A CONTRIBUTION TO THE MORPHOLOGY OF THE HUMAN URINOGENITAL TRACT.

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In two previous communications I discussed the questions of the origin of the hymen and vagina. I there attempted to show that the lower ends of the Wolffian ducts enter into the formation of the former, and that the latter was Müllerian in origin only in its upper two-thirds, the lower third being formed by blended urinogenital sinus and Wolffian ducts. In following this line of inquiry more deeply it resolved itself into a much wider question—viz., the morphology of the human urinogenital tract, and this has occupied much of my spare time for the last five years. It soon became evident that what one required to investigate was really the early history and ultimate fate of the Wolffian body and its duct, as well as that of the Müllerian duct, and this led one back to the fundamental facts of development in relation to bladder and bowel. The result of this investigation will therefore be considered under the following heads:—

I. The Development of the Urinogenital Organs, Rectum and External Genitals in the Human Fœtus up to the end of the first Month. The Development of the Permanent Kidney is not considered.

II. The Condition of these Organs at the 6th to 7th Week.

III. The Changes at the 14th Week and at the 24th.

IV. The Structure and Origin of the Adult Human Vagina.

V. The Genital Tract in the Marsupialia.

VI. The Analogues of the Human Male and Female Genital Tract.

VII. The Relation of the Views advanced to certain Developmental Arrests.

VIII. On the Nature and Development of Mucous Membranes.

IX. Summary.

I have to explain that the greater part of the work was done in the Laboratory of the Royal College of Physicians, Edinburgh. Most of the microscopical specimens and of the microphotographs were made by Mr J. Hume Paterson, and those of the early chick by Mr Richard Muir. The incubation of the chick embryos was under the charge of my late assistant, Dr Allan Brough, and was carried out at the Laboratory of the Royal College of Physicians. Some of the work was carried out in my practical room, Surgeons' Hall. The clinical casts were made by myself on suitable cases prior to operation. To the Laboratory Committee, and to all the workers mentioned above, I have to express my great indebtedness.

I have also to state that the University of Edinburgh gave me a most generous grant from the Moray Fund towards the considerable expense involved in the work done, and also an additional grant for the plates of this paper, and I beg to tender my hearty thanks for their munificence.

I must now finally enumerate the material used in this investigation. It divides itself into (*a*) that of the human fœtus, and (*b*) the adult specimens and fœtuses of lower mammals.

(*a*) 1. Human embryos, 3 mm. and 4 mm. in serial sections.
2. Human embryo, serial sections, 28th day.
3. Pelvis of human embryo, serial sections, 6th and 7th week.
4. Pelves (central slabs) of human female fœtuses at 14th and 28th week, serial sections.
5. Male fœtuses at 8th week, 12th week, 14th week, and 18th week (central slabs, serial sections).
6. Prostate and adjacent parts in full-time male fœtus (serial sections).

These were the successful specimens. As all embryologists know in regard to early human fœtuses, the tissues are often not fresh enough for exact microscopical work, and I have had

several disappointments in this way. It is a safe plan, therefore, not to cut and stain all the serial sections unless the early ones show the tissues to promise well.

(*b*) The genital tract in the adult rabbit, and especially in the rat-kangaroo, two specimens: Bennett's kangaroo, one specimen; Wallaby kangaroo, one specimen; pelvis of Bennett's kangaroo, one specimen from Professor Symington of Belfast; many specimens of early pig and rabbit embryo were also cut in serial sections, as well as adult specimens of mole.

The specimens were thus numerous, several thousands of microscopical slides requiring careful examination.

I also examined a series of early chick embryos prepared by Mr Richard Muir.

In determining the scope of this examination, I was guided by the following criteria. In endeavouring to settle morphological questions as already defined one should know—

1. The development of the urinogenital organs in the embryo.
2. The structure of these organs as modified in the female adult.
3. The structure of these organs as modified in the male adult.

These criteria I can fulfil with a fair amount of detail in the human fœtus and adult. In the other groups of mammals the work is necessarily only partial.

I. The Development of the Urinogenital Organs, Rectum and External Genitals in the Human Fœtus up to the end of the first Month. The Development of the Permanent Kidney is not considered.

The development of the urinogenital organs is intimately bound up with the origin of, and further changes in, the primitive gut.

If we examine the sections of the caudal end of a four millimetre human embryo as figured by Keibel (fig. 1), we see the parts of the primitive gut known as the end-gut and the entodermal cloaca. Anteriorly the latter is bounded by what is

known as the cloacal membrane, reaching from the body end of the future navel to the limit between entodermal cloaca and end-gut. This boundary has at first no mesoblast, is related in part to the primitive streak, *i.e.*, is developed from its posterior end, and is probably due to a drawing out of the blastopore.

A few words may be added on this point so as to make the matter quite clear. In the development of the amphioxus we have first a cell proliferation which leads to the formation of a hollow sphere—the blastula (fig. 2). This invaginates and gives a double-layered structure (ectoderm and endoderm)—the gastrula—with an aperture of invagination—the blastopore (fig. 3). This gastrula stage is supposed to hold good for vertebrates in general (Haeckel and others).

In the germinal area of the rabbit we get an axial thickening of the ectoderm—the primitive streak—which develops lateral thickenings and also an aperture at the anterior end, the neurenteric canal which forms a communication between endoderm and ectoderm.

In the early human embryo (2 mm.), Graf Spee has found the *canalis neurentericus* which unites the endoderm of the umbilical vesicle with the ectoderm, and represents the blastopore of the gastrula stage (fig. 4). Keibel in his sections of embryo E B (caudal end; greatest length, 3 mm.), figures the cloacal membrane and remains of the primitive streak on it, so that it is probable that the cloacal membrane represents or is derived, in part at any rate, from the posterior end of the primitive streak, along with a drawing out and union of the edges of the blastopore (which in itself lies in the anterior part of the streak), and this would explain the want of mesoblast at first. The cloacal membrane extends up as far as the root of the future navel and back to the front of the future anus, as one of the malformations I have to consider later on tends to demonstrate. The development of the cloacal membrane is of great interest, as its patency in the new-born fœtus gives rise to the rare condition known as extroversion of the bladder, and explains cases of split pelvis, split clitoris, etc., as I shall indicate further on (*v.* paper following, p. 376).

Before detailing the further changes, I wish to remark on the unsatisfactory nature of the nomenclature in relation to

the primitive gut. The term 'entodermal cloaca' is apt to be confused with the term cloaca, used legitimately enough at a later stage of development for the common inferior aperture in the six weeks' embryo or in the permanent organs of the ornithorhynchus. I beg to suggest that we might speak of the 'end-gut' as the *pars ultima*; of the 'entodermal cloaca' as the *pars penultima*; of the 'cloacal membrane' as the *anterior gut membrane*, short for *anterior penultimate gut membrane*.

Into the so-called entodermal cloaca the Wolffian ducts open. These have their origin from the ectoderm, as has been shown for the guinea-pig by Graf Spee, and by Kollmann for the human embryo.

In an eight millimetre fœtus (sagittal mesial section) further changes are shown by Keibel. The end-gut (pars ultima) (fig. 5) is in course of disappearance, while from the lower end of the Wolffian duct the ureter is taking its origin. The penultimate gut (entodermal cloaca) now becomes divided by coronal (side lateral) folds into an anterior and posterior part, the closure proceeding from above down; the posterior division forms the rectum ultimately; the anterior, part of the bladder and the urinogenital sinus (figs. 6–9). In the guinea-pig a peritoneal dip separates the upper parts of these organs (Keibel).

In the guinea-pig, where the allantois is very transitory, and at any rate where no entodermal allantois is present at the time the bladder develops, the urinary viscus arises, according to Keibel, from the anterior division of the penultimate gut. In the human embryo the stalk of the allantois is usually described as giving origin to the bladder, but we must remember that in the human embryo the allantois is quite rudimentary, and that it seems more exact to describe the bladder as also originating in the human embryo from the front division of the penultimate gut (entodermal cloaca), with probably only its upper part allantoic. The folds so dividing off the primitive gut are coronal, as Keibel's sections show. He also points out that the epithelial lining of the two divisions so formed is different, prior to division, that of the future rectum being more columnar (figs. 6 and 7).

This view of the origin of the bladder, which we owe to

Rathke, Lieberkühn, and Keibel, is a very valuable one, and explains completely the normal anatomy and the various malformations connected with the bladder and rectum. Keibel's 8 mm. section (fig. 5) shows the ureter budding off from the Wolffian duct and developing from below up, and it may be asked how the ureter and the Wolffian duct become separated at their lower ends. They do so by the development of the trigone of the bladder, and thus the ureteric openings come to lie above those of the vasa deferentia in the male, or that of the hymen in the female.

II. The Condition of these Organs at the 6th to 7th Week.

For this stage I have a perfectly preserved 6 to 7 weeks' fœtus obtained by extirpation of a pregnant uterus which was also cancerous. Of the pelvis of this fœtus I have several serial transverse sections by Dr Lovell Gulland, while for a mesial section of a somewhat later date I take that published by Keibel (8th week).

In the transverse sections of my specimen, 48 in number, the following conditions exist:—

1. A cloaca—ectodermal cloaca—is present (sect. 38–44).
2. The urinogenital sinus is present, and has the Wolffian duct openings in it (sect. 31), with the eminence of Müller in the section above (sect. 30) (figs. 11, 12 and 13).
3. The genital cord has formed (sects. 25 to 32) with three canals in it, the central one being the coalesced Müllerian ducts; the two lateral ones the Wolffian ducts (fig. 12).
4. The broad ligaments with Müllerian ducts and ovary are present (sects. 10–23).
5. The Wolffian bodies are present with the Wolffian ducts (sects. 10–22), and in a state of retrogression (fig. 15).
6. The permanent kidney[1] is developed (sect. 18 and upwards) (fig. 14).
7. The ureter is present, but no connection with the bladder can be traced.

[1] By a mistake in my early paper, this was lettered as Wolffian body.

These sections show well that the processes which bring about the complete urinogenital sinus, bladder, etc., are due to development from above and below, as in sections 34–37 we have no connection between urinogenital sinus above and the part being formed from below. We have at this stage a real cloacal arrangement, the urinogenital sinus and bowel opening into a large undivided space—the cloaca. How has this arisen? So far as I know, the intermediate stage has not been found in the human embryo, but from what Retterer has figured in the rabbit embryo (figs. 16 and 17), we may have an epithelial ectodermic plug formed, pyramidal in section, with its apex towards the lower portion of the urinogenital sinus to meet the coronal partition of the primitive gut, and by the breaking down of this centrally we get the condition of the 6 to 7 weeks' fœtus produced (fig. 18).

We have now to consider how the permanent condition of the pelvic organs in the adult is brought about. How is the perineum formed? This we now take up.

