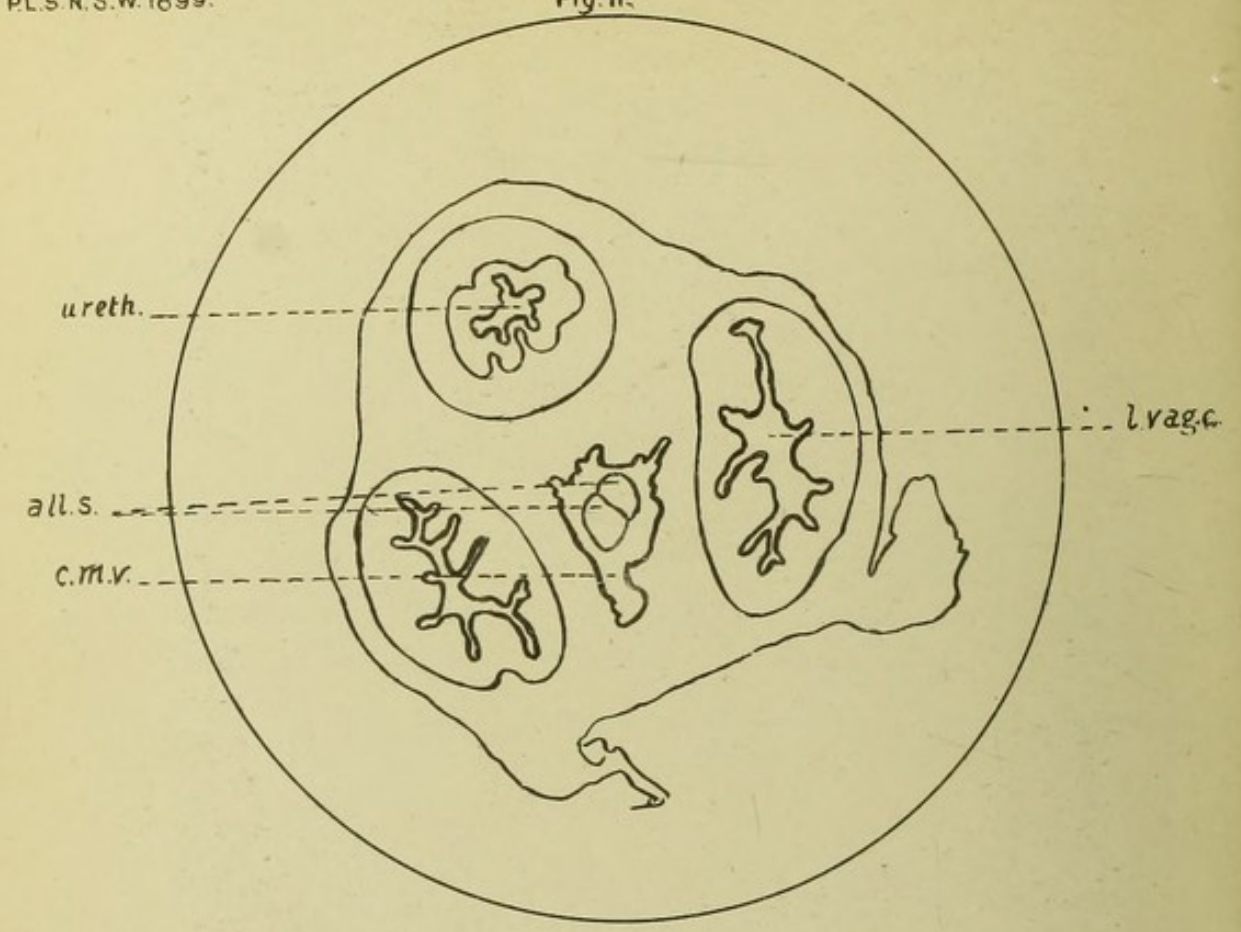

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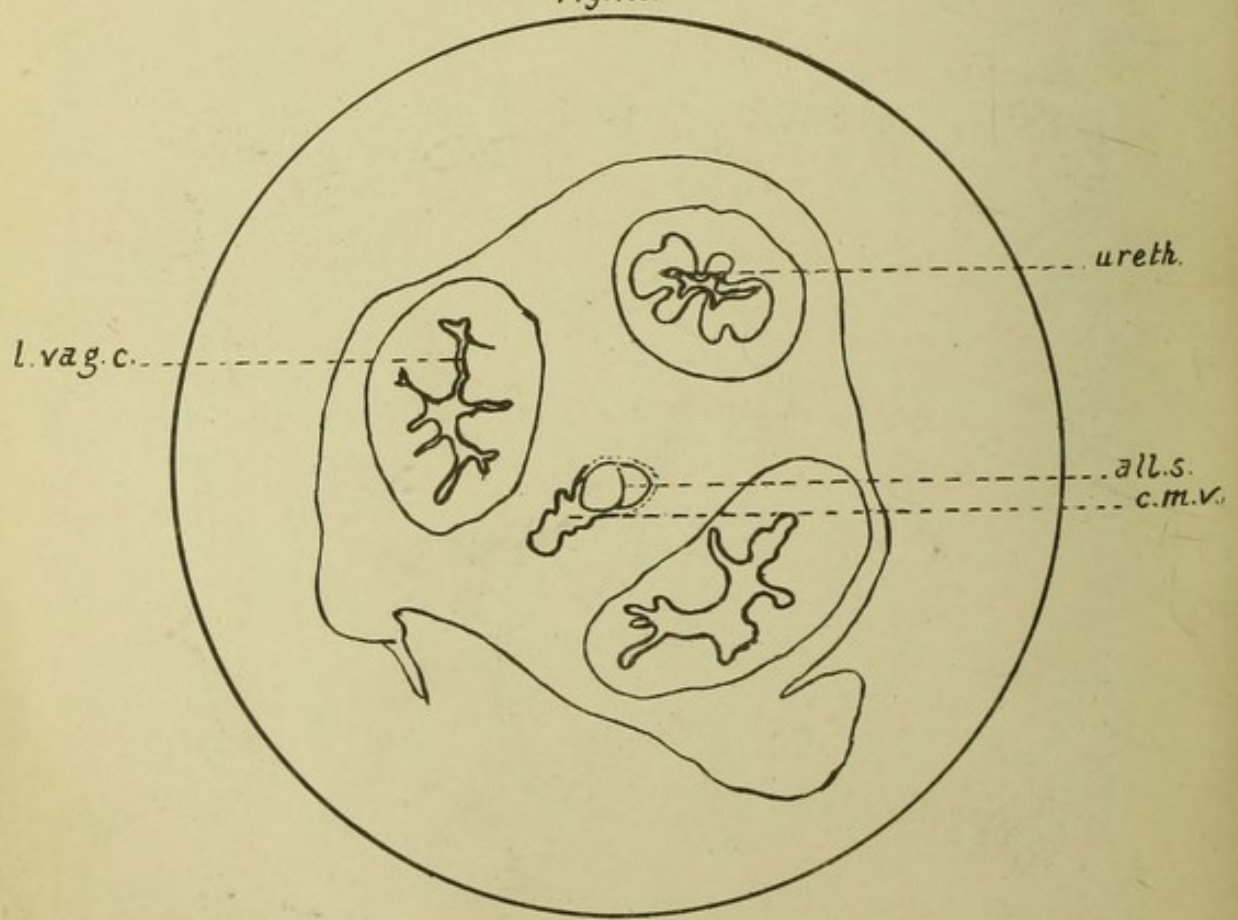
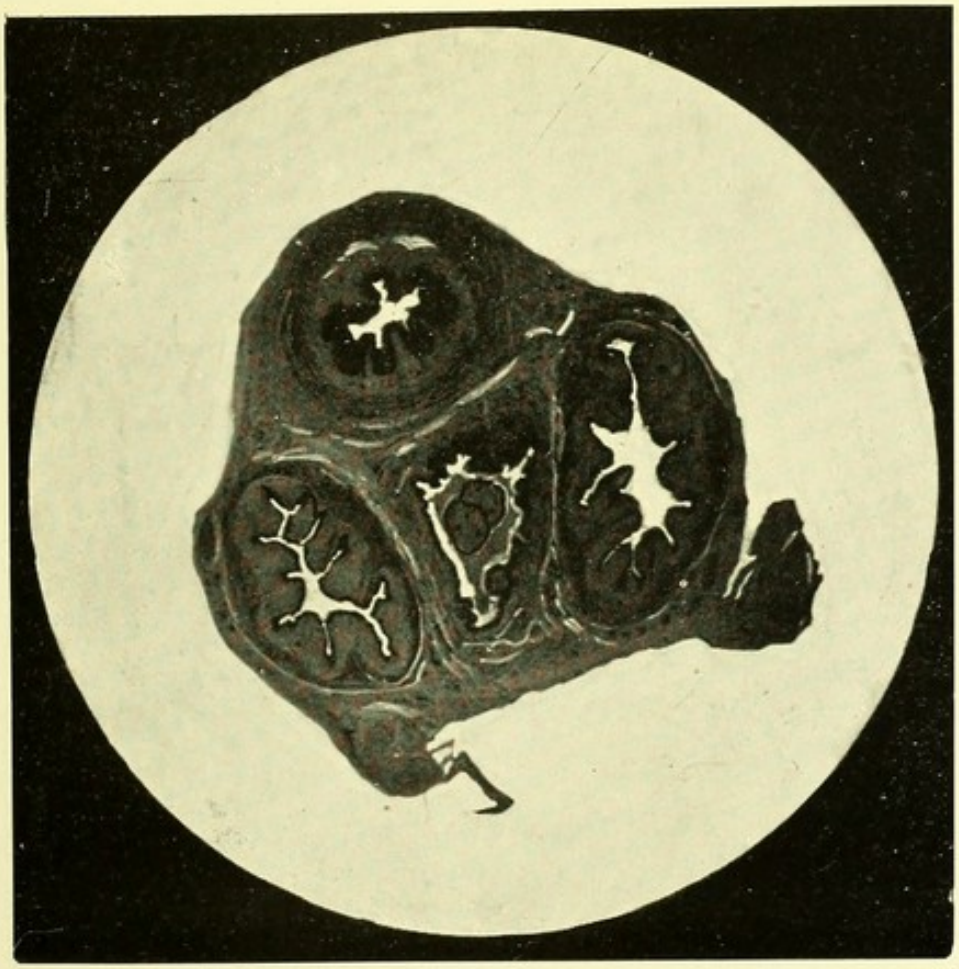




