THE STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS OF THE FEMALE AFRICAN ELEPHANT

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[Plates 15 to 18]

CONTENTS

The anatomy of the reproductive tract has been studied in several foetuses and one young calf.

The external genitalia are characterized by the position of the vulva immediately behind the umbilicus, and a long urogenital canal extending from the vulva to the vaginal opening, which is within the pelvic girdle. The clitoris is relatively large; its tip is partially enveloped in a fold of skin which is referred to as a preputial fold by some writers, but no true prepuce is formed in either sex.

The uterine horns of the foetus traverse a 'ram's horn' flexure such as is found in many ungulates, and the mesometrium is produced into elaborate lappets the significance of which is not known.

The blood vessels in the region of the kidneys and ovaries were found to be complex and variable in plan. The abdominal reproductive organs are described.

The external musculature of the reproductive tract is described. The retractor clitoris (penis) muscle is of unusual form; the muscles of right and left sides do not meet below the rectum and they do not extend far along the genital canal. The ischio-cavernosus muscle is prominent, as is the levator clitoris muscle which appears to have an important function. These muscles are of comparable size and identical disposition in both sexes, at least in foetal stages. The arrangement is contrasted with that in the horse and with that in the hyena, and the significance of the differences is discussed. The bulbo-cavernosus muscle is similar in disposition in both sexes but it is smaller in the female, where the corpus spongiosum is much less prominent. The urethral muscle (compressor of Cowper's gland) is absent from the female, where Cowper's gland is relatively minute.

A corpus spongiosum is present in the female and is fairly prominent in the foetus, though not comparable in bulk with that of the male. It does not extend to the tip of the clitoris (or of the penis in the male) but does partially invest this organ near its tip by a lateral extension which is served by an elaborate network of nerves and blood vessels homologous with, and similar to, the blood and nerve supply of the true glans penis typical of many mammals.

The corpora cavernosa of the clitoris are invested by a thick tunica albuginea, which also invests the strong median tendon into which the levator muscles insert, and extends part way around the roof of the urogenital canal.

The two separate uterine cornua unite to form the body of the uterus but the lumina remain separate for most of its length. Implantation usually occurs in this part of the uterus. The two lumina open simply into a common cavity which in turn opens into the vagina, the os uteri being marked by a relatively massive papilla and a prominent sphincter muscle in the foetus. The obstruction evidently becomes progressively less prominent as development proceeds.

The vaginal opening into the urogenital canal is complex in early stages and in some foetuses the opening was not patent. The canals of Gaertner were identified in the foetus and were also found in the calf, where they were relatively minute.

Introduction

The general anatomy of the elephant, other than that of the skeleton, has not yet been described in detail. The reproductive organs of the male have been very much more fully described than those of the female, largely because Dr N. B. Eales's foetal specimen of *Loxodonta africana* was a male, and Schulte (1937) described the urino-genital system of an adult male Indian elephant. Petit (1924) contributed a note on the openings of the vas deferens and the ducts of the seminal vesicles. Neuville (1937) reviewed existing accounts of the female reproductive organs of African and Indian elephants and added some observations regarding the external genital opening. These accounts apparently comprise everything published on the subject between the year 1900 and the present writer's contribution (Perry 1953), giving a brief account of the structure of the female reproductive tract of the African elephant and discussing points raised by Neuville. Among earlier accounts, those of Watson (1872 to 1875 on the male, and 1881 and 1883 on the female) are particularly useful. The only foetal material hitherto described in detail consists of the single specimen dissected by Eales (1925 to 1929) to whose account extensive reference will be made below in comparing the female with the male in respect of the homologies of the reproductive organs. The present paper is based on the dissection of several foetal specimens of *Loxodonta* and one very young calf. Dr Eales's observations have been confirmed in many particulars and contradicted in none, and it is hoped that this account may supplement her work in some respects.