The course of the changes described here is known in part from human embryos, aided by a knowledge of what takes place in the embryos of lower mammals, and also by a consideration of certain rare malformations in the adult female due to defective cloacal changes. On this subject the most valuable papers are by Rathke, Reichel, von Rosthorn, Keibel, Tourneux, and Retterer. Reichel in his paper describes a case of a patient 25 years of age who was admitted to the Klinik complaining of incontinence of fæces. Prior to her marriage, three years before, her condition in regard to this had been normal. On examination, anus, labia minora and majora were found normal, but a fistula ran between the rectum and the fossa navicularis, the external opening being below the hymen. The perineum was short and badly developed. The fistula was undoubtedly due to coitus. Von Rosthorn and Caradec relate similar cases. In von Rosthorn's case the lower end of the fistula admitted two fingers.

Reichel gives a good account of the development bearing on this particular point. He confirms Rathke's description in 1830 as to the closing of the cloacal opening. This happens as follows:—

From a mesial skin-fold the genital eminence develops, giving rise to clitoris and penis. From two lateral folds below it, we get the labia with the genital furrow between, the cloacal pit lying posteriorly. Two eminences develop at the side of the cloaca, and by their junction in the middle line, and union with the septum dividing bladder from rectum, above, we get the perineum formed, and *the cloaca with its bowel opening obliterated.* In the cases narrated by Reichel and von Rosthorn the cloaca has remained in part, but the bowel opening has become closed at the apex of the cloacal pit. Marital relations had caused a breaking down of the tissue between bowel and the rest of the cloaca, and thus an incontinence of fæces was established.

The permanent anus is not developed from the bowel opening into the cloaca. This closes, as has been described, and the permanent anus develops as follows :—

The development of the anus is well seen at the stages between the second and third and a half month, and we also get a very clear view of how the epidermis, by passing in deeply, forms a lumen. The sagittal sections show the epidermis passing in as a series of tubular ingrowths (fig. 19). When at the top of the anal orifice, the superficial cells cease, and the deep cells pass up in two layers to meet the epithelium of the Lieberkühnian glands. The anus is thus formed like the prepuce—viz., *the epidermis, deep layer and superficial layers, passes in; the superficial cells (now central) desquamate, and thus the lumen forms.*

I may finally, under this division, briefly consider the question of the production of the cavities or spaces already alluded to. I have mentioned the formation of the primitive gut, the division of the entodermal cloaca into bladder and rectum, and, finally, the formation of the ectodermal cloaca at the 6th week. Each of these shews a different mechanism.

1. *The primitive gut is formed by the ventral infolding of the early embryonic area—i.e.*, by head, tail, and lateral folds converging centrally to the site of the future navel.

2. *The bladder with the urinogenital sinus and the rectum are formed by mesoblastic folds which pass partly from above and partly from the sides.* They are thus partition folds, and there is no central breaking down.

3. *The cloaca—ectodermal cloaca, it may be termed—is formed*

in all probability in a way much used in the developing embryo, as we have seen in the development of the anus, and shall see when we take up the development of the prepuce and vagina. The active ectoderm by proliferation forms a plug, cylindrical or pyramidal, the deeper active cells forming the outer surface except at the free base, the centre of the plug or cylinder being made up of cells less active and tending to be shed. Thus, after a plug has formed, the centre breaks down, and a cavity or slit forms. This is cavity—or slit—formation by ectodermic action, and is sharply contrasted with the method of formation of cavities by splanchnopleuric folds where no breaking down happens. As a broad fact, therefore, the ectoderm forms orifices or open slits, by the breaking down of a solid plug; the mesoderm, cavities or lumina by partitions (figs. 6–9 and 10, 11, 18 and 19).

III. The Changes at the 14th Week and at the 24th.

The changes that take place at or about the 14th week are of very great importance and of the highest interest. We undoubtedly need graduated specimens filling up the stages between the 8th and 14th week, but even with these gaps not yet made good, the changes at the 14th week are of a very evident and pronounced nature. Thus, on viewing a mesial section of a female fœtus at the 14th week, and comparing it with that at the 7th week, we see that the cloacal condition has disappeared, the urinogenital sinus has shortened, the hymen is in process of formation, the relations of urethra and vagina are more like those of the adult condition, a permanent anus is in course of formation, and the prepuce of the clitoris is being developed.

The mechanism of the formation of the rectum and bladder, of their external openings and the formation of the permanent anus, have already been given (pp. 334–337), and need not be discussed. We must take up, however:

1. *The formation of the preputium clitoridis.*
2. *The development of the hymen, and the changes in the vagina and uterus.*

3. *The formation of the female and male urethra, and the changes in the urethral orifice.*

1. *The formation of the preputium clitoridis.*—In the early stages, prior to the 3rd month, the genital eminence is covered by an unbroken layer of epidermis, and sections show no attempt at preputial formation. If, however, sections be examined between the 3rd and 5th months, a remarkable condition is found. In sagittal mesial section (fig. 20) one sees the glans formed and bounded by cells continuous with the deep layer of the epidermis. The preputial aperture has formed, but is filled with a solid plug of cells, while between the glans surface and the inner surface of the prepuce we have also a solid layer. This is often represented, but most erroneously, as a fusion of the epithelial surfaces of the glans and prepuce. In coronal section one sees a remarkable horse-shoe arrangement, the outline of the horse-shoe being mapped out by deeply-stained cells, whilst between these we have less deeply stained cells. In certain lateral sections, again, we get an analogous arrangement, but a circular one.

These appearances shew that the prepuce is developed as follows:—At the apex of the glans the epidermis passes in, following the glans outline.[1] The active epidermic cells, more deeply stained, rest on the glans and the inner preputial surface; between these lie the less deeply-stained cells corresponding to the more superficial cells of the epidermis. We see here, then, very well illustrated, how the epidermis forms lumina. In the epidermis at this stage we have an active deep layer, and above it the less active cells with a tendency to desquamate. When the epidermis has passed in as described, the central cells in the horse-shoe arrangement, for instance, desquamate, and we then get the movable prepuce in the child. The prepuce is thus formed by *the epidermis passing in round the glans, with its active cells deep, its less active and desquamating ones central; the desquamation of the latter makes the mobile prepuce.*

It is usually said that the prepuce grows forwards from the glans root, that the inner surface adheres to the glans and then

[1] I have sections to show that the glans is formed first in the male, at any rate.

breaks down. This is quite an erroneous description, and leads to serious pathological errors in surgery. Adherent prepuce is not an adhesion really, but a hindered central desquamation.

In one specimen I found the cells passed in not yet desquamated; but it was interesting to note that the central cells were flatter than the others. The glans clitoridis is imperforate in the human female.

2. *The development of the hymen and the changes in the vagina and uterus.*—We now take up one of the most interesting points in this investigation, as the results under this heading are opposed to current views, and appear to me to clear up several hitherto obscure points.

These changes occur at the 14th week, and have hitherto been described as a metamorphosis of the lining of the part of the Müllerian ducts forming the Anlage of the vagina. The lower end of the fused ducts, especially, is said to become distended, owing to epithelial proliferation. This proliferation causes perforation into the urinogenital sinus, thus forming the hymen.

Klein says: "Der Hymen ist jener Theil des Beckenbodens welcher durch den spätestens im Anfang des drittens Monats erfolgenden Durchbruch des Müllerschen Gänges und durch die vom dritten bis fünften fötal Monat erfolgenden ampulläre Erweiterung des Endtheiles der Vagina abgegrenzt und verdünnt wurde." Nagel's (p. 100) description is as follows: "Bei Embryonen aus dem 3 Monat beginnt eine Vermehrung und Anhäufung der oberen Schichten des Epithels, welche zuerst dicht oberhalb des Orificium vaginae auftritt, wodurch die Vagina an dieser Stelle (bei Embryonen von 7–10 cm. Rumpflange) eine bauchige Erweiterung erfährt. Durch diese Erweiterung ensteht der Hymen."

Tourneux and Legay state: "Au commencement du 4° mois lunaire, chez le fœtus humain (7·5–10·5) la portion inférieure ou vaginale du canal génital (moitié environ) est tapissée par un epithelium pavementeux stratifié qui se continue par une transition graduelle avec l'epithelium de la portion supèrieure ou utérine."

In a very well-preserved female fœtus of the third and a half month which I examined by serial sections, using the Paraffin method and staining with Logwood and Eosin, I found a series

of conditions which threw quite a novel light on the development of the hymen. I found that at the site of the hymen two epithelial bulbs developed. These measured, in the specimen shown at fig. 21, ·3 mm. × ·2 mm.; as they near the middle line they are larger, and they measure as much as ·5 mm. × ·4 mm.—*i.e.*, may be double the former size. They lie, in the main, lateral to one another, are composed of epithelial cells exactly like those of the adult vagina, and have their structure and relations well shewn in fig. 21. The origin of these bulbs of epithelium had now to be settled, and, on examining the sections carefully, I at last came on the Wolffian duct ending in the smaller one (fig. 21). This enabled me to clear up the matter, as evidently these bulbs, which I now term the 'Wolffian bulbs,' are derived from the Wolffian ducts, and as these, according to all recent embryological work, are derived from the ectoderm; this layer is the source of the epithelium of the bulbs. The sections of this fœtus further shewed that the epithelial cells of these proliferated into the Müllerian vagina, mapped out the fornices and passed into the lower third of the cervical canal, blocking these up and rendering them solid for a time, as Tourneux and Legay have well figured.

The central cells, which, both in the Wolffian bulbs and in the Müllerian vagina, are the more advanced, soon begin to desquamate, and in this way a central lumen forms. The view advanced, however, by such able observers as Nagel, Klein, and Tourneux and Legay, requires careful consideration. Their view is that the vaginal epithelium is the result of a transformation of the original Müllerian lining, while I urge that we have an actual eruption of cells from the Wolffian bulbs into the Müllerian vagina: that indeed the mechanism is like what I have described in the development of the prepuce and anus. I would urge that the mere transformation of cells would not necessarily involve the coalescence that renders the vagina and its fornices at first solid, while the explanation I have given does.

In order, however, to establish the opening of the hymen, an active involution of epithelial cells in the urinogenital sinus takes place, and thus by the distending bulbs above, and the epithelial involution from below, the entrance of the vagina—*i.e.*, the

hymeneal orifice—is formed. *Thus the hymen is formed by a special bulbous development of the lower ends of the two Wolffian ducts aided by an epithelial involution from below of the cells lining the urinogenital sinus* (fig. 20).

The hymen bilamellatus described by Schaeffer at the fifth month is probably due to the persistence of the upper and lower margins or edges of the bulbs, and disappears in the more advanced fœtus. Schaeffer's statement is: "Jeder Hymen wird mehr oder weniger deutlich im 5 Monate als bilamellatus angelegt." I have not, however, as yet had an opportunity of examining this transitional form.

The whole of the developmental changes might be summed up now as follows: Formation of primitive gut, seen in embryos of 20th–23rd day (fig. 1); division of primitive gut into bladder (with urinogenital sinus) and rectum, and withering of end-gut about 20th–30th day (fig. 5); communication of bladder and rectum with exterior (formation of cloaca) by breaking down of hypothetical plug (in human species) before sixth week (figs. 16, 17, 18); closure of cloaca by Reichel's Analhöcker and formation of perineum, 7th–8th week; urinogenital sinus with Müllerian ducts related to it and Wolffian ducts opening into it, no anus, at 8th–9th week; hymen formed, anus formed, preputium clitoridis in course of formation, Müllerian vagina being relined, and uterus now single; 3rd to 4th month (figs. 20, 21).