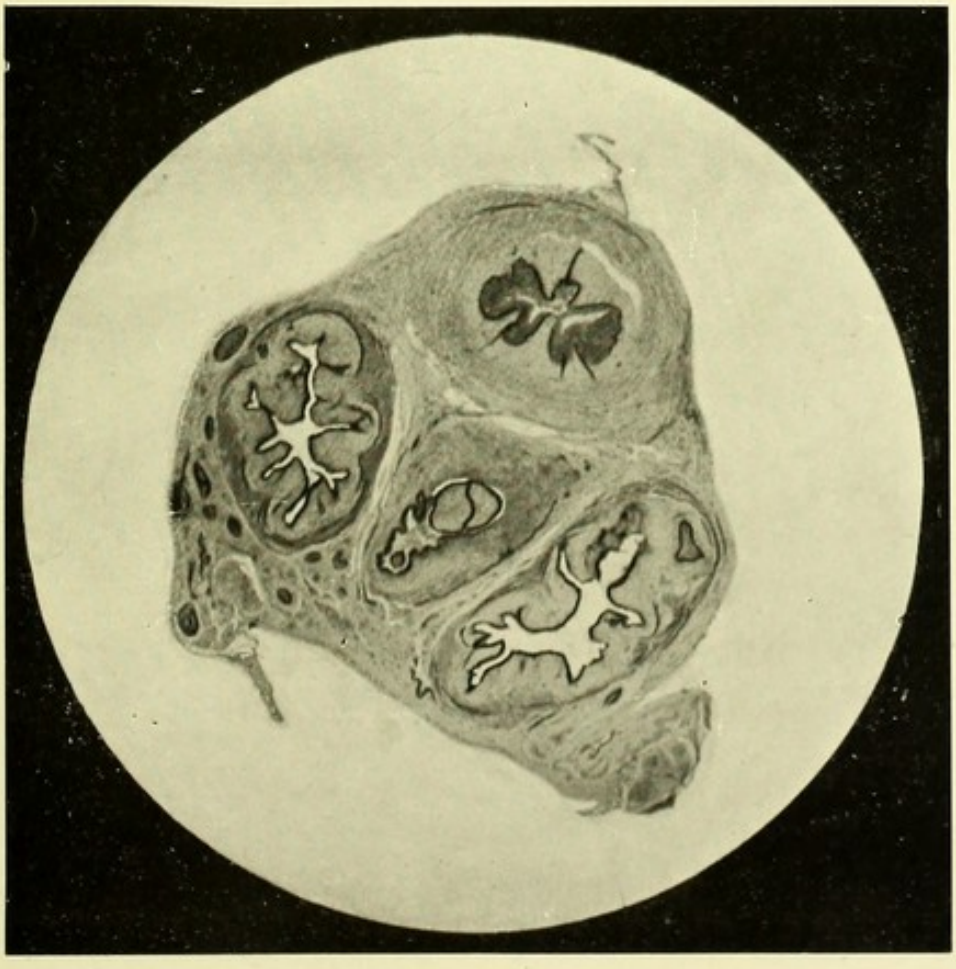
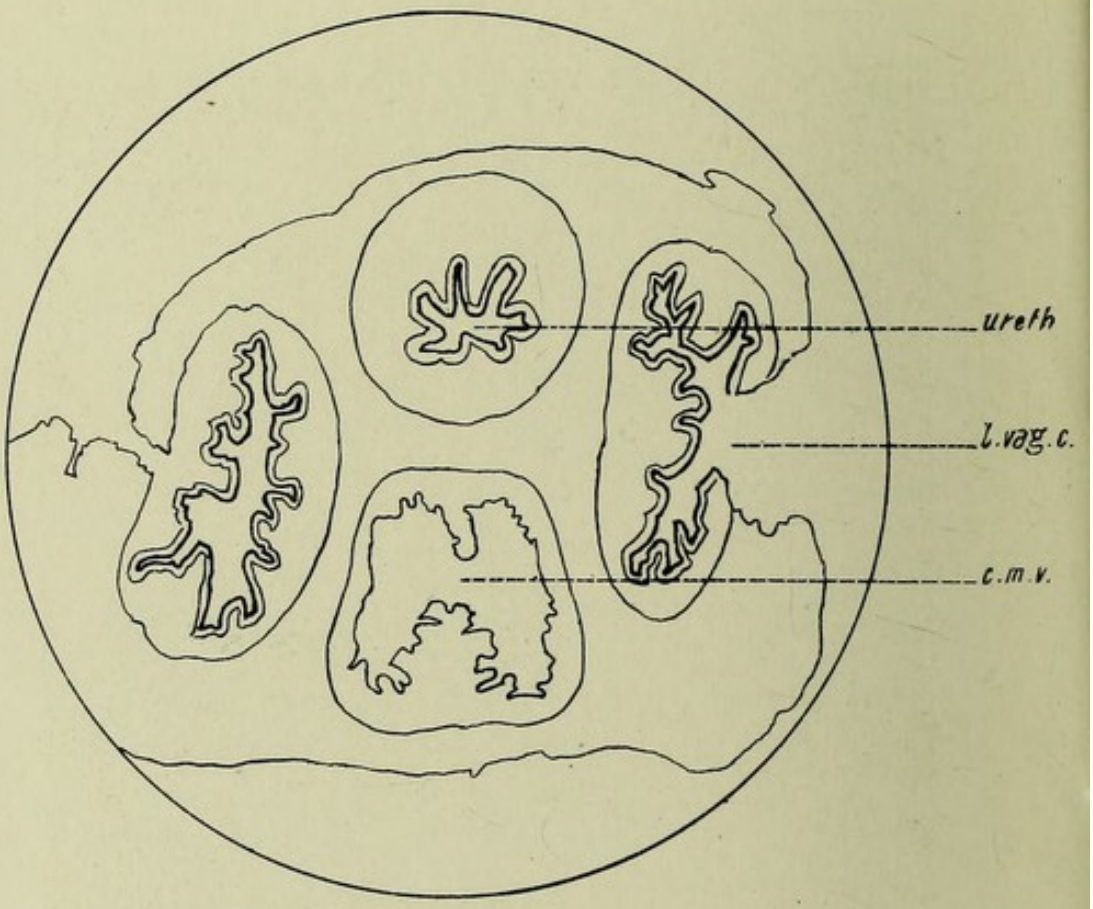


Fig 13.



PERAMELES OBESULA.

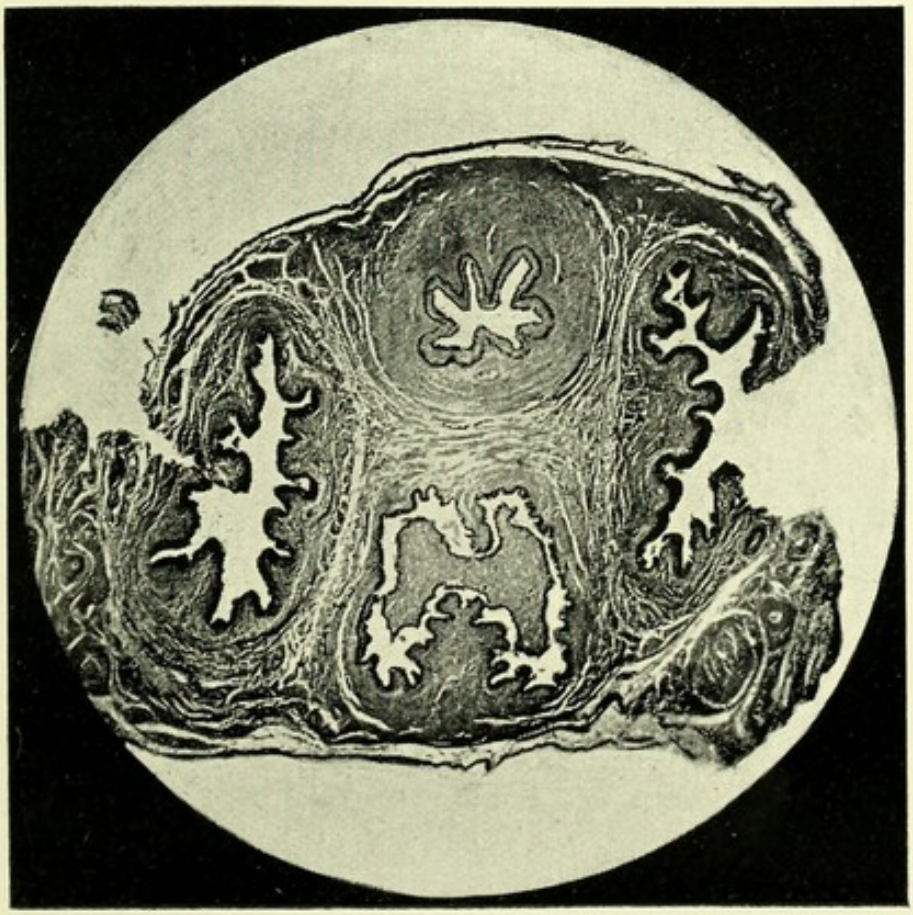


Fig 14.