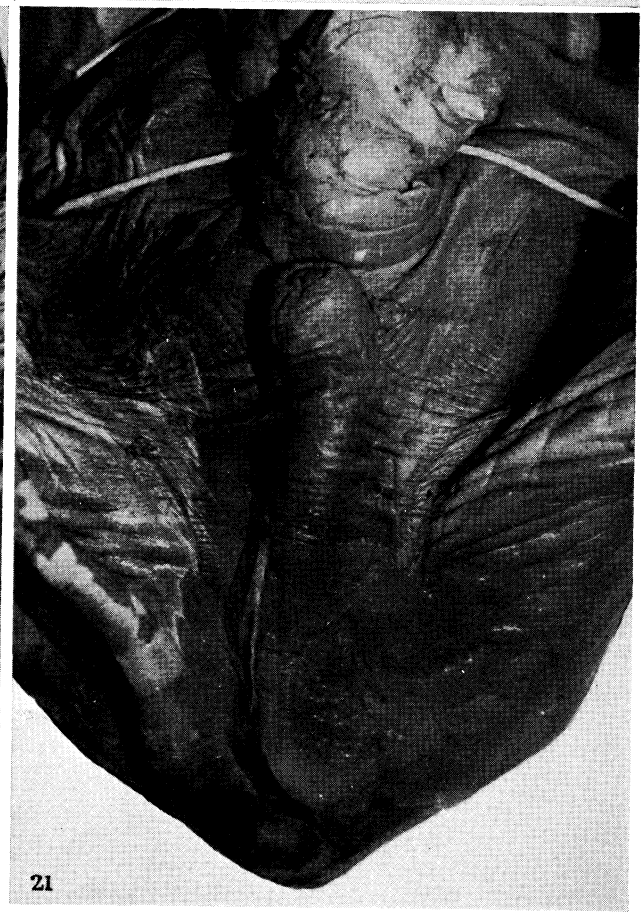
Material

The abdominal and pelvic region of a 3 kg foetus (E147f) shown in figure 19, plate 15, was dissected in some detail. The observations were supplemented by the dissection, and by transverse sections, of the reproductive tracts of a 2 kg foetus (E15f) figure 18, plate 15, and one of 6 kg (E138f) after their removal from the specimen. A very young female calf (E119) was obtained in Africa and its reproductive tract was dissected out in the field immediately after death, photographed (figure 23, plate 16) and preserved in formalin for transport to England. Transections and histological preparations of this specimen have been made.

The development of the ovaries and of the peritoneal structures associated with them has been described in a previous paper (Perry 1953). The foetal gonad undergoes great enlargement in late pregnancy, presumably under the influence of maternal hormone. The ovary and testis of a late foetus were compared with the ovary of a young calf (E134, a little younger than E119, referred to above), the foetal gonads being about four times as heavy as those of the young calf. The foetuses used in the present study were at a considerably earlier stage of gestation than that at which this gonadal enlargement occurs.

The external genitalia

The genital tract of the female elephant is carried round the perineal region to open under the belly at a position very similar to that of the tip of the penis of the male. The vaginal orifice is within the pelvic girdle, and the perineal and abdominal part of the tract



FIGURES 18, 19. Two of the female foetuses referred to in the text. E15f (figure 18) weighed about 2 kg. E147f (figure 19) weighed about 3 kg. Both to same scale (× approx. $\frac{1}{3}$).

FIGURE 20. The perineal region of the specimen shown in figure 19 (slightly reduced).

FIGURE 21. The perineal region of a male foetus (E60f) weighing about 3·5 kg. Scale as figure 20.