These periods are only approximate. An excellent table is given by Wendeler, and Nagel's papers should be consulted for his views as to the formation of the perineum.

IV. The Structure and Origin of the Adult Vagina.

So far as the structure of the vagina in the adult is concerned, I wish to direct attention only to two points—viz.,

(*a*) *The relations of the normal hymen.*
(*b*) *The naked-eye arrangement of the vaginal rugæ and columns.*

I shall then discuss the Anlage, or fundamental origin of the vagina.

(*a*) *The relations of the normal hymen.*—If a normally-developed *virgo intacta* be examined carefully while under chloroform and in the lithotomy posture, as one has often an opportunity of doing in operative cases—*e.g.*, in dilatation for dysmenorrhœa—and if care be taken not to disturb the parts unduly, it can be easily noted that the so-called hymeneal entrance is a vertical slit, and that the edges of the slit are in contact (Cullingworth). This can be well seen in the sections of the four-months' fœtus, where we can observe the vertical slit in the centre of the epithelial proliferation of the hymen (fig. 22).

How this arises is easily understood when we consider what has been already stated as to the development of the hymen. The vertical slit is due to the coalescence and central breaking down of the laterally placed Wolffian bulbs, and the so-called crescentic hymen as well as the oval form are made by the examining fingers separating the vertical edges.

(*b*) *The naked-eye arrangement of the vaginal rugæ and columns.*—On examining the vagina in adults, preferably in a multiparous married woman, one notices a distinct difference in the upper and lower straits. The lowest inch of the vagina is narrowed and has rugæ or columns, in the main running longitudinally. Above this the vagina is transversely wider and has its rugæ transverse. This difference to the naked eye is very striking, and has not hitherto been sufficiently noted. The anterior and posterior columns I consider not as septal remains of the Müllerian portion of the vagina, but as the remains of the original partition between the Wolffian bulbs.

While, then, the hymen is derived from the Wolffian bulbs, as I have indicated, it may be asked what evidence there is as to the extent of the participation in vaginal formation of the urinogenital sinus. As we have already seen, the Müllerian ducts in the early fœtus end in the eminence of Müller; the Wolffian ducts open below them. It follows, therefore, from what has gone before, that the upper portion of the urinogenital sinus enters into the formation of the vagina, and that the lower end of the vagina is due to a blending of Wolffian ducts and urinogenital sinus. This lower portion measures, in the adult, about an inch. I base this estimate on the different naked-eye

structure of this part of the vagina, what may be termed its columnar portion, and on the fact that in certain rare forms of atresia classed with atresia hymenalis, a transverse septum is found an inch from the actual hymen (*v.* also p. 365).

In the two-months' fœtus the urinogenital sinus is relatively long, has the Wolffian ducts at its upper part, and the bulbs developing from them block it therefore, and probably block the lower portion of the urethra too. The involution from below perforates both obstructions, and this view explains, I believe, the apparent urethral hymen seen so often. The urinogenital sinus of the early fœtus is therefore represented in the adult by the vestibule, lower portion of the urethra, and lower third of vagina.

In the adult human vagina the Anlage is therefore as follows:—

(1) The upper two-thirds of the vagina are derived from the ducts of Müller.

(2) The lower third is due to the coalescence of the upper portion of the urinogenital sinus, and the lower ends of the Wolffian ducts.

(3) The epithelial lining of the vagina is derived from the Wolffian bulbs, which again are epithelial proliferations of the lower ends of the Wolffian ducts. The vaginal mucous membrane is thus epiblastic.

The outline of the human vagina from a developmental point of view is indicated in fig. 23.

The Relation of the Origin of the Vagina to its Lymphatic Supply.

I take this part as it affords a very interesting comment on the view I have advanced.

As is well known, the lymphatics of the external genitals and lower third of the vagina and urethra pour into the inguinal glands—*i.e.*, these receive the lymphatics of the genital tract whose Anlage is the urinogenital sinus, while the lymphatics of the upper two-thirds or Müllerian portion of the vagina join with those of the cervix uteri to enter the hypogastric glands.

How far the vascular and nervous supply of the pelvis is

moulded on this central fact I have not yet had time to determine exactly, but it might be considered in the case of some of the lower animals first—*e.g.*, in the dog. I may point out, however, that the pudic artery and nerve supply the lower end of the genital tract and external genitals, but the exact upper boundary of this supply I have not had time to look into. It is probable, however, that the urinogenital and rectal tract may be divided into two great parts, an upper and lower. The latter comprises external genitals, lower end of urethra, lower third of vagina and anus: the former, the rest of urethra, the bladder, upper two-thirds of vagina, uterus and tube, and rectum. Herman records a remarkable case where from nerve or vascular influence this lower part alone seems to have sloughed. Von Lingen has also drawn attention to a number of cases where a cast of the upper part of the vagina and vaginal portions of the cervix, comprising mucous membrane, submucous and some muscular fibre, has sloughed off. He points out that this part is supplied by the cervico-vaginal branch of the uterine artery, and one supposes that thrombosis of this branch must have occurred. These pathological cases form an interesting comment on the view I have given.

3. *The formation of the female and male urethra and the changes at the urethral orifice.*—In the female the urethra is developed from the lower end of the anterior division of the primitive gut. It is possible, as I have already suggested, that during the formation of the hymen the urinogenital sinus becomes blocked, and the urethra at its lower end perforated from below again (*v.* p. 344).

The male urethra is formed from the primitive gut in the same way down as far as the colliculis seminalis, the hymeneal analogue. Below this, where the adult female is, as it were, hypospadic, the male urethra is closed. As, however, this same hypospadias exists in the embryo in both sexes, the question arises as to how the male urethra becomes ultimately closed on its inferior aspect. The usual statement is that the parts analogous to the labia minora in the female unite by their edges and thus close in the canal. Of this method of closure there is only a fair amount of proof, and it does not explain how the male glans becomes perforated.

Three of my specimens were available for studying this question. The first was a male fœtus between the second and third months; the second, a male at the third and a half month; and the third, one at the fourth month.

In the first and second the closure was going on, but there was no perforation of the glans; in the third the perforation of the glans was going on (figs. 24, 25, and 26). In regard to the closure of the inferior aspect of the spongy portion of the urethra, it can be noted that the greater part of the posterior closure was due to a gradual growth forwards of epidermis and deeper tissue towards the frænum, and probably forming a solid closure. Behind the frænum the deep and superficial layers of the epidermis passed in and back, the superficial cells being central and tunnelling back to meet the higher part of the urethra. These appearances are illustrated by figs. 24, 25, and 26. The posterior part of the urethra thus seemed to be closed as usually described, but certainly tunnelling goes on from before backwards, the active epidermis passing in and back, and by central desquamation forming a lumen. The changes closing in the posterior part are more difficult to follow, but those in front are certain.

Sections at the fourth and a half month show the prepuce in course of formation, as I have already described. There is, however, a remarkable condition to be noted at the apex of the glans, where the epidermis passes in as a solid plug to cause perforation of the glans there and to meet the canal behind (fig. 26).

Thus, in the male urethra the canal is formed down to the perineum by the urinogenital sinus; below this we get the canal completed by a gradual and apparently solid closure of the ridges from behind forwards. Immediately posterior to the frænum the epidermis passes in and back, making a lumen, as already described; finally, the glans is perforated by an epidermal plug, and thus the continuous canal formed.

Further observation is, however, needed on these points, which are subsidiary to the present inquiry.

V. The Genital Tract in the Marsupialia.

I have examined the genital tract in seven specimens. Two of these were what is termed the Rat Kangaroo (*Hypsiprymnus*), two were Wallaby kangaroos, and three were specimens of Bennett's kangaroo (*Macropus Benneti*). I am indebted to the Marquis of Bute for the Wallaby kangaroos, to Professor Symington for the pelvis of one of the Bennett's kangaroos, and to Professor Kelly of Baltimore for one of the opossum. The rat kangaroos were obtained alive, and I was thus enabled to get the genital tract fresh and in good condition for microscopical examination. In one I therefore had serial sections made of the whole genital tract, so that the complicated structures might be traced accurately. This involved the preparation of about two thousand slides on this question alone. The other specimens were examined for their naked-eye relations, and drawings made.

I purpose, therefore, under this heading to consider—

1. *The naked-eye anatomy of the Kangaroo genital tract.*
2. *The microscopical serial sectional anatomy of the genital tract in the Rat Kangaroo.*

1. *The naked-eye anatomy of the Kangaroo genital tract.*— In the *Marsupials* we have a very remarkable arrangement in the vaginal portion of the genital tract. The uterus is bicornuous, and each horn has its lower opening or os uteri. The vagina has two lateral canals, which may arch and meet above, this portion lying between bladder and uterus like a second bladder. Below, these so-called lateral canals open into the urinogenital sinus. In addition, a median portion is present, and this communicates above with the lateral canals, while below it may end as a *cul-de-sac*, or in some species open into the urinogenital sinus. In the central portion, the double os uteri opens. Lister and Fletcher discuss the condition of the median portion in the Macropodidae carefully, and give a table of the various species, and the arrangements in each as to this point. Some allege that the opening is not present in the same animal in its early life. Figs. 27, 28, and 29 give the variations, so far as known, in the different species of marsupials. These authors also figure the relations of the Wolffian ducts and ducts

of Müller in an embryo of *Macropus rufus*, and remark that the arrangement of the Müllerian ducts is the same as in the adult opossum.

In my own specimens (fig. 27) the naked-eye arrangement of the organs in one of the rat kangaroos (*Hypsiprymnus*) is shown. The following are the measurements:—

Length of genital tract from ovary to lower end of bowel, 7 cm.
Length of cornua, 7 mm.
Diameter of central canal, 5 mm.
Diameter of lateral canal, 3·5 mm.

In the opossum (*Didelphys dorsigera*) we have a double uterus, two lateral canals, a lower unpaired portion into which the former opens, then the urinogenital sinus.

In Macropus, figured by Owen, we have two lateral canals: a central blind pouch, with double cornua and ovaries.

A very important point is the relation of the ureters. These pass inside the lateral canals, and lie outside the median pouch when this is present (fig. 29). In the opossum (*Didelphys dorsigera*), the central portion of the tract is not well marked, and may be only represented by the upper part of the lateral canals where the os uteri of each side opens, or by the lower mesial portion above the urinogenital sinus. In this opossum the ureters lie to the inside of the lateral canals.

The opinions hitherto expressed on these remarkable structures making up the vaginal segment of the genital tract in marsupials have all been to the effect that the lateral canals as well as the central part are Müllerian.

Tourneux and Legay say: "Chex les marsupiaux, la non fusion des conduits de Müller (*Didelphys dorsigera*) est la consequence d'une disposition spéciale des urétères, qui, au lieu d'embrasser dans leur courbure le cordon génital s'engagent dans l'epaisseur même de ce cordon, entre les conduits de Müller qu'ils separent" (*op. cit.*, p. 376).

Brass says: "Wir . . . . von einer dreifachen Vagina sprechen können" (p. 36).