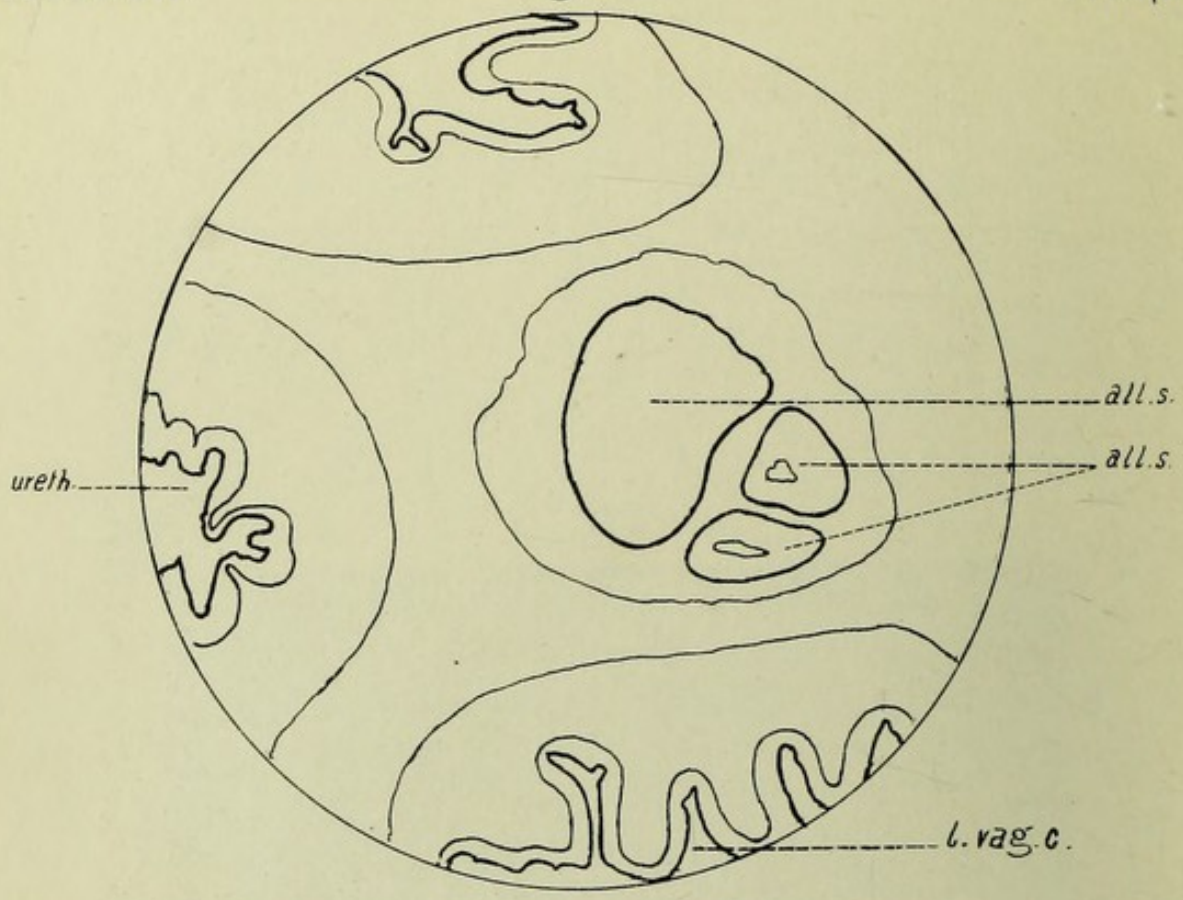


Fig. 18.

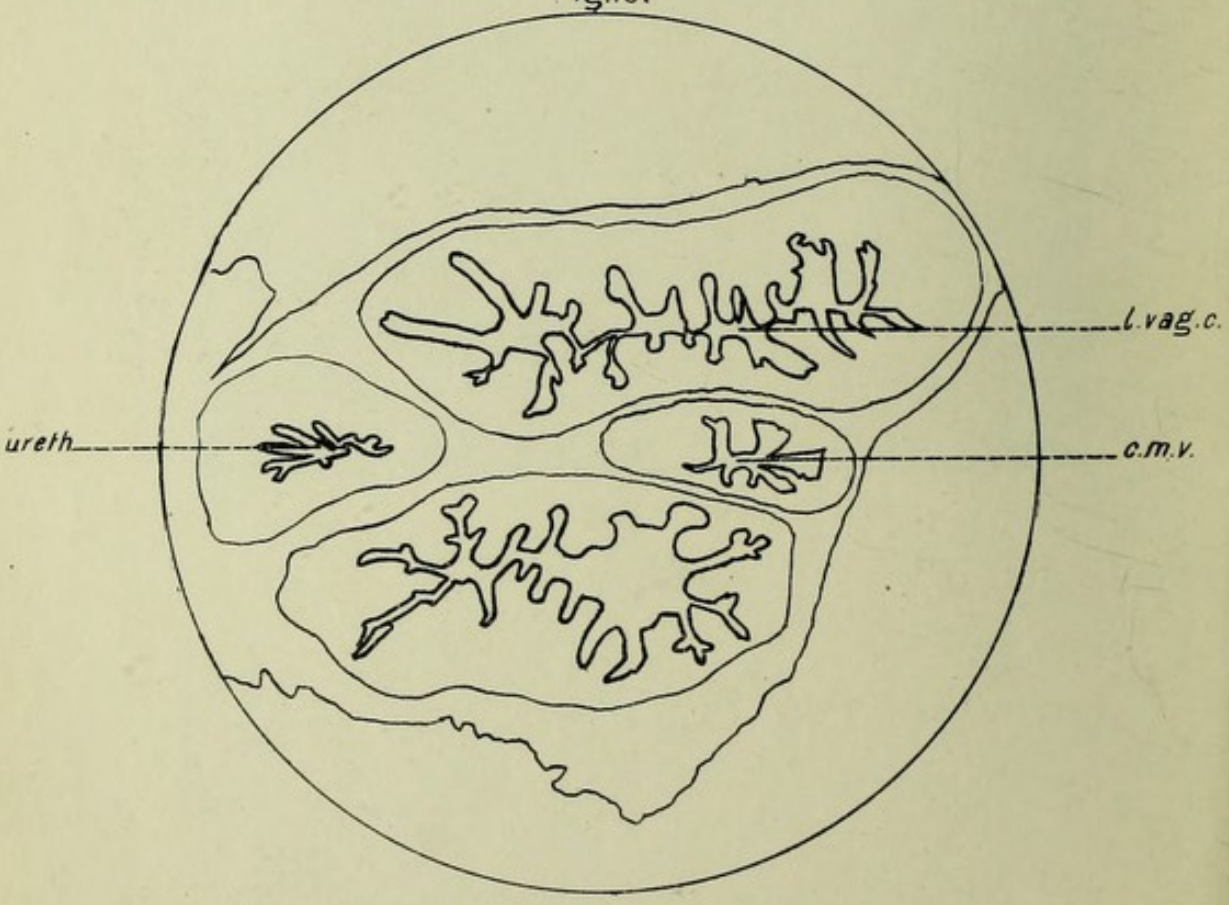
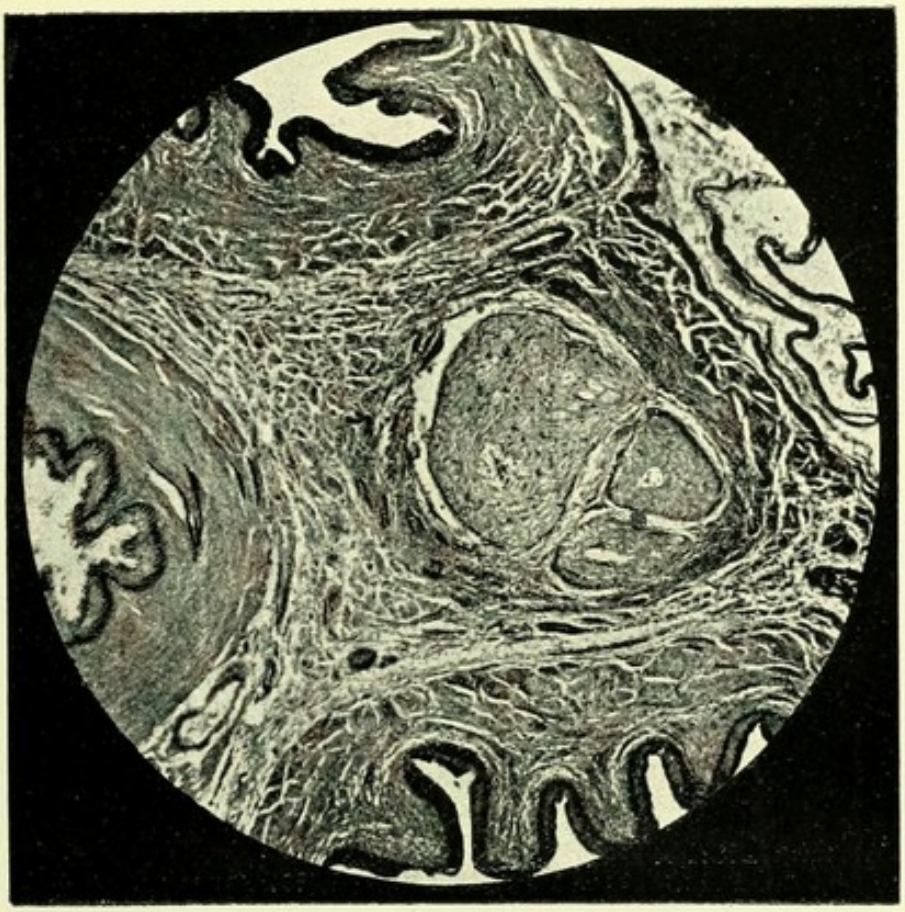


Fig. 14. P. obesula Fig. 18. P. nasuta (?)