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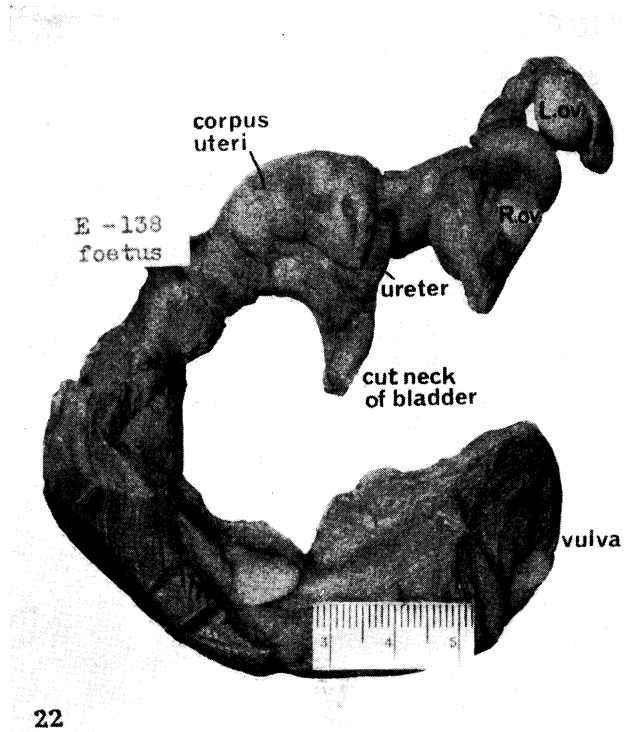
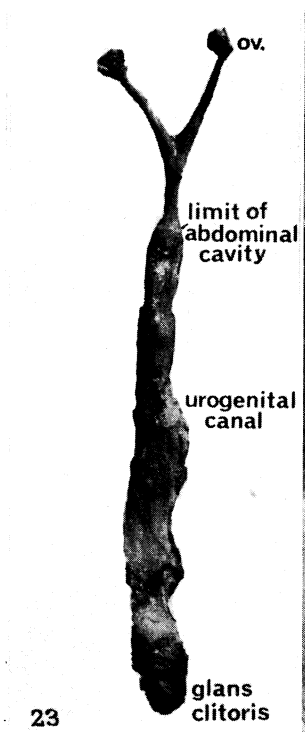




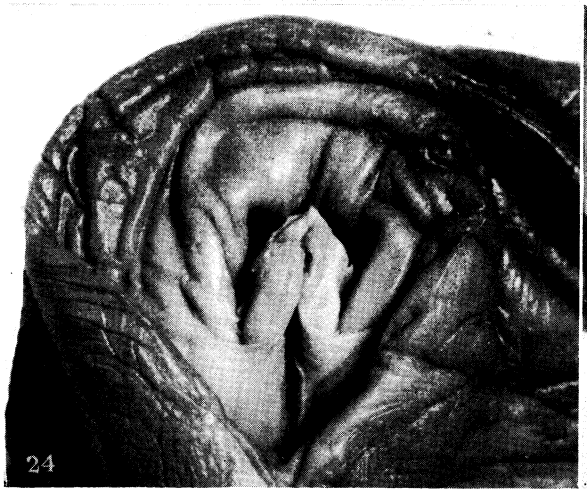


FIGURE 22. Reproductive tract of a female foetus (E 138f) from the right lateral aspect. ($\times \frac{4}{5}$.)

FIGURE 23. Reproductive tract of a young calf (E119) photographed from the dorsal aspect after dissection in the field. The diagrammatic drawings in figures 3 to 17 are from this specimen. Measurements are given in the text. ($\times \frac{1}{9}$ approx.)

FIGURE 24. Vulval region of a 6 kg female foetus (E138f) ($\times 3$ approx.).

FIGURE 25. Perineal region of a male foetus (E20f) of about 50 g. (Scale as figure 24.)

FIGURE 26. The 'ram's horn' flexure in the uterine horns (E147f), showing the 'mesometrial lappets'. ($\times \frac{1}{5}$.)

FIGURE 27. Abdominal cavity of a female foetus (E147f) opened in front of the umbilicus. Rectum cut across; liver and alimentary canal removed. (Approx. actual size; see text.)

FIGURE 28. Further dissection of the foetus shown in figure 27. The dorsal ligament has been cut and the umbilical stalk turned aside. Cf. figure 1. ($\times 1\frac{1}{2}$ approx.)