The conclusion I have come to in regard to the morphology of the vaginal tract in the marsupials is that the lateral canals

represent the Wolffian ducts, and that the mesial *cul-de-sac* is Müllerian. The evidence for this is as follows:—

Naked eye.—That the central portion is Müllerian is quite evident. It has the os uteri of each horn at its upper part; Owen further figures the remains of a septum in the mesial portion. The lateral canals occupy the position of the persistent Wolffian ducts, have the ureter on their inner aspect, and open below into the urinogenital sinus.

The permanent arrangement in the marsupials is what we find in the human embryo at or about the sixth to seventh week of intrauterine life. We have, therefore, in the marsupials the primitive developmental condition of the urinogenital ducts remaining, instead of coalescing, as in the higher mammals; the Müllerian element may be less evident, as in the opossum, or both elements may be well represented, as in the Macropodidæ.

As to the function of the lateral canals, it has been ascertained that the seminal fluid is transmitted by them, and that the fœtus in certain cases passes along them (Hill). According to some authors the fœtus passes by the central portion even when this does not open into the urinogenital sinus, and Hill records a case where the fœtus did not pass by the lateral canals but into the connective tissue between them, the central pouch being absent.

Microscopical.—The microscopical structure varies in the case of the central and lateral canals, the former being lined with a single layer of columnar epithelium, like that of the human cervix uteri, while the latter are lined with many layers of squamous epithelium. This, however, is considered more fully presently.

An important point is the relation of the ureter to the vagina in the adult female mammal, as well as that of the ureter to the urinogenital ducts in the mammalian fœtus. With the present tendency of biological thought one would expect these relations to be on a common plan. In the kangaroo adult the ureters pass inside the lateral canal and outside the central vaginal canal before entering the bladder. Their relations are well seen at fig. 27. There one can note the ureters passing down from the kidney to run behind the cornua, and, at a lower level, to

penetrate the bladder wall after passing inside the lateral canals; the central vaginal canal lies between them.

Lister and Fletcher figure a diagram of an early fœtus of *Macropus rufus*, and state that the ureters pass outside both Müllerian and Wolffian ducts, an arrangement, they say, like that of the adult didelphys. There must be some error here, as whatever view one takes of the origin of the vaginal canals in the opossum, the ureters pass to the inner side of the lateral canals.

The question of these relations has now to be raised in regard to the human fœtus. Here we get opinions at variance with what I find in the specimens I have examined. Nagel says: "The ureters lie to the outside of the Wolffian ducts" (in fœtus of 8 mm.).

In an embryo figured by Keibel from His' collection (embryo L.O. 25 mm., female, 8½–9 weeks), Keibel states that the ureters lie lateral, the Wolffian and Müllerian ducts mesial. A section of this is figured, and also serial sections to illustrate the relation (figs. 90–100, Keibel). An examination of these (Keibel, pp. 100 and 103) seems to me to bear a different interpretation. Fortunately the fœtus of which I figure transverse sections is about the same age and size as L.O., and is practically the same in structure.

From the study of these and a third specimen, which I owe to the kindness of Mr Stiles, the following seems to me a more correct view.

(1) At the genital cord, where in the human fœtus the Wolffian ducts are placed together, with the blended and therefore now single Müllerian ducts between, *we get the ureters lateral.* One cannot compare the fœtus at this level with the adult kangaroo type, as the canals are too approximated.

(2) Higher up in the fœtus we get the following relations—viz., to the outside, the Wolffian duct; somewhat internal to this the Müllerian duct, and much further towards the middle line the ureters (*v.* fig. 90 of Keibel.) As one passes down the sections the Wolffian and Müllerian ducts lie closer together, and the ureters are thrown to the outside. The bladder is high, however, in the kangaroo—*i.e.*, lies in front of the cornua; in the human female it is deeper; the ureters, therefore, enter the kangaroo bladder higher up.

This is manifestly the level (*v.* sheet and fig. 90, Keibel) one must compare with the kangaroo and human fœtal tracts, as here the ducts are separated and not approximated.

We have thus at a certain stage of the development of the human fœtus, and at a certain level of the fœtus, an arrangement of the ureters and urinogenital ducts analogous to what one would expect in the kangaroo if the lateral vaginal canals be really Wolffian and the central Müllerian.

This question, however, requires further working out.

2. *The microscopical serial sectional anatomy of the genital tract in the Rat Kangaroo.*—The structure and relations of the parts were very well brought out in one of the specimens by means of serial sections of the entire tract. These were cut with the Cambridge rocking microtome and stained in the usual manner with logwood and eosin. The organs examined were the ovary, tube, cornu, lateral canals, central portion of vagina, urethra, bladder, ureter and intervening tissue, the rectum and anal glands.

The *Ovary.*—This measured 5 mm., and was set in the pavilion of the tube like an egg in a cup. Its connective tissue was continuous with that of an attached fimbria.

The following structures make up the ovary, and need no comment. The germ epithelium is well marked over the outer surface, except where the tube was attached. Graafian follicles were present in abundance, and with the ordinary mammalian constituents of tunicæ fibrosa et propria, membrana granulosa, with yelk and ovum. One peculiar feature in the ovary was at the hilum, where, amid a group of endotheliomatous cells, a canalicular system lined with epithelial cells was present where the tube grasped the ovary (fig. 35). Careful study of the serial sections seemed to me to show that this was continuous with the epoophoron, and was thus the paroophoron.

The ovary in this animal thus varies from the human ovum in two remarkable points—viz.,

1. The paroophoron ends in the centre of the ovary near the hilum.
2. The ovary is inserted in part into the pavilion of the tube, like an egg in a cup.

It is interesting, therefore, to note that the early indifferent sexual gland had become an ovary, but had retained a large part of what would become the vas deferens in a male specimen.

The *tube* calls for little remark, as it resembles in many points that of the human tuba Fallopii. It has a mucous membrane consisting of columnar epithelium on a basis of connective tissue and thrown into folds, especially in its outer part. Circular and longitudinal unstriped muscular fibres form the wall, which is covered externally with peritoneum. The cornu has a very well-formed and thick mucous membrane with many glands (fig. 30). The interglandular connective tissue consists of a homogeneous basis and connective tissue corpuscles. The epithelium lining the glands is well formed and columnar, with large nuclei and nucleoli. In the lower part or cervix the epithelium is columnar and narrow like the cervical epithelium of the human uterus. The muscular wall is thinner than that of the mucous membrane, and has longitudinal (outer) and circular muscular fibres, with some interlacing ones. The interglandular connective tissue passes into the wall, and thus vessels enter the mucous membrane from it. Near the tube and ovary the epoophoron is seen well developed, and consists on section of many tubules lined with epithelium of a columnar but somewhat flattened type.

The *central vaginal portion* is lined with narrow columnar epithelium like that of the cervix, while that of *the lateral canals* is squamous and many-layered. This is well seen on T.S. (fig. 31), when one can further note that the muscular wall of the lateral canals is much thicker than that of the central Müllerian (three to four times). *A common muscular coat surrounds the lateral and central portions.* The urethra is seen cut in front in this T.S., and the blood-vessels lie at the posterior angle of junction of the central and lateral portions.

The bladder, ureter, rectum and anal glands present no novel features.

So far as the microscopical anatomy goes the cell structure is not rudimentary, but like that of higher mammals.

VI. The Analogues in the Male and Female Genital Tract.

While it is generally believed that the analogy between the male and female genital tract is a very close one, the exact details have by no means been worked out, and excellent observers are at variance on several points.

Exact analogues have yet to be determined in regard to those organs which are rudimentary in the one sex and fully developed in the other. Thus it is as yet disputed how far the vas deferens of the male is represented in the female; how much of the vagina is represented in the male, and so on. This practically means that we must consider not only the adult anatomy of the genital organs, but also their development, and this resolves itself, in the main, into a consideration of the development of the urinogenital organs. I shall therefore consider the subject as follows:—

A. *The development, immediate and ultimate, of the urinogenital organs so far as known in man.*

B. *The significance of the temporary development of the Wolffian bodies in the human embryo.*

C. *The ultimate fate of the urinogenital organs in the male and female; the male and female analogues.*

D. *The homology of the male and female sexual function.*

A.—*The development, immediate and ultimate, of the urinogenital organs, so far as is known, in man.*

The development of the rectum, bladder, and urethra has been considered in a previous section (pp. 332–335), and we have therefore only now to take up the development of the Wolffian bodies and ducts, and of the Müllerian ducts in the early stages. On this part of our subject there is a very large amount written, and what I give here is based on this and on my specimens at the fourth and sixth week. These were examined by serial sections.

If we take a five weeks' embryo, as Coste so beautifully figures, we find that in the pleuro-peritoneal cavity the temporary organs known as the Wolffian bodies have developed.

They occupy the greater part of the length of this cavity, reaching from the heart, downwards and backwards, to the caudal extremity. As is well known, we have, in the lower vertebrates, these bodies consisting of two parts—the pronephros or head kidney, and mesonephros or Wolffian body proper. In the human embryo it is disputed as to whether the pronephros is really represented. In my specimen of a month old I found at the top of the Wolffian body a pit with a small tubule at its deep end, and this seemed to me to be pronephric in its nature (figs. 32 and 33). It was, at any rate, the only part of the Wolffian body which had a free peritoneal opening for its tubule. Another view would be, of course, that it is the beginning of the duct of Müller.

In the lower mammals we get very instructive examples of the minute anatomy. I have examined this in several specimens of the chick, and rabbit, and pig embryo (many specimens in serial transverse and longitudinal section), and found Minot's description correct. The mass of its substance is made up of tubules lined with epithelium, and opening towards the surface of the organ into the Wolffian duct. At the other end of the tubule is a Malpighian corpuscle with a thin lining of epithelium —the capsule of Bowman. We have no exact information as to the mechanism of their excretion, but they are evidently analogous in their function to the permanent kidneys.

Along the outer free peritoneal surface of the Wolffian body runs the Wolffian duct, the collecting tubules opening into it (fig. 34; *vide* also Kollmann, p. 399). The Wolffian duct opens below into the urinogenital sinus (figs. 11 and 12).

The Müllerian ducts in embryos of 7–13 mm. develop at the fifth week as peritoneal involutions on the lateral aspects of the Wolffian bodies, running first to their outer edge and then to the inner surface. They course down and back in close relation to the Wolffian duct, and ultimately end blindly on the back of the urinogenital sinus, immediately above the Wolffian duct openings, and form there the eminence of Müller (fig. 11). The Müllerian duct, as Sedgwick long ago asserted, I consider to be probably of pronephric origin, for reasons to be afterwards given. Gregg Wilson's papers may be referred to for a summary on this point.

A very important point has now to be considered—viz., that in connection with the mesonephros a sexual gland develops, the future testis or ovary, as the case may be.