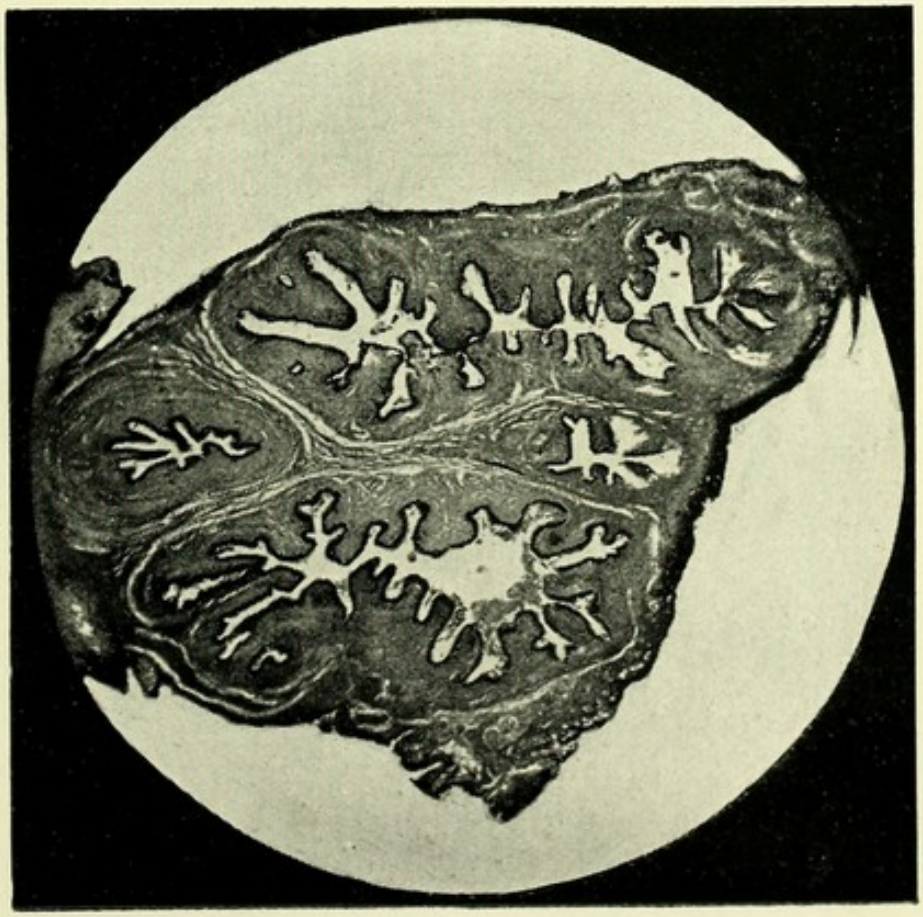


Fig 20.

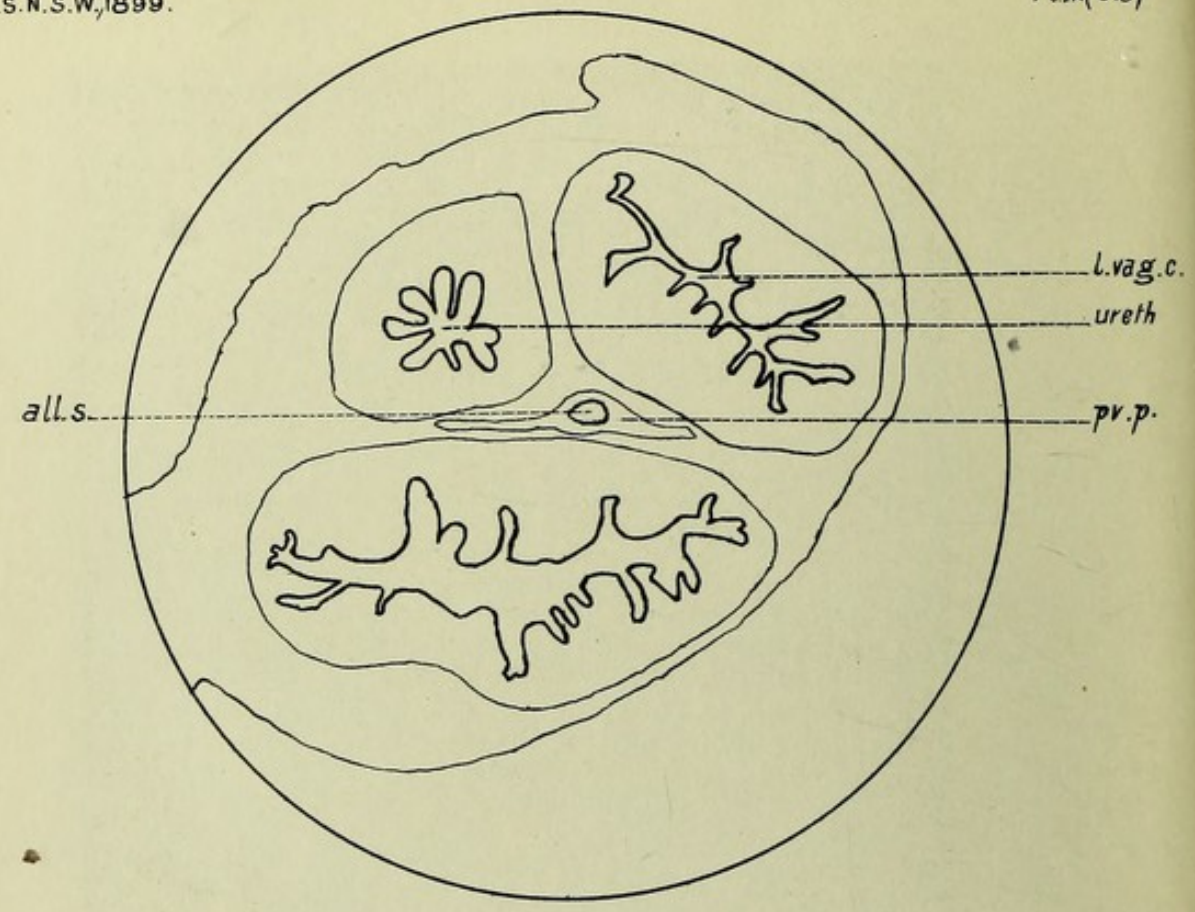
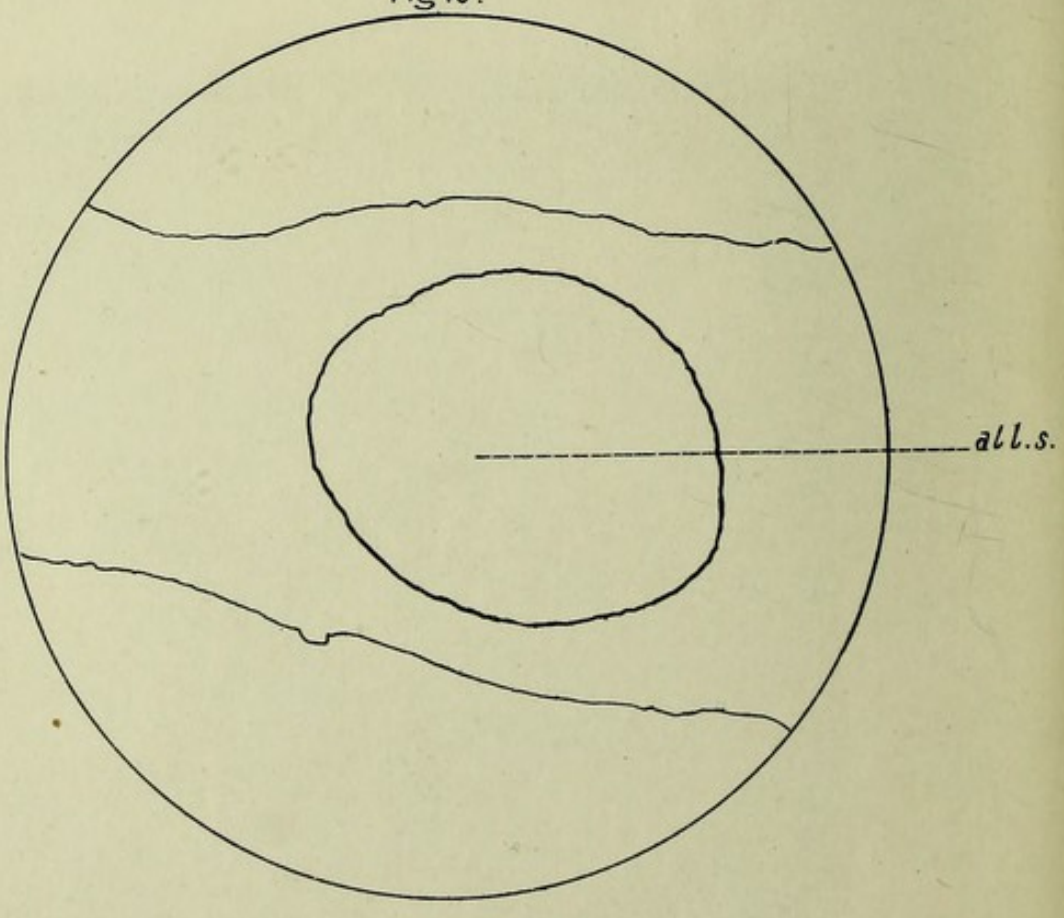
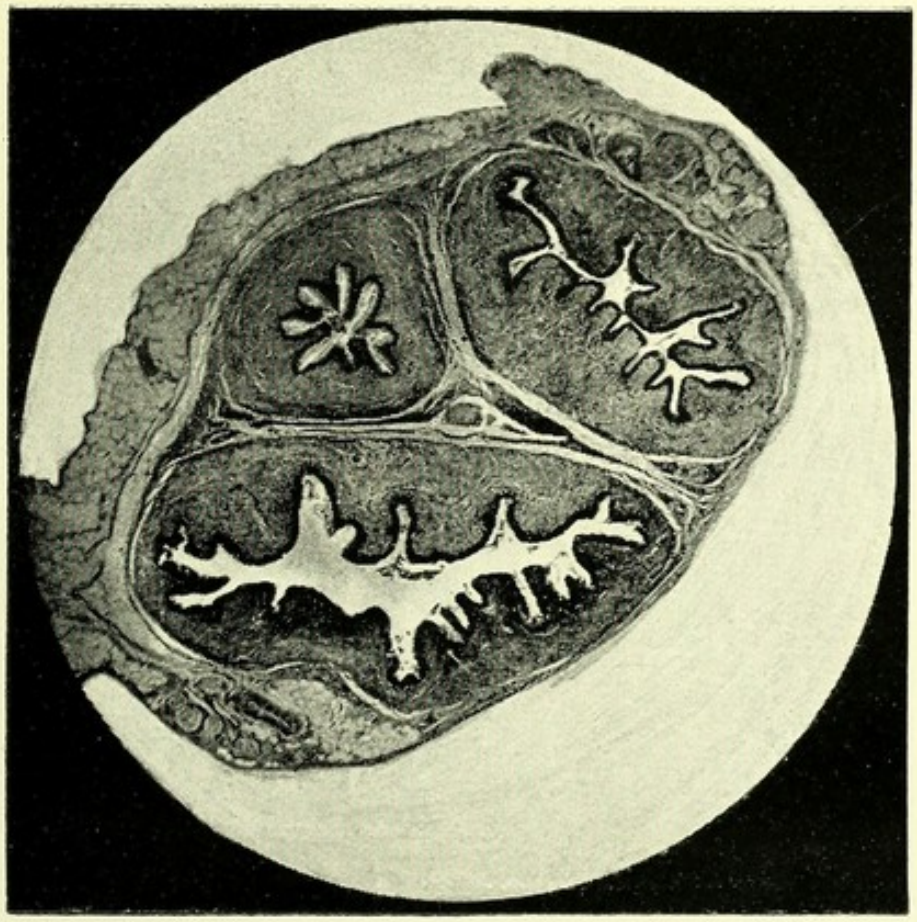
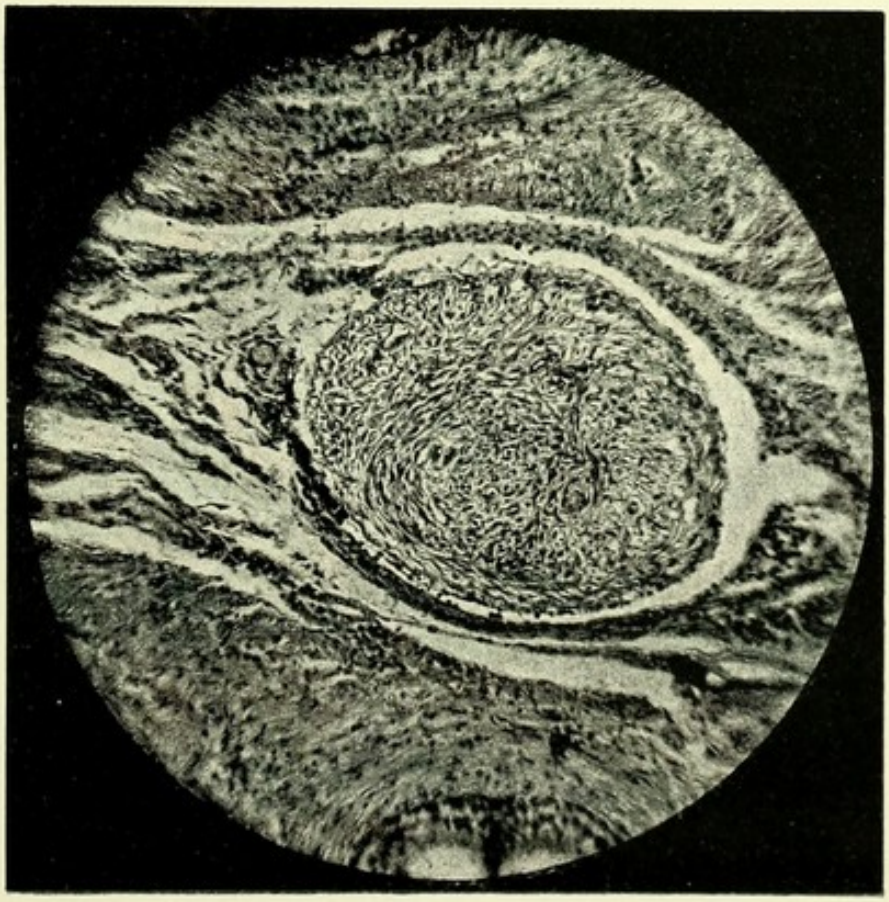