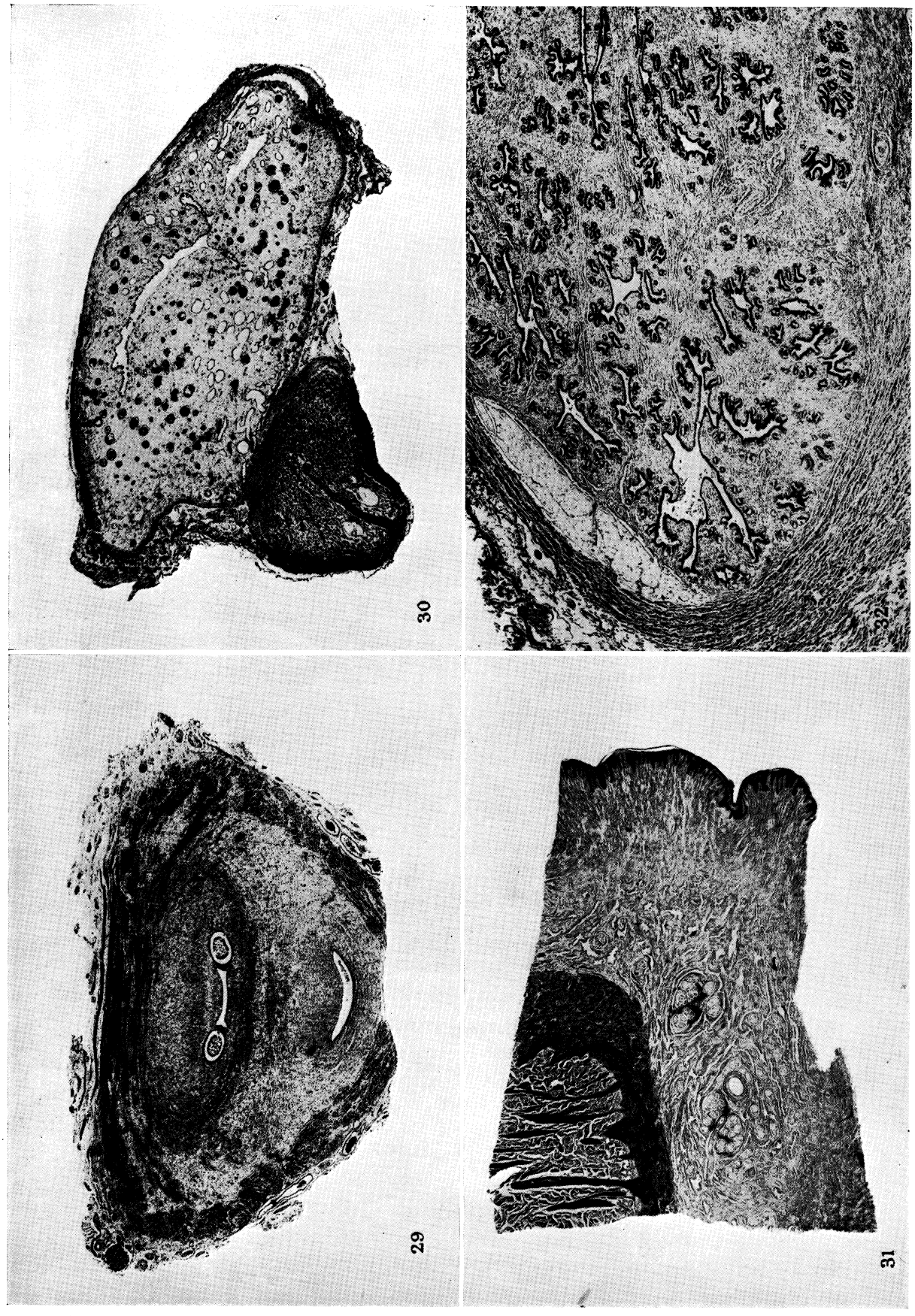


FIGURE 29. Transverse section of the reproductive tract of the foetus shown in figure 18, in the region of the os vagina. (×10.)
FIGURE 30. Transverse section at about the middle of the body of the clitoris of the foetus shown in figure 18. (×15.)
FIGURE 31. Transverse section through the clitoris of a young calf (E119) shown in figure 23. (×7.)
FIGURE 32. Transverse section of part of Cowper's gland of a young calf (E119). (×27.)

consists of a greatly elongated vestibular portion, the urogenital canal. The length of the clitoris is proportional to that of the urogenital canal, and in the relaxed condition the clitoris and penis are not greatly different in length, although the penis is a considerably more massive organ. In the writer's experience, African hunters have on several occasions reported the shooting of a cow elephant as that of a bull, although they knew that greater interest attached to female specimens. The reporting of a bull as a cow would have been ascribed to a desire to please, but this mistake was in fact never encountered. It seems probable, indeed, that the discrepancy between the numbers of male and female elephants reported as shot by African hunters of the Game Departments, is at least partly attributable to error in identification.