The indifferent sexual gland first arises in the human fœtus about the end of the first month (fig. 34). Nagel has figured it in fœtuses of 12 mm., and Coste has an excellent drawing of it at the same period. It is due to a thickening of the cœlomic epithelium over the mesonephros, and by the ingrowth of this epithelium the ova or seminiferous tubules, as the case may be, arise. In the male, tubules connect the Wolffian duct with the seminiferous tubules, and in this way the Wolffian duct becomes the seminal duct (epididymis and vas deferens). This phase of development in the male need not further concern us, especially as many of the points in regard to the development of the testis require elucidation. As to the development of the ova and Graafian follicles, a good deal of dispute exists; but the most generally accepted view is that the ova are derived from an indipping of the cells of the germ epithelium into the connective tissue of the ovary, and that the cells of the membrana granulosa have also a similar origin. Foulis, on the other hand, believes in an outgrowth of the stroma snaring in the germ-epithelium cells, and that the membrana granulosa cells arise from the connective tissue. My specimen of a month old shews the sexual gland present, and ova in course of formation.

B.—*The significance of the temporary development of the Wolffian bodies in the human Embryo.*

As is well known, the mesonephros has only a temporary development in the Amniota, but persists as a permanent kidney (kidney and testis in the male) in the Anamnia. Thus, in the human fœtus the mesonephros reaches its full development during the second month and then withers, leaving traces only, although the duct has a more permanent adult function. The question arises, therefore, Why do we get this temporary development in the human fœtus? Why does the true kidney not develop earlier?

The usual view is based on the Darwinian theory, and would regard the mesonephros as an ancestral inheritance, used, so far

as is necessary, in the development of the organs, but still ancestral.

The view I would advance is as follows: The development of the ovary and testis is one intimately bound up with that of the mesonephros. The mesonephros may, indeed, be considered as a sexual excretory organ. In the Amniota the development of the sexual organs is completed early in fœtal life, and the after function of the ovary or testis is to provide a comparatively small number of ova or spermatozoa at long intervals, in mammals at any rate.

In the Anamnia, however, the ovaries and testes produce a very large number of their characteristic products, and thus the great local activity of these organs leads to a retention of the mesonephros as an excretory organ in close vascular relations with the sexual organs.

The persistence of excessive ovarian and testicular activity in the Anamnia is to be associated with the persistence of the mesonephros.

On this point Noël Paton's researches on the Salmon are of value, and the following quotations put the matter briefly:—

"Yearly, or at longer intervals, the fish appear on our coasts, apparently from the deeper waters, and ascend the rivers there somewhere between October and January to deposit their spawn milt. Having done so, they descend the river as kelts and again disappear in the sea, to return either in the same or in the following year to the fresh water.

"What force urges the fish to leave its rich feeding ground in the sea? Is it necessary that it should enter fresh water in order to perform the act of reproduction? Does it require or procure any food during its sojourn in the river; and if not, how is it able to maintain life and to construct its rapidly growing genital organs? In the female the growth of these is enormous. In April or May the ovaries constitute only about 1·2 per cent. of the weight of the fish. In November they are no less than 23·3 per cent. In a fish of thirty pounds, in the spring they weigh about 120 grammes, in November they weigh over 2000 grammes. The increase in the testes in the male is not so marked, but is sufficiently striking. In April or May their organs are about 0·15 per cent. of the weight of the fish, while in November they are 3·3 per cent."

C.—*The ultimate development of the urinogenital organs in the male and female tract: the male and female analogues.*

In the fœtus, whatever be its sex, we have a double set of organs, viz., pronephros and mesonephros, with the mesonephric or Wolffian duct and the Müllerian ducts. We have now to discuss the ultimate development of these in the two sexes, and to state the analogous parts (fig. 34).

In the human female the Müllerian ducts form the Fallopian tube, uterus, and vagina, according to the generally accepted view.

From what I have already advanced, I regard this as only in part correct, and would modify it as follows. The Fallopian tubes, uterus, and upper two-thirds of the vagina are Müllerian, the lower third of the vagina is blended urinogenital sinus and Wolffian ducts. The hymen is developed from the lower ends of the Wolffian ducts. Inasmuch, therefore, as the hymen is developed from the Wolffian bulbs, as I have already indicated, it is evident that the hymen corresponds with the lower ends of the vasa deferentia in the male, and this gives us a most valuable point of comparison between the male and female urinogenital tracts. Hitherto there has been a want of exactitude in our knowledge, owing to the belief that the Wolffian ducts in the female disappeared in their lowest parts, and were therefore practically not represented in the female genital tract. In investigating this point I examined serial sections of male pelves between the second and third month, at the third and a half month, at the fourth month, and at the fourth and a half month. The following were the conditions found:—

(*a*) The apparent uterus masculinus at the second and third month is really due to fusion of the vasa deferentia.

(*b*) At the fourth month the prostatic gland had developed.

(*c*) At the fourth and a half month I found, near the termination of the vas deferens, a hitherto undescribed bulb of epithelium exactly like the Wolffian bulb of the female. It is remarkable indeed to note this bulb in the male with epithelial cells exactly like those of the adult vaginal mucous membrane. The vas deferens ended near, but not in it, in this specimen.

(*d*) The so-called sinus pocularis in the adult male seems to

me, therefore, not to represent the uterus, but the hymeneal end of the vagina, practically those parts of the Wolffian ducts which with the urinogenital sinus form, as I have indicated, the lower third of the vagina.

(*e*) The ducts known as Skene's ducts in the female urethra are really analogous to the prostatic glands of the male. They do not represent any part of Gärtner's canal (Wolffian duct), but are merely prostatic. Of this I have no doubt now. The prostatic glands in the male develop from the urinogenital sinus, and in the female the only prostatic element is to be found in Skene's ducts and the small glandular recesses seen round the urethral meatus.

I must point out, however, that it will be necessary to examine serial sections of full-time male and female fœtuses to determine more exactly the analogues of the seminal vesicles, and the more exact anatomy of the common ejaculatory ducts.

So far as I have traced the development in the male, the prostatic openings of the ejaculatory ducts are the lower ends of the Wolffian ducts.

The following table, modified from Quain, gives shortly the views advanced here as to the male and female genital analogues.

We may now trace the analogous parts more in detail. From what I have already said it is evident that the analogues of the female and male tract are most definitely settled in the upper portions. The disputed points are mainly as to the lower.

The fact that the analogue of the hymen is the vasa deferentia termination in the male colliculus seminalis, enables us, by superposition of diagrams of the early fœtal organs and fully developed adult ones in sagittal mesial sections, to clearly establish practically all the analogues. Thus from the hymen on along the vestibule to the glans clitoridis, is equivalent to all in the male urethra below the colliculus seminalis; and if the ventral surface of the male organ were split from this point to the urethral orifice, the female construction would be so far imitated. As to the analogue in the female of the vesiculæ seminales, I have not been able to settle this to my satisfaction, the best opinion yet advanced being that of Bland Sutton, who holds that Skene's tubules represent them. That the ovary and testis are analogues and homologues is evident, but in the

Table of Corresponding Parts of the Genito-Urinary Organs of the Two Sexes, and the Embryonic Organs from which they are developed. (Modified from Quain.)

	Embryonic Organ.	Female Organ.	Male Organ.
Genital Ridge:	Germinal Epithelium	Graafian Follicles and Ova	Epithelium of Seminiferous Tubules.
	Mesoblast of Ridge	Stroma of Ovary	Connective Tissue of Testicle.
Müllerian Duct:	Superior Extremity	Fimbriated Extremity of Fallopian Tube	Hydatids of Morgagni.
	Middle Part	Fallopian Tubes	Cornua Uteri Masculini, which sometimes occur.
	Inferior United Part	Uterus and Vagina (*upper two-thirds*)	Uterus Masculinus and Vagina (*two-thirds*).
Wolffian Body:	Superior Tubes	Smaller Tubes of Epöophoron; Parovarium	Vasa efferentia and Coni Vasculosi.
	Inferior Tubes	Paröophoron	Paradidymis (Organ of Giraldés).
	Outgrowths from Upper Malpighian Corpuscles	Interstitial cells near hilum of Ovary,	Walls of Seminiferous Tubules (?) and rete testis.
Wolffian Duct:	Superior and Middle Parts	Main Tube of Epöophoron	Vas deferens (in part).
	Inferior Part	Duct of Gartner	Vas deferens (in part).
	Lower Ends	*Wolffian Bulbs and Hymen*	*Colliculus seminalis.*
	Outgrowths from Posterior Part	Ureter; and uriniferous Tubules of Kidney	Ureter; and uriniferous Tubules of Kidney.
Urinogenital Sinus:	Upper Part	Urethra	Prostatic portion of Urethra, as far as Verumontanum.
	Middle Part	*Lower third of Vagina*	Lower prostatic and membranous part of Urethra.
	Lower Part	*Vestibule*	
	Epithelial involutions on each side of Sinus (lower end)	Glands of Bartholin	Glands of Cowper.
	Genital eminence and folds	Clitoris and Nymphæ	Penis.
	Integument on either side of orifice of Sinus	Labia Majora	Scrotum.
	Outgrowths from Upper Part	*Skene's Ducts*	Prostate.

(The italicised parts show the modifications advanced.)

present state of dispute as to the development, it would be rash to attempt to push analogies here in detail. In regard to the urinogenital sinus, it has to be noted that in the early fœtus we have as its upper boundary where the eminence of Müller lies, on its posterior wall. The hymen forms at the Wolffian ducts opening, and not at the eminence of Müller, as usually stated. I think it probable that the Wolffian bulbs block the urinogenital sinus, and that the lumen is re-established as a double one, urethral and vaginal, by involutions from the sinus below. Thus in the female, the vestibule, lower third of the vagina, and lower end of the urethra represent the original sinus urinogenitalis. In the male, of course, all below the colliculus seminalis represents it, with this difference that it forms a real canal, and not practically a hypospadias as in the female, the penis being greatly developed as compared with the clitoris. The upper portion of the urethra and the bladder in the female, and all above the sinus pocularis in the male, are of course derived from primitive gut and allantois.

I need hardly indicate that the labia majora represent the scrotum split sagittally and mesially, and that the labia minora are the ununited edges of the urethral groove.

Above the colliculus seminalis the task of identification of the analogues is fairly easy. No part of the vas deferens is normally represented in the human female until we come to the interval between tube and ovary, where we have the main tube and tubules of the epöophoron (parovarium). The tubules of the Wolffian body are represented in the female by the paröophoron tubules at the hilum, and by the epöophoron or parovarium higher up.

In the male we get remnants of the Wolffian body in connection with the testicle, the well-known organ of Giraldés, or paradidymis. The ducts of Müller, strictly speaking, are not in my opinion represented in the male at all, except by the hydatids of Morgagni and the rare cornua uteri or uterus and vagina occasionally found. (Primrose.)

The sinus pocularis represents, I believe, the junction of Wolffian ducts and part of urinogenital sinus. Of course, if one holds to the vagina being Müllerian in all its extent, the sinus pocularis will represent the lower part of the Müllerian ducts.

We have now to try to understand the reason for this apparently extraordinary development of the genital organs. It seems remarkable that we should have apparently a double genital tract to start with, and that each sex should, in its adult and normal condition, retain traces, so far as we know, functionless, of the opposite sex.