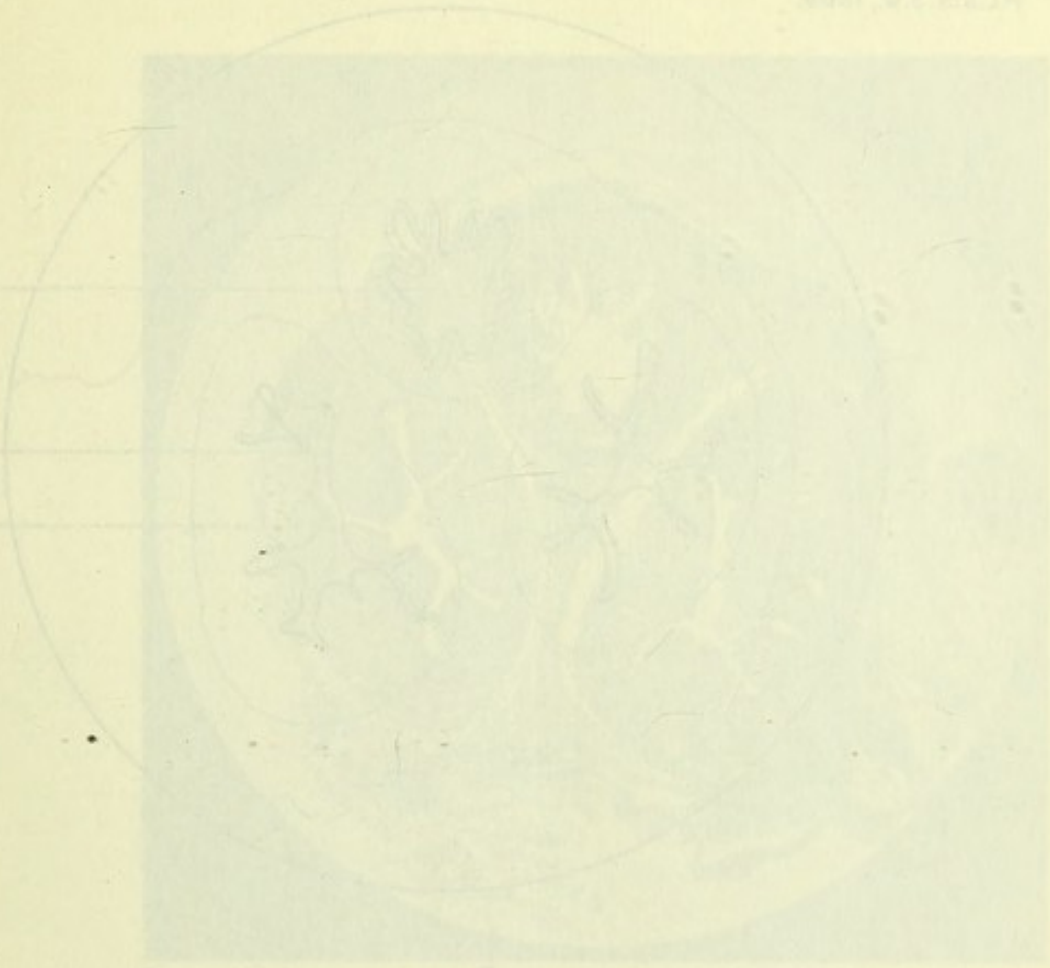
Fig 19.



PERAMELES NASUTA (?)