Figures 20 and 21, plate 15, show the perineal region of a male and a female foetus. The male was the slightly older foetus and the two photographs have been printed to the same scale. The difference between the sexes is often much less marked than it is in this instance, and in several cases it has been necessary to expose the internal genitalia before the sex of a preserved foetus could be determined. It will be seen from the photograph that the male appears to have a definite prepuce. In the adult the appearance is different; as stated by Schulte (1937) the adult has no prepuce and the glans penis is not visible when the penis is not erected. The distal portion of the penis of the foetus shown in figure 21 in fact appears to have been rendered more than normally prominent by pressure on the posterior region during its fixation in formalin. The possibility of such distortion has always to be borne in mind when dealing with preserved material even when it has been carefully transported. The preputial fold, however, is clearly seen in all the male foetal specimens, and is evidently homologous with a similar fold surrounding the genital opening in the female. The preputial fold of the foetal (male) elephant is single, and appears to represent the external part of the prepuce of the horse, the internal part, or prepuce proper (Sisson 1953) being absent. The preputial fold of the female foetus, seen in figure 20, plate 15, seems to persist in the adult. Such a structure was described by Neuville (1937). The only elephant foetuses as yet examined which were younger than those described above, were males. The peritoneal region of one of them (E20f) is shown in figure 25, plate 16. This foetus weighed about 50 g (the specimen E60f, figure 21, weighed about 3·5 kg). The preputial fold is clearly seen as a ridge at the base of the glans penis. The invagination dorsal to the glans was already well developed, and the photograph also shows a well-defined raphe. This latter feature was not so clearly seen on another specimen of a similar age, or on one younger specimen, but there was nothing to suggest that it was an artifact resulting from compression during fixation and storage. Figure 24, plate 16, shows the vulval region of a female foetus somewhat older than that shown in figure 20, plate 15. This was photographed after the genital tract had been dissected out of the specimen together with a band of skin in the perineal region, but it clearly shows the development of the skin fold referred to above. The invagination dorsal to the glans clitoris is also seen.

The genital opening itself appears to be in an exactly similar position in male and female elephants. In the specimens shown in figures 20 and 21 the genital openings are close to the umbilicus. The scar of the umbilicus lies a little way anterior to the genital opening in the adult, a difference which is probably due to changes in the proportionate sizes of these

parts of the body during growth. It is more significant that in the younger foetal stage shown in figure 25 the genital tract does not reach so far forward as it does in later stages. The condition in the youngest foetus examined (approximately 2 g) is very similar to that shown in figure 25.

The implications of the unusual arrangement of the female genitalia with regard to the process of copulation have been discussed in an earlier paper (Perry 1953). The elephant resembles the hyena in that the external genitalia of male and female are superficially similar in both species. In the immature hyena, the clitoris is actually similar to the penis in size but it will be shown that in the musculature of the penis and clitoris the elephant differs from the hyena as described by Matthews (1939) and it will be suggested that the difference is related to the fact that these organs are pendulous in the hyena whereas in the elephant they are closely applied to the abdominal wall.

Dissection of the foetal reproductive tract (♀)

(*a*) *General*

The linear proportions of the female reproductive tract of the foetus and of the young calf are shown in figures 22 and 23, plate 16. The former was photographed after storage in formalin, and was arranged approximately as it would have been *in situ*, for comparison with the drawing of the lateral aspect of a dissection, shown in figure 2. The tract of the very young calf (figure 23) was dissected out in the field very soon after the specimen was obtained, and was photographed in the fresh condition. The right and left uterine horns were about 12·5 cm long and the abdominal portion of the tract below the junction of the horns was about 10 cm long, whereas the length of the intra-pelvic and vestibular parts was about 56 cm. Figure 22, plate 16 and figure 2 together show how the neck of the uterus and that of the allantoic bladder fit closely against the rim of the pubic symphysis. Figure 2 is based upon the dissection of a 3 kg foetus (E 147f), further details of which are shown in the drawing in figure 1 and in the photographs (figures 27 and 28, plate 17).