In the early human embryo we have a very remarkable condition present, which I may recapitulate as follows :—

1. A very rudimentary pronephros or head kidney (?).
2. A well-marked mesonephros, or Wolffian body proper, with a duct.
3. An indifferent sexual gland developed in connection with the mesonephros. When this is an ovary, we get—
4. A special female genital duct, the Müllerian retained. Should this gland be a testis, we get—
5. The Wolffian duct persisting as its vas deferens.

This, however, does not exhaust the peculiarities, as we find that when the sex is female we get parts of the mesonephros and its duct normally persisting as well-marked vestiges, and aiding in hymeneal and vaginal development, as I have already described. When, however, the fœtus is of the male sex, we get hardly any trace of the Müllerian duct except Morgagni's hydatid; that is to say, the adult female has more representative traces of the male sex than the male sex has of the female. This seems to me very remarkable, and worth investigation.

The testis and vas deferens develop from or in connection with the mesonephros, which is the strongly developed portion of the Wolffian bodies. What develops the Müllerian duct or its Anlage? The present current answer is that the Müllerian duct develops later than the Wolffian, and apparently is developed by an invagination of the cœlomic epithelium, *i.e.*, of the epithelium of the peritoneal cavity. As I have already hinted, it may develop from the rudimentary pronephros as in some of the lower mammals. At any rate, the Fallopian tube and ovary are formed on a Wolffian type, as we have the funnel-shaped opening and the duct passing down as uterus and vagina, finally to blend with the Wolffian duct at the hymen. It has,

of course, long been held by some observers that the duct of Müller was pronephric. (Sedgwick.)

We may say, then, that the early fœtus is not hermaphroditic or double-sexed. There is never ovary and testis, but only an indifferent gland at first. The essential point seems to be that we first get the Wolffian bodies or temporary kidneys formed, and these are developed apparently as sexual kidneys, which wither in advanced vertebrates when the ova and spermatozoa are fairly formed. They are utilised, as far as possible, in the development of the conducting parts of the genital tract, and thus from pronephric epithelium the Müllerian duct probably arises, while the whole of the mesonephric duct and part of the mesonephric tubules are utilised for the testis.

The conducting part of the genital tract is thus practically an adaptation of the Wolffian scaffolding, and the persistence in the female of such well-marked functionless portions as the epöophoron and paröophoron is to be associated with the fact that the mesonephros is the best developed part of the Wolffian body, its duct is taking part in the development of the female fœtus as late as the third and a half month. If we grant the pronephric Anlage of the Müllerian duct, the more marked atrophy of the latter in the male is to be correlated with its origin from a more rudimentary part of the Wolffian system.

D.—*The homology of the male and female sexual function.*

An interesting parallel can be drawn between the male and female sexual functions. The female supplies an ovum which is discharged along the Fallopian tube, and, if impregnated, is developed, as a rule, in the uterus. The ovum is a modified cell from the specialised cœlomic epithelium, *i.e.* is a peritoneal cell, and is passed along a duct which, if not pronephric, is at least modelled on a pronephric or mesonephric type. The discharge of the ovum is probably a specialised Wolffian function. The spermatozoon is also part of a modified peritoneal cell, and is discharged along the vas deferens, *i.e.* Wolffian duct. The discharge of the spermatozoon is thus practically a specialised Wolffian function.

VII. The Relation of the Views Advanced to Certain Developmental Arrests in the Urinogenital Tract.

I take up only those cases which are, for whatever reason, permanent developmental arrests, and I consider specially only some of the rarer ones which have come under my own personal observation. For clearness, however, I shall repeat a resumé of normal developmental stages. Normal development may be summed up as follows:—

Stage.	*Date.*
1. Division of primitive gut into bladder, rectum, and urinogenital sinus; cloacal membrane present; withering of end gut (pars ultima), ...	20th to 23rd day.
2. Communication of pelvic end of urethra and rectum with exterior by formation of ectodermic plug; its breaking down, and thus existence of ectodermic cloaca,	4th to 6th week.
3. Closure of cloaca by Reichel's Anal-höcker, ...	7th to 8th „
4. Urinogenital sinus completely formed with ducts of Müller related to it, and Wolffian ducts opening into it, . .	8th to 9th „
5. Hymen formed, anus formed, preputium clitoridis in course of formation; Müllerian vagina being relined from Wolffian bulbs, ...	3rd and 4th month.

I need not recapitulate the well-known facts as to the appearance of the ducts of Müller, and their time of fusion so as to form the uterus and tubes (*vide* Hart and Barbour, 5th edit., p. 291).

The special malformations I have been able to study belong mainly to the rarer forms, and comprise—

1. *Fœtus without urinogenital system.*
2. *A pediculated tumour attached to the perineal region of a female infant, which on removal and microscopical examination proved to be a piece of isolated bowel, probably persistent end-gut.*
3. *Two cases of transverse septum vaginæ dividing the vagina into a lower third and upper two-thirds.*
4. *A case of atresia of the lower third of the vagina, the rest of the tract being developed.*

5. *Case of vertical ridge on the anterior vaginal wall, with another corresponding ridge on the upper two-thirds of the posterior vaginal wall.*

1. *Fœtus with no urinogenital system.*—This remarkable specimen, for which I am indebted to Mr Miles, was an eight-months' fœtus with no permanent anus, and no representative of external genitals except a strap-like projection of skin from the pubes about an inch long.

On sagittal mesial section I found no bladder, only primitive gut; a rudimentary allantois above the pubes, no internal genitals, and no ureters or kidneys.

I do not purpose discussing this remarkable case fully, but merely point out that it justifies—

(1) The consideration of the urinogenital organs as forming a correlated system.

(2) The views of Lieberkühn and Keibel as to the development and origin of bladder.

These investigators derive it from the primitive gut, and only its apex from the allantois. If in this case we had some early destruction of Wolffian duct, it would account for the absence of ureter and kidney. In some cases, however, a rudimentary kidney has been noted by Ballantyne, and this points to the kidney not being entirely a Wolffian duct derivative. The non-division of the primitive gut into its rectal and bladder portions is difficult to explain.

2. *A pediculated tumour attached to the perineal region of a female infant, which on removal and microscopical examination proved to be a piece of isolated bowel, probably persistent end-gut.* —This rare and, so far as I know at present, unique case occurred in the practice of Dr Inch of Gorebridge. When I saw it with him, the child was a week old and was in every respect healthy and normal, except that while it had the genitals of a female child, there was attached to the skin surface between anus and vagina what seemed to be a scrotum with an anterior opening, into which a probe passed for a short distance.

The annexed diagram (fig. 36) shows that the child had the external female genitals normally developed, except that the preputium clitoridis was split into two halves. So far as I

could ascertain, the cavity of this tumour communicated with no organ, and gave no secretion. It seemed to me to be scrotal at any rate, with or without testicle, and I thought it best to consider matters before removal. I could find no such case recorded, and could advance no thorough explanation of its nature. As the parents were greatly distressed at this strange malformation, and as I was certain it had no communication with any organ or with peritoneum, I ultimately removed it, first transfixing and ligaturing the neck. The child did not suffer afterwards, and is now quite well. On laying open the tumour, I found the cavity already alluded to, but nothing else except fat and skin.

On microscopical examination I was very much astonished to find the cavity lined with Lieberkühnian follicles, and no testicular tissue present. We have, therefore, to explain the strange anomaly of such a rare and unusual condition.

If we take Keibel's diagrams (figs. 1 and 2) of the lower end of an early human fœtus 3 mm. long, we see displayed the structure known as the cloacal membrane. This is the anterior boundary of the part of the primitive gut known as the entodermal cloaca, from which, as I have already explained, the rectum and bladder are formed by coronal partitions (figs. 6–9). This cloacal membrane extends from the root of the navel back to the top of the portion of the primitive gut, which atrophies usually. The aberrant tumour I have just described seems to me to be the persistent end-gut; and if this be the case it is of importance as helping to determine the posterior end of the cloacal membrane.

The value of my case, if my view be right, is this, that it establishes in the new-born child the posterior boundary to which the cloacal membrane extends, viz., to the vagina. It also shows that the split clitoris is not a proof that the glans develops from two halves originally.

3. *Two cases of transverse septum vaginæ dividing the vagina into a lower third and upper two-thirds.*—This is the rarer form of so-called atresia hymenalis vaginæ. We have the external genitals developed normally, a hymen present as in one of my cases where the patient was a girl at puberty, with the vagina apparently an inch long, and evident pressure symptoms and retention of urine. When I saw her the urinary retention had

been relieved, and there had been a discharge of much tarry blood from the vagina. As a tumour had previously protruded at the vulvar orifice, I examined carefully, and found the hymen and external genitals developed, while an inch from the hymeneal edge a transverse septum could be felt with a lacerated tear through its substance on the left side. When this laceration was dilated I could pass my finger into the rest of the vaginal canal—the real Müllerian portion. The rest of the genital tract was normal.

The second case was that of an adult woman who had menstruated scantily and with pain. In her the same condition of a transverse septum an inch from the hymen existed, and of the condition I was able to take a cast. There was evidently a small aperture in the septum, as I could dilate a sinus and make a lateral canal admitting the finger. I did not detect a cervix. The uterus bimanually seemed unicornuous, and the ovaries were both present.

Each of these cases had, therefore, the lower third of the vagina present—*i.e.*, that part derived from the blending of the urinogenital sinus and Wolffian ducts. Such cases are only to be understood in the light of the origin of the vagina as brought forward in the present investigation.

4. *Case of atresia of the lower third of the vagina, the rest of the tract being developed.*—In this case, that of a prostitute in the Royal Infirmary, whom I saw through the kindness of Mr Caird, there was an interesting persistence of a vertical ridge both on the anterior and posterior vaginal walls. The ridges differed, inasmuch as the posterior one ceased about an inch from the vaginal entrance, while that on the anterior wall ran along the whole distance, and had quite an excrescence at its lower end. The ridge on the posterior wall probably represented the remains of the Müllerian septum, while that on the anterior was the remains of the septum between the Müllerian ducts and Wolffian bulbs.

We can thus give the probable antenatal date of the deformities recorded:—

1. Congenital perineal bowel tumour in 3rd–4th week.
2. Septum vaginæ (transverse), 6th week–8th week.
3. Vertical ridges, 4th week.

VIII. On the Nature and Development of Mucous Membranes.

There is admitted difficulty in defining what we mean by 'mucous membrane'; and Bland Sutton states that practically there is no difference between skin and mucous membrane. Hair, he believes, can grow on mucous membrane; and in his work on Dermoids he considers the Graafian follicles as practically mucous follicles—*i.e.*, with the power of producing skin products.

A study of the development of the prepuce of the clitoris and penis, and of the development of the permanent lining of the vagina, seems to me to throw some light on this question, and therefore I purpose to consider it at this stage. I accordingly consider—

(1) *The behaviour of mucous membranes when everted.*

(2) *The development of the anus and of the prepuce of the clitoris and penis.*

(1) *The behaviour of mucous membranes when everted.*—The gynæcologist has good opportunity of observing this in certain clinical cases. Thus, in prolapsus uteri and in tears of the perineum sufficiently extensive to involve the anus and rectum, he can observe how the exposed mucous membranes alter or remain moist when exposed to unusual friction or irritation.