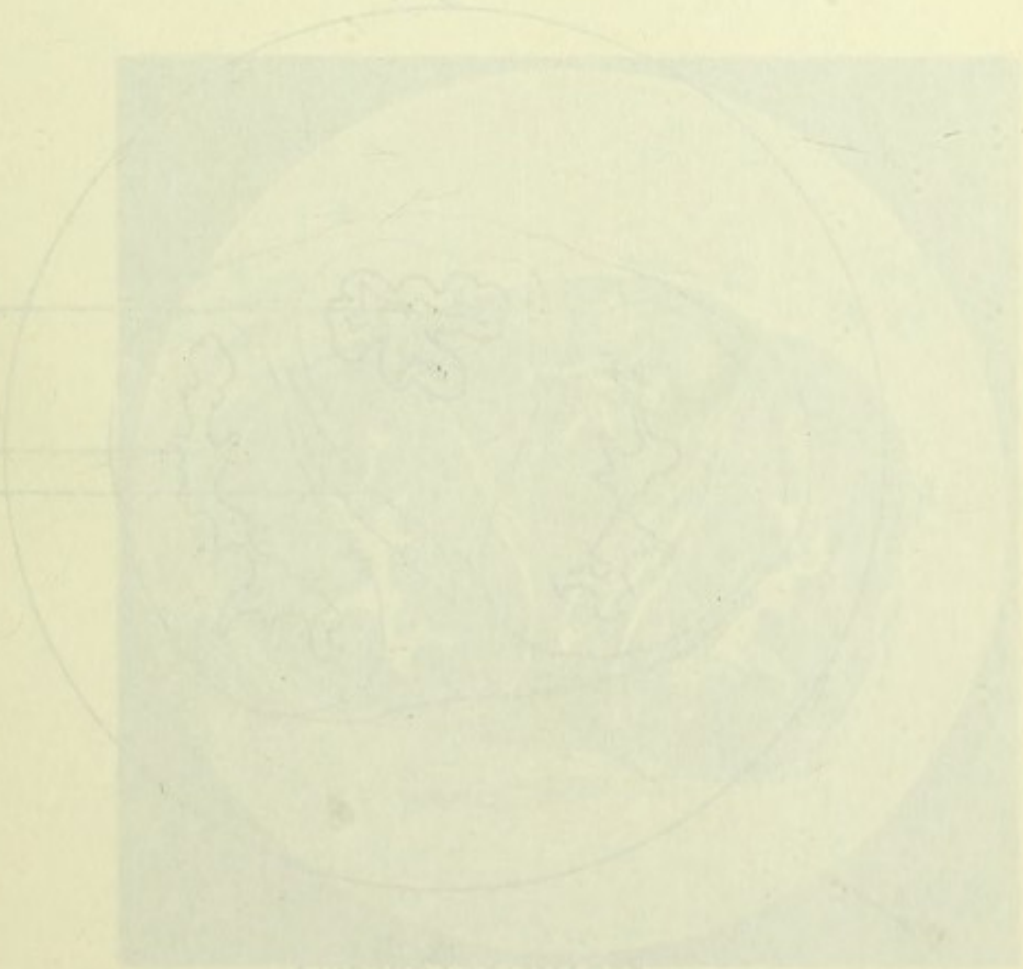


Fig 21.

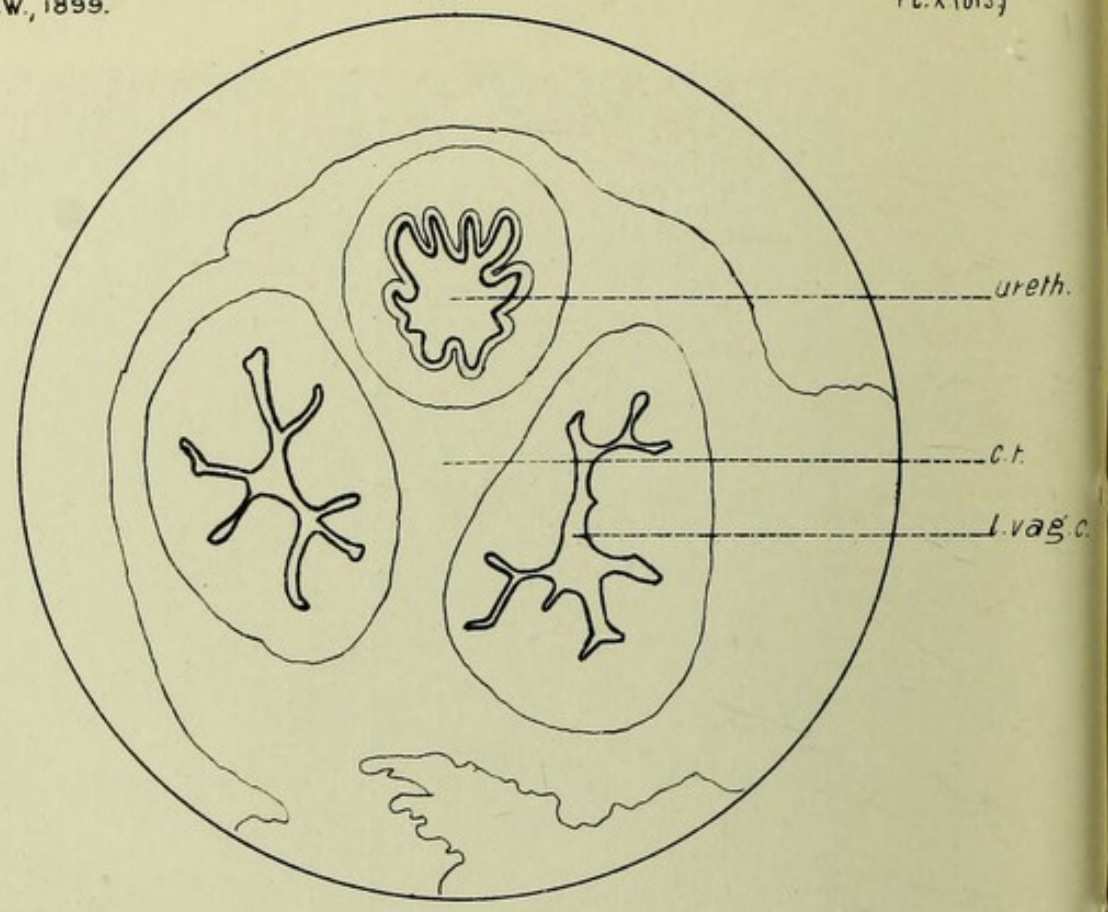
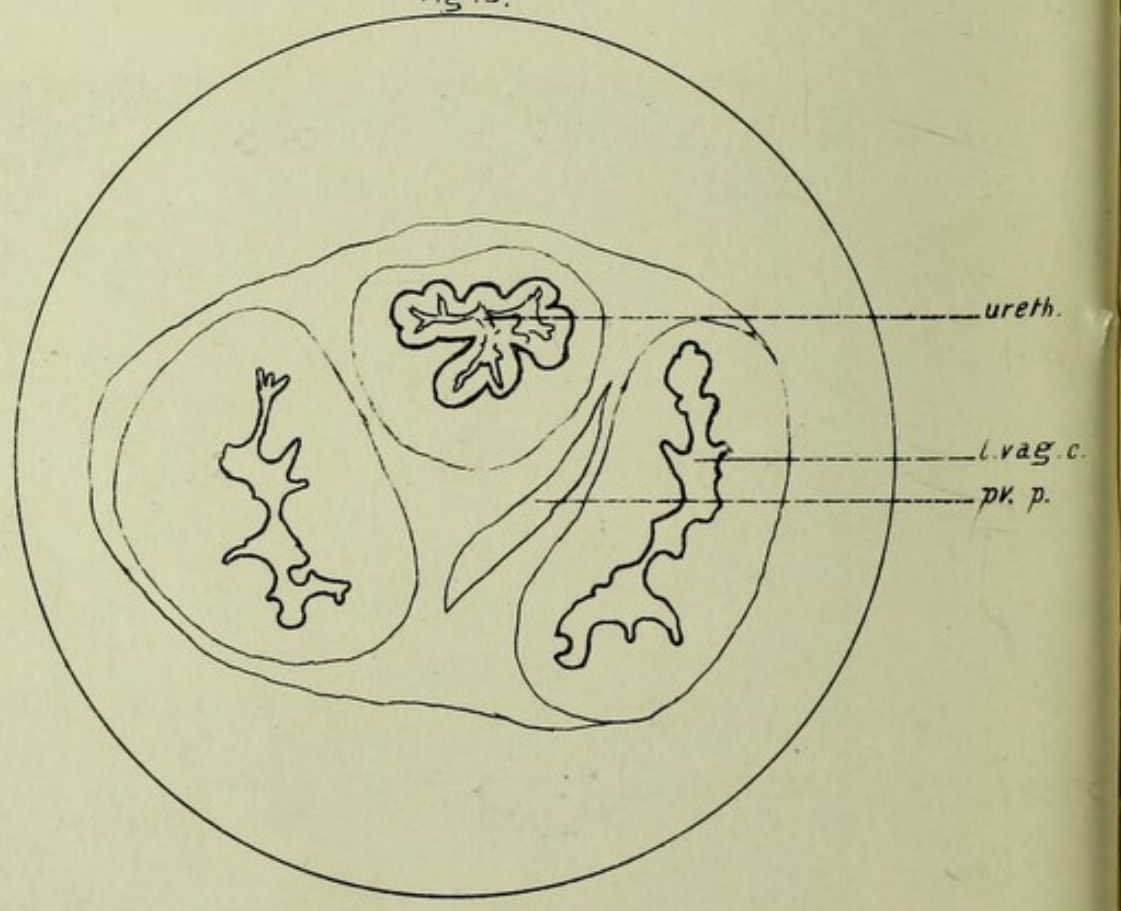
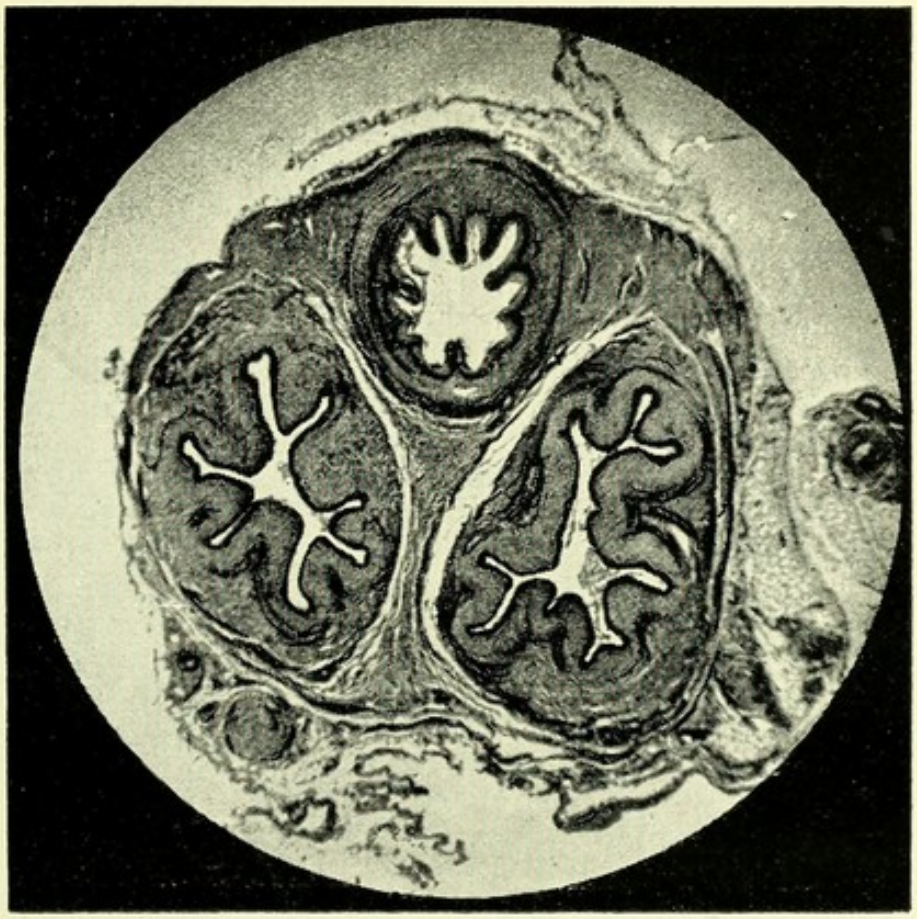
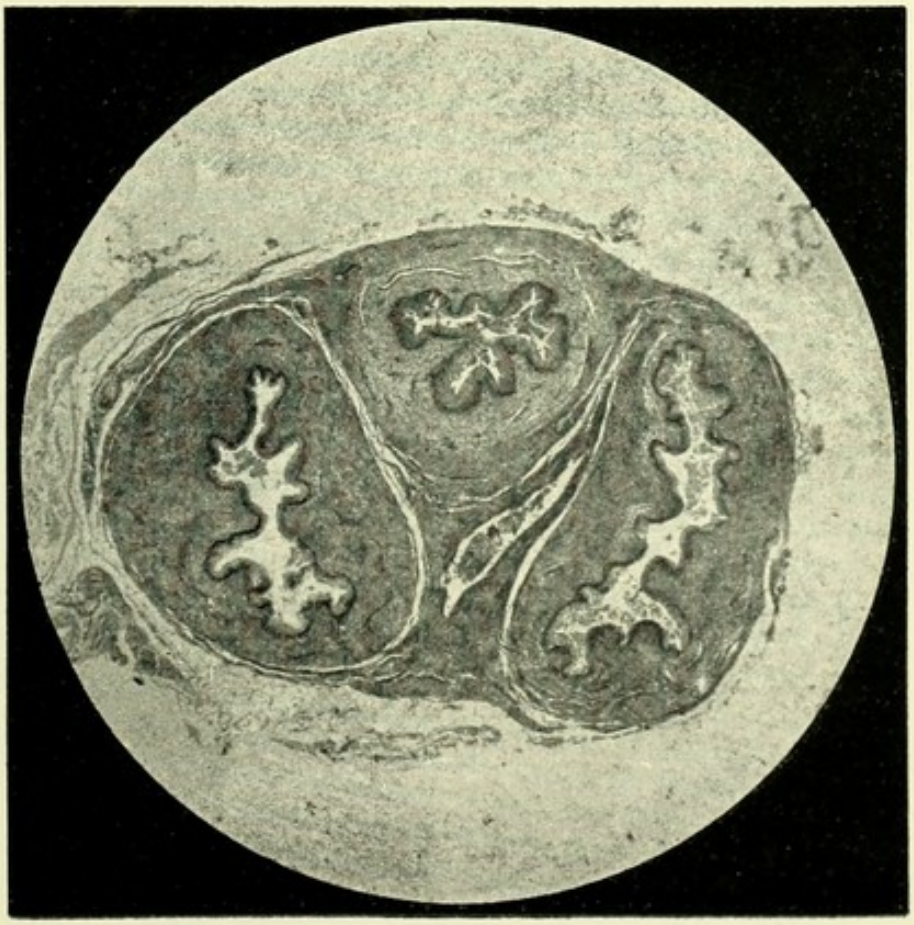