(*b*) *The abdominal cavity*

Figure 27 shows the posterior part of the abdominal cavity of an elephant foetus (E147f) opened ventrally and with the intestines removed, the rectum being cut across at the level of the kidneys. It will be seen that the ovaries lie immediately posterior to the kidneys, the right kidney being only very slightly cranial to the left one in position. There are comparatively bulky peritoneal structures in the neighbourhood of the ovary, partially enclosing it. When the peritoneum was removed, to expose the kidneys, their lobular form was revealed (figure 28, plate 17). The body of the uterus and the basal part of the uterine horns traverse a characteristic 'ram's horn' flexure (figures 26 to 28, plates 16 and 17). Figure 27 shows the large paravesicular fossae within the pelvic girdle, separated medially by the dorsal ligament which suspends the bladder and the umbilical arteries.

A curious feature of the reproductive tract is the extension of the mesometrium to form a number of irregularly shaped folds or lappets, shown in figure 26. By analogy with the term 'superior mesosalpinx' (Zuckerkandl 1897) these structures might be regarded as forming a 'superior mesometrium', i.e. it is as though the uterine horn traversed the mesometrium at some distance from its free edge, the latter being produced into irregular

folds. These mesometrial lappets do not contribute to the ovarial sac and do not appear to assume any constant form. They were found to be relatively well vascularized but their development and function are obscure.