The vaginal lining is generally described as mucous membrane, although many consider it as more correctly presenting greater affinity to skin. In the natural condition its free surfaces are moist and rose-coloured, but when these are everted, as in prolapsus uteri, they take on all the dryness and appearance of ordinary skin. The same holds good for the glans penis after circumcision. In marked contrast with this is the condition of the rectal mucous membrane in complete anal tear. Here the everted mucous membrane of the rectum retains its fresh red colour and moisture, and never approximates in appearance to skin. The anal lining, however, is hardly distinguishable from skin. All these surfaces are, however, indiscriminately classed as mucous membranes, although their behaviour under altered conditions of friction and pressure is so different; and the question may be asked, What is it that makes the difference? The

answer to this involves some questions of development which we must now recapitulate.

(2) *The development of the anus and of the prepuce of the clitoris and penis.*—The lining of the rectum is a hypoblastic structure, while that of the anus is epiblastic. In the three and a half months' fœtus one can see the epidermis passing in at the anal site, and at the top of the anus gradually passing into that of the Lieberkühnian follicles (fig. 19). The superficial cells of the epidermis so passing in are necessarily central, and as they desquamate, form the lumen.

The views advanced by embryologists as to the development of the prepuce are discordant, and in some respects unintelligible. Milnes Marshall, for instance, says: "The prepuce appears towards the end of the third month as a fold of skin round the base of the glans, and is at first interrupted ventrally by the urethral groove" (p. 597, 1893). Minot (pp. 517–9, edit. 1897) gives two accurate, though rather ill-defined drawings, and says: "The prepuce appears as a slight ridge which overgrows the glans, the epithelium of the inner surface uniting as the fold blends with the epithelium of the glans—the two epithelia fusing into one solid plate."

With this description I disagree, and the account I urge as a more correct one is already given at page 339.

There is thus a close parallel between this development of the prepuce and that of the vaginal lining. The vaginal lining is derived from the Wolffian bulbs, and they render the previous Müllerian lumen of the vagina solid, and when central desquamation takes place a fresh lumen is formed. The Wolffian bulbs are of course epiblastic in origin (*vide* p. 341).

To understand the difference in behaviour of the mucous membranes when exposed to pressure, we must remember their origin. The so-called mucous membranes of the inner surface of the prepuce, anus, and vagina are epiblastic in origin, and revert to epidermis when eversion is permanent. They should be thus classed as epiblastic mucous membranes or mucocutaneous surfaces (Turner). Rectal mucous membrane, on the other hand, is hypoblastic in origin, is a true mucous membrane with a mucous secretion, and takes on no squamous character when everted permanently.

In regard to the relining of the vagina from the Wolffian bulbs, I wish to point out that in the ureter and bladder we have a mucuous membrane made up of a many-layered epithelium. The interesting query suggests itself as to the origin of this lining. The ureter splits off from the Wolffian duct and is thus epiblastic. The bladder, however, is allantoic at its apex, derived in the main from the primitive gut (*vide* postea, p. 381), and is thus hypoblastic in origin. Is it relined through the epiblastic ureter as the vagina is through the Wolffian duct? It would be interesting to know what naked-eye changes took place in that mucous membrane of extroverted bladder after the ureters had been transplanted with the rectum. Probably the exposed bladder would become skin-like and lose its moist condition.

IX. Summary.

1. The genital organs in the adult mammal arise from, and in connection with, the Wolffian bodies, the Wolffian duct and the ducts of Müller.

2. In the lowest female mammal examined (rat kangaroo as type of Marsupials) the urinogenital ducts are least modified; *the Wolffian ducts being represented by the lateral vaginal canals and epöophoron, while the paröophoron is present as a duct in the centre of the ovary.* The Müllerian ducts are present as the Fallopian tubes and uterine cornua, while the central vaginal canal represents the rest of the Müllerian tract. The urinogenital sinus is present apparently unaltered, and the whole arrangement is like the human fœtal condition at the sixth to the seventh week.

3. In the adult human female the genital tract has the Wolffian body represented by the epöophoron (normally present) and by traces of the paröophoron at the hilum of the ovary. The Wolffian duct is represented normally near the epöophoron and rarely by occasional traces in the broad ligament and uterus. The lowest segment of the vaginal portion of the Wolffian duct forms the hymen by the coalescence of bulbous proliferations there, and cells from these replace the primitive lining of the Müllerian vagina.

The vagina is Müllerian only in its upper two-thirds; the

lower third is formed by the coalescence of the Wolffian bulbs and urinogenital sinus.

4. Between the lowest and highest female mammals there are gradations in the representation of the Wolffian ducts in the genital tract. This still requires determination. It is known that the Wolffian ducts persist to a marked extent in the cow and sow (Gartner's canal), and additional mammals must therefore be examined as to the point.

5. The colliculus seminalis of the adult human male is the analogue of the hymen and lower third of the vagina. The Müllerian ducts are not represented in the adult human male so far as is known—except by the hydatid of Morgagni and some rudiments near the testis.

6. Skene's ducts in the female urethra are prostatic analogues, but the nature and analogues of the vesiculæ seminales are as yet not accurately determined.

7. The spermatzoon is a specialised pleuro-peritoneal cell. and its excretion is practically a specialised Wolffian function.

8. The ovum is a specialised pleuro-peritoneal cell, but its excretion is along a duct formed later than the Wolffian one, and cannot be represented as a specialised Wolffian function, unless we hold that the Müllerian duct has a pronephric Anlage.

9. In the formation of the lumina of the preputium clitoridis, vagina, male urethra (spongy portion and glans), and permanent anus, the epidermis between the 2nd and 4th month of fœtal life is the active agent. First a solid plug of epidermis passes in, with its superficial cells central, its more active ones deep; desquamation of the central cells ensues, and thus the lumen remains lined with cells of an ectodermic origin.

10. True mucous membrane is hypoblastic in origin.

DESCRIPTION OF PLATES XXXV., XXXVI.

Fig. 1. Vertical mesial section of caudal end of 4·2 mm. fœtus (Keibel). Note formation of primitive gut with Wolffian duct opening into posterior part: cloacal membrane, *a*, is anterior boundary of entodermal cloaca (pars penultima of primitive gut); tail gut, *b*, present.

Fig. 2. Blastula stage of Amphioxus (Hatschek), $\frac{220}{1}$.

Fig. 3. Gastrula stage of Amphioxus (Hatschek), $\frac{220}{1}$.

Fig. 4. Dorsal view of 2 mm. human embryo, $\frac{14}{1}$. P.S., primitive streak; N.T., neurenteric canal entering yolk sac; N.G., neural groove; H.P., head end of embryo, $\frac{14}{1}$ (Graf Spee).

Fig. 5. Embryo, H.*s.f.*, 6·5 mm.,; *a*, tail gut withering; *b*, ureter budding off from Wolffian duct (Keibel).

Figs. 6–9. T.S. of 4·2 mm., human embryo, showing stages of division by coronal partition of primitive gut into rectum and bladder (Keibel); *r*, rectum; *b*, bladder.

Fig. 10. To show view that bladder originates from allantois (Allen Thomson). *r*, rectum; *b*, bladder; *u.g.s.*, urinogenital sinus.

Fig. 11. Genital cord in 6–7 weeks embryo (30 mm.), showing in front the urinogenital sinus with eminence of Müller, *below* which the hymen forms (T.S.); *s*, urinogenital sinus; W, Wolffian duct; *m*, duct of Müller.

Fig. 12. Genital cord immediately below that of fig. 11 (T.S.) shows urinogenital sinus with Wolffian ducts opening into it. This is site of future hymen.

Fig. 13. Genital cord below that of fig. 12 (T.S.), to show Anlage of H-shape of adult vagina near vaginal orifice; urinogenital sinus in front, and behind, Wolffian ducts on each side of canal of coalesced Müllerian ducts.

Fig. 14. T.S. of 6–7 weeks embryo to show kidney and Wolffian body. *k*, kidney; W.B., Wolffian body.

Fig. 15. T.S. of 6–7 weeks embryo to show ovary formed on Wolffian body. *o*, ovary; W.B., Wolffian body.

Fig. 16. Vertical mesial section of fœtal rabbit, 10 mm., 13th day, to show primitive gut with partition forming to divide off bladder and rectum, and passing down to meet epidermic plug (Retterer).

Fig. 17. Vertical mesial section of tail end of rabbit, 14th day, showing division of primitive gut into rectum and bladder, and union of partition with epidermic plug (Retterer). *e.p.*, epidermic plug.

Fig. 18. Sagittal mesial section of human embryo, 25 mm., to show ectodermic cloaca, *c.l.* (Tourneux).

Fig. 19. Development of permanent anus by inward passage of epidermis, and central desquamation at about third month. *a*, anus; *r*, rectum.

Fig. 20. Sagittal mesial section of three and a half months embryo to show formation of prepuce of the clitoris and development of hymen. S U G, urinogenital sinus (part to form vestibule); W.B., Wolffian bulb; UR, urethra; *ep.*, epidermic plug to form prepuce ($\frac{8}{1}$).

Fig. 21. Wolffian bulbs; note Wolffian duct ending in smaller one. W.D., Wolffian duct ($\frac{200}{1}$).

Fig. 22. Coronal section of pelvis of four and a half months fœtus in line of pubic arch, to show hymen. Note two lateral parts of hymen, one from each Wolffian bulb. H, hymen; B.*g.*, Bartholinian gland.

Fig. 23. Outline of formation of vagina, showing upper two-thirds originating from the ducts of Müller, the lower third from urinogenital sinus and Wolffian bulbs. *c.c.*, cervical canal; A, Müllerian part; B, part derived from Wolffian bulbs and urinogenital sinus.

Figs. 24 and 25 show sagittal mesial section of penis of three and a half months fœtus. Fig. 25 shows epidermis (*a*) passing in behind fraenum under a higher power.

Fig. 26. Section of glans penis, showing formation of prepuce and tunnelling of glans, near full time. *p*, prepuce; *ur*, urethra.

Fig. 27. Genital tract of Rat Kangaroo. K, kidney; U, ureter; C, cornu; *l.c.*, lateral canal; *m*, central part.

Fig. 28. Genital tract of Macropus Benneti (Brass).

Fig. 29. Genital tract of Wombat (Brass).

Fig. 30. Uterus of Rat Kangaroo to show mucous membrane (*m*).

Fig. 31. Genital cord of Rat Kangaroo. *l.c.*, lateral canal; *m*, central vagina; *u.r.*, urethra.

Fig. 32. Sagittal lateral section of four weeks human embryo (10 mm.) to show Wolffian body. Note apparent pronephric tubule (*a*) at top of Wolffian body. Tubules, glomeruli, and duct of mesonephros are seen. W.D., Wolffian duct.

Fig. 33. Pronephric tubule of above.

Fig. 34. Nagel's diagram of urinogenital organs in human embryo, *modified by prolongation of lower ends of Wolffian ducts.* *m.d.*, Müller's duct; *w.d.*, Wolffian duct; *w*, Wolffian body; *s.g.*, Sexual gland; *w.b.*, Wolffian bulbs.