Fig 15.



PERAMELES OBESULA.





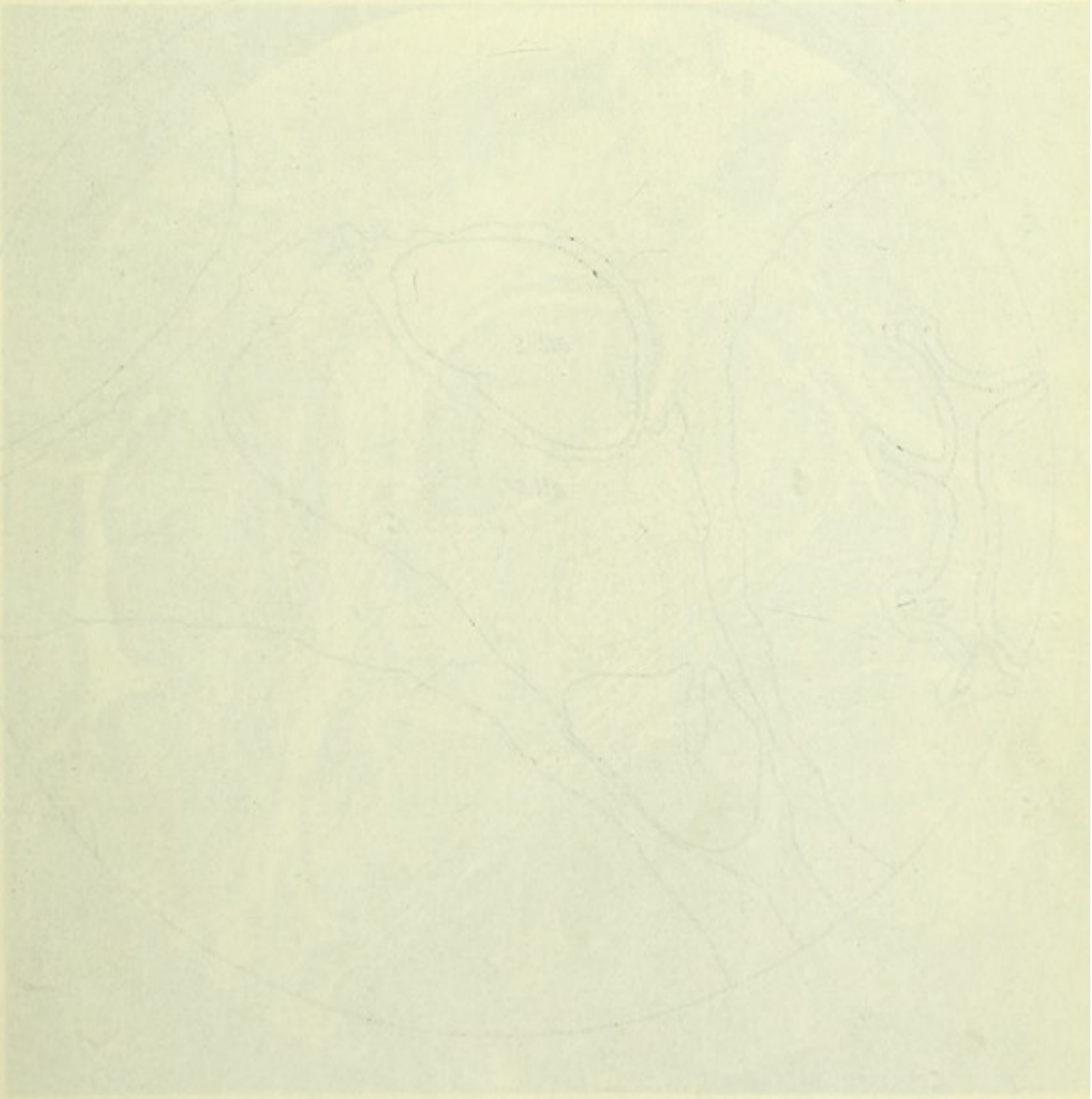
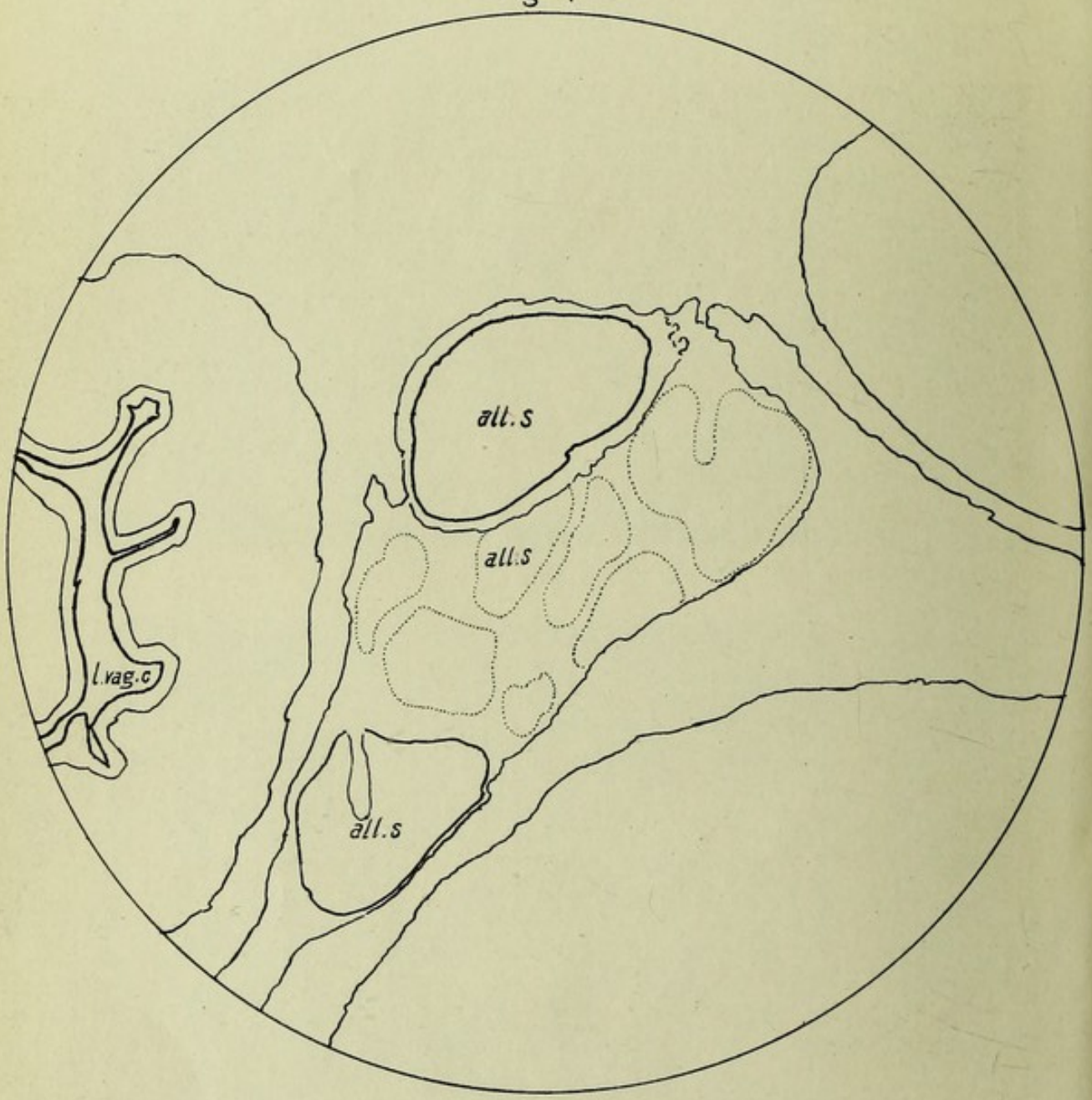