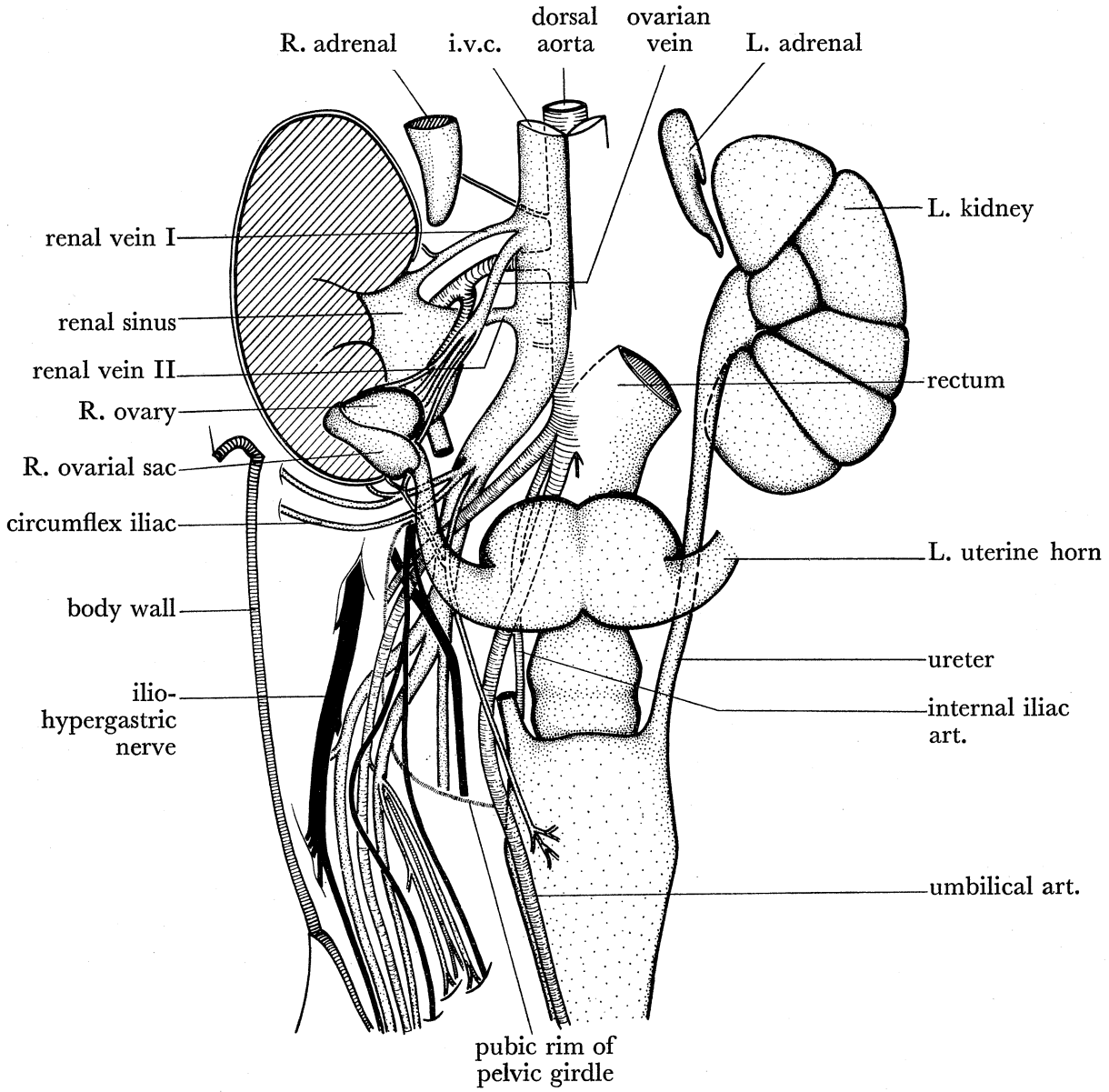


FIGURE 1. Reproductive tract and adjacent structures in the abdominal cavity of a female foetus about mid-pregnancy.

The reproductive tract and adjacent structures in the abdominal cavity, seen from the ventral aspect, are shown in the drawing, figure 1, where the relative dimensions of the various parts are derived from direct measurement of the specimen. Some degree of foreshortening occurs in the photographs (figures 27 and 28) and distorts the proportions to some extent. This drawing should be compared with Eales's (1929) diagrams of the arterial and venous systems of a male foetus. It was partly because the general lay-out of these systems is so clearly shown by Eales's diagrams that it was decided to attempt to present the structure more pictorially in this figure and to include both arteries and veins, as well

as the abdominal organs, in one drawing. The abdomen was opened by a transverse incision immediately anterior to the umbilicus, so that the urachus and the umbilical arteries are carried in a directly posterior track, whereas in the intact animal they would be so curved as to pass through the abdominal wall at a point approximately ventral to the ovaries.

The adrenal glands of the elephant are large organs of somewhat complex shape; that of the left side is shown in figure 1. The smaller lateral lobe is characteristic of adult as well as foetal stages. The adrenal glands of a very large specimen (Quiring 1939) together weighed 940 g.

The lobed structure of the kidney has been described by Eales (1929). The lobules, as she says, 'fit as closely together as if the cuts of a sharp knife had produced them'. The pattern of the lobulation of the left kidney shown in the drawing (figure 1) is that actually observed in the specimen. The number of lobules appears to be constant, six in the right kidney and seven in the left, one of which is small and not visible from the ventral aspect. The shape and relative size of the renal lobules evidently varies somewhat in different individuals. Eales remarked on the relatively short length of the ureters, shown in figure 1 and in figure 28, plate 17.

The blood vascular supply in the region of the kidneys and ovaries comprised an unusual system of arteries and veins in the specimen dissected, which differed slightly in this respect from the male specimen described by Eales. It is probable that some of the complexities, such as the fan-like branching of the ovarian vein, would be resolved to some extent in the course of further development. There was, on both sides, a large venous distension in the region of the hilum of the kidney, from which two veins led to the inferior vena cava. The larger of the two occupied the position usual for the renal vein, the other was anterior to it, and ran obliquely forwards to join the inferior vena cava at a point anterior to the ovarian vein. In Eales's specimen the spermatic vein entered the inferior vena cava posteriorly to the renal vein. Thus although the more posterior of the two renal veins in the present specimen was the larger and had the appearance of being the definitive vein, its relation to the gonadal vein differed from that of the single renal vein in the specimen described by Eales. The ovarian artery is a branch of the renal artery, and the course of the main vessels in the posterior part of the abdominal cavity is shown in figure 1.

(*c*) *The musculature of the reproductive tract*

The extrinsic musculature of the reproductive tract of a mid-term foetus is shown in figure 2, a composite drawing mainly based on the dissection of the specimen E