Fig. 35. Ovary and tube of Rat Kangaroo, with Wolffian duct (W) in centre of ovary.

Fig. 36. Diagram of persistent end-gut in new-born child. *a*, tumour with lumen; *b*, vaginal entrance; *c*, labium majus.

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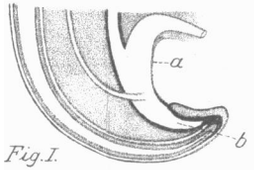
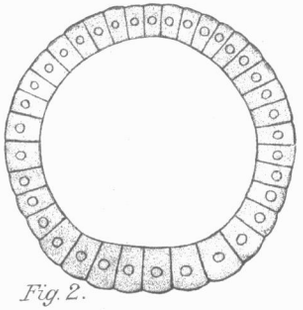


Fig. I.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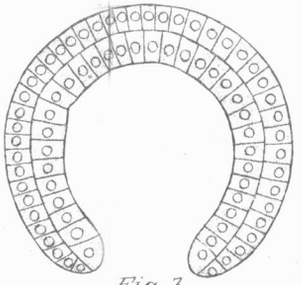
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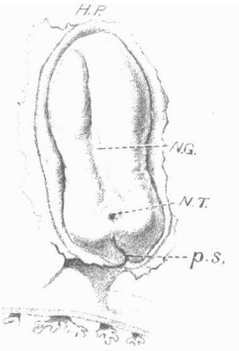

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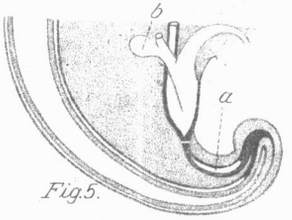

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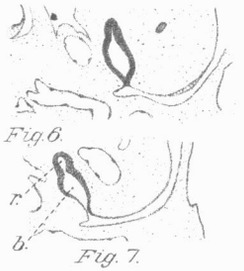

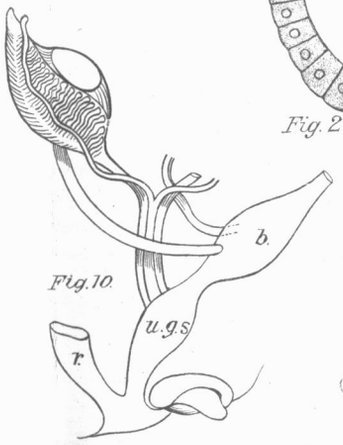

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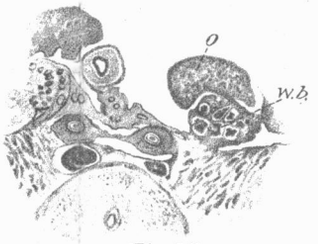


Fig. 15.


Fig. 8.

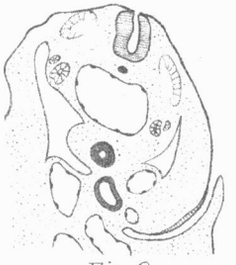
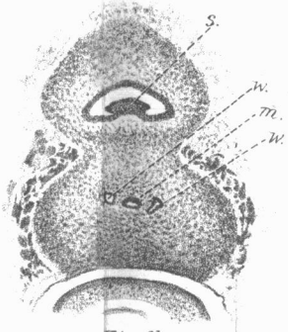


Fig. 9.


Fig. 13.

Fig. 18.



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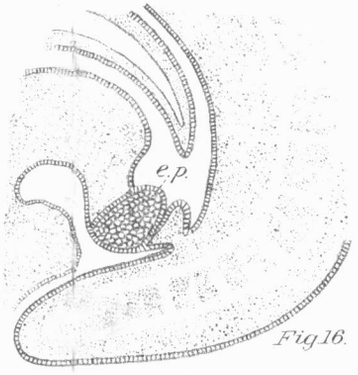

Fig. 16.

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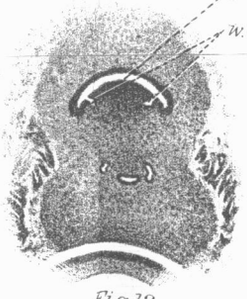
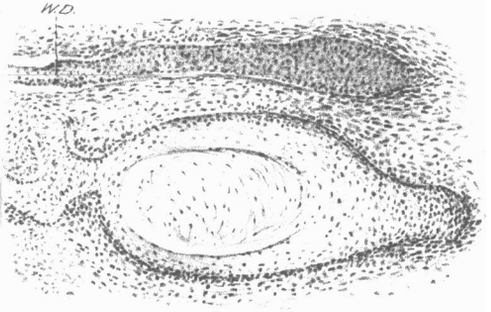


Fig. 12.

Fig. 14.

Fig. 17.

Fig. 20.



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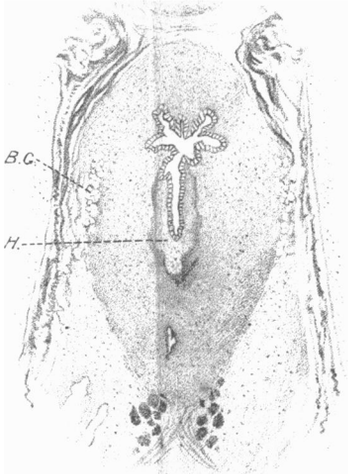

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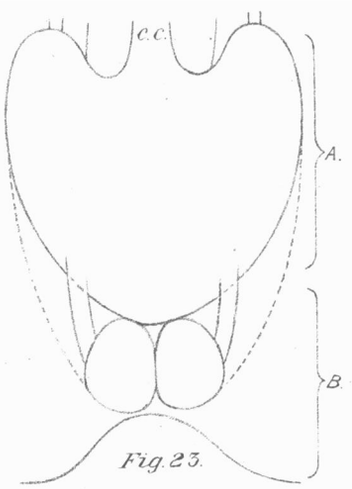

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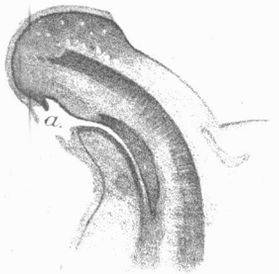
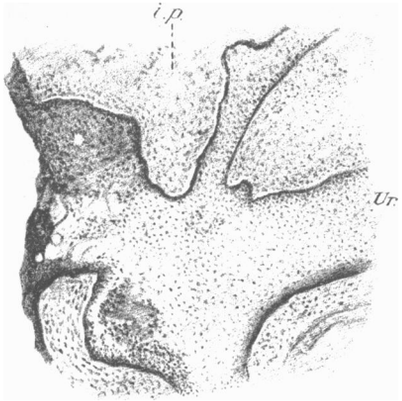


Fig. 24.

Fig. 25.



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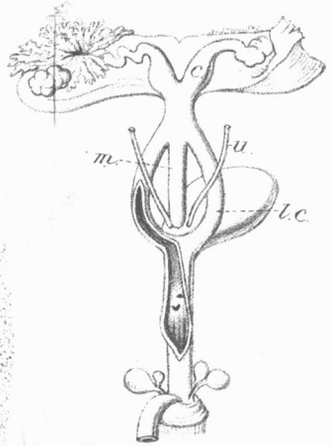

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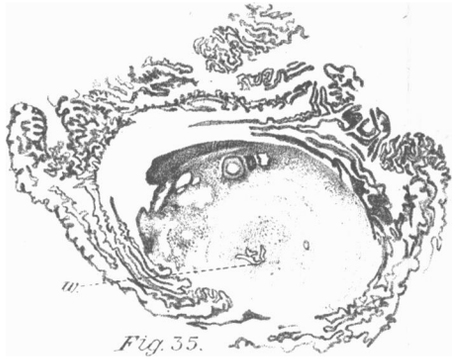

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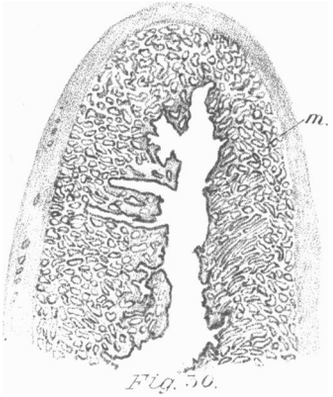

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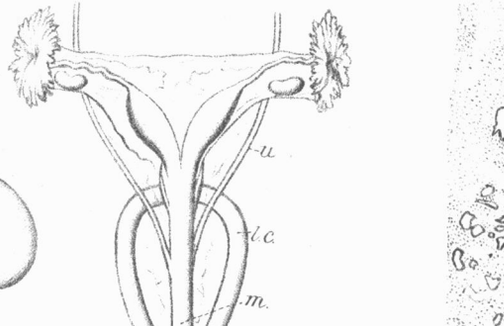

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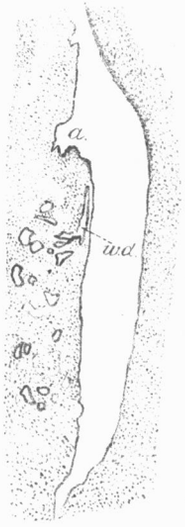

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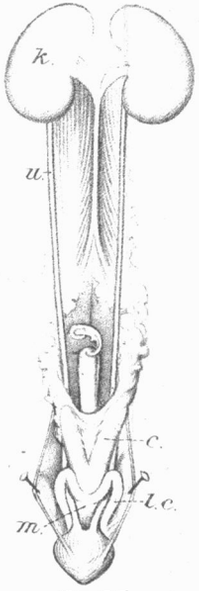

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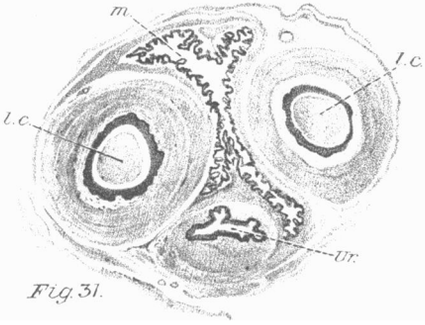

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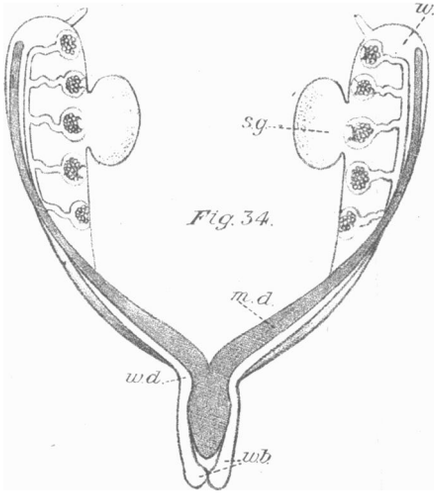

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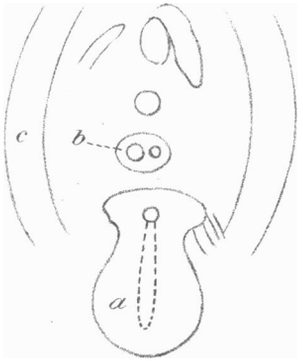

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