Fig 17.



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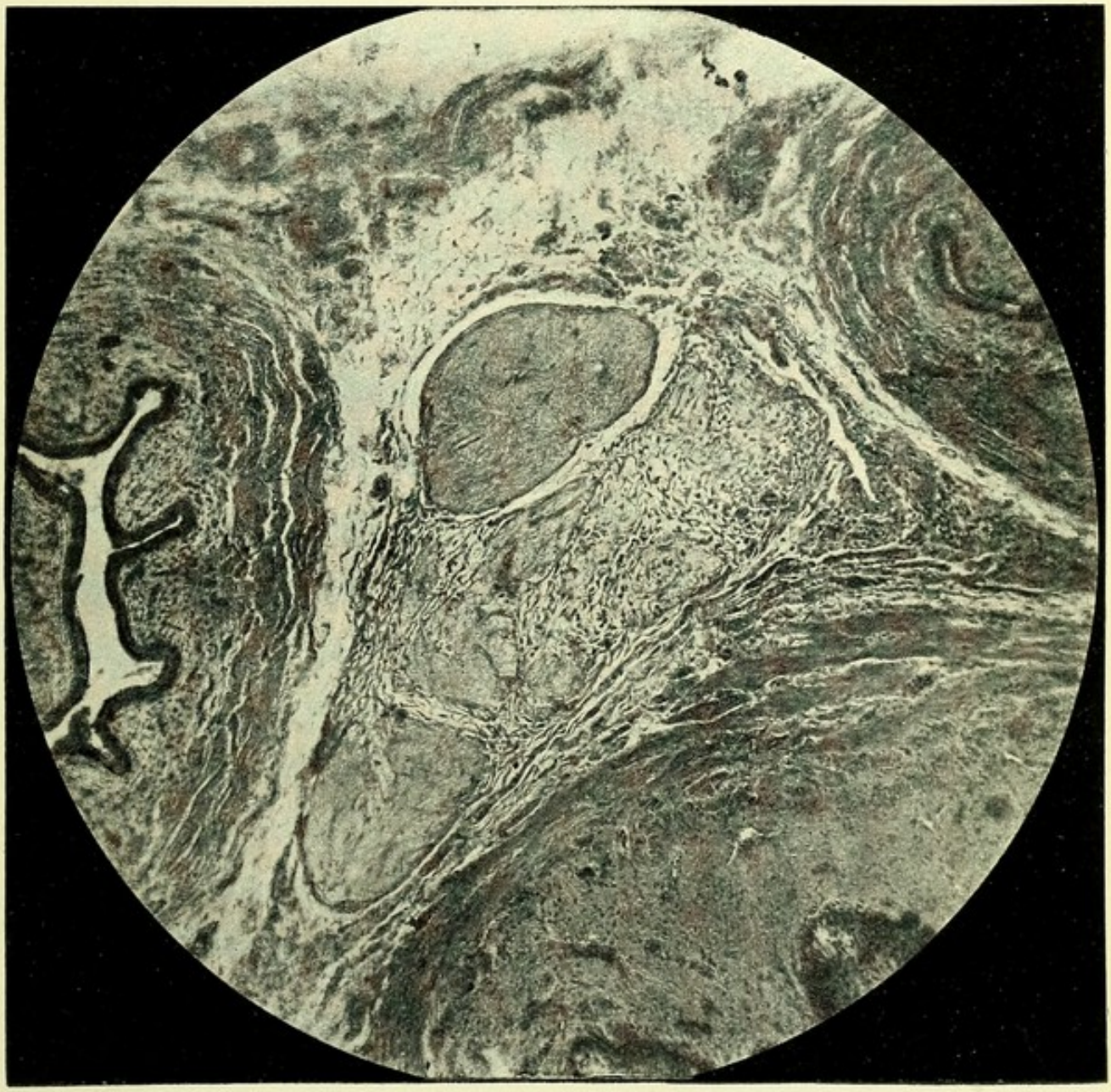

Fig.16.

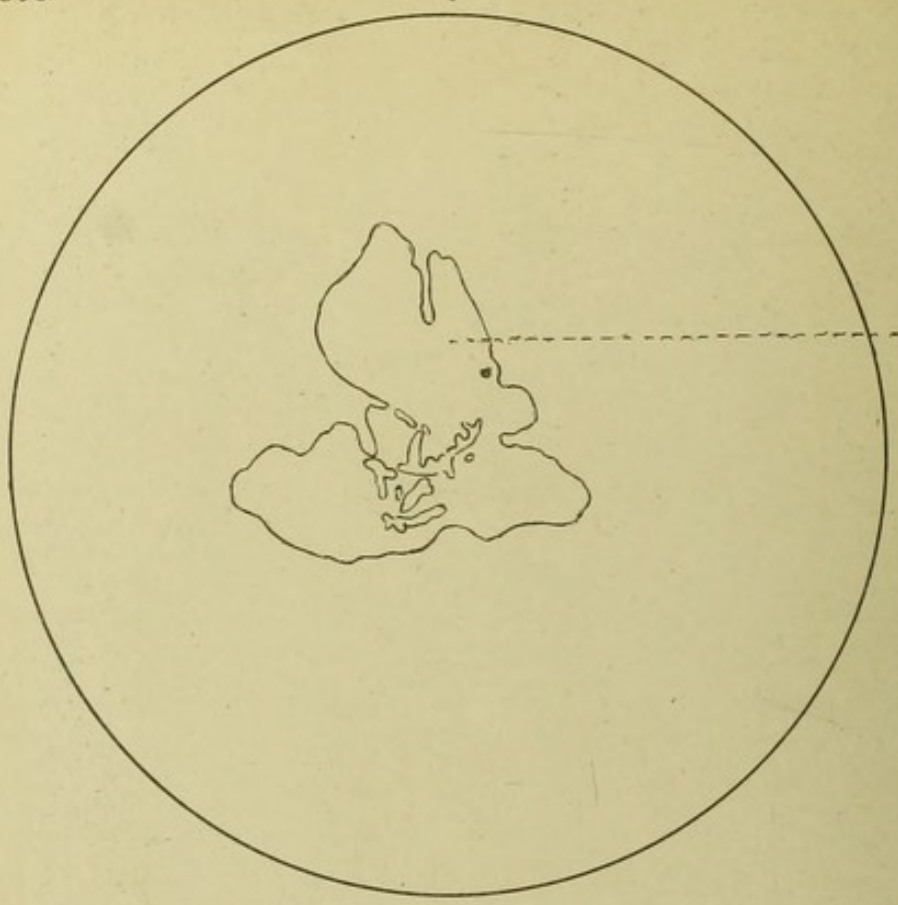

Fig.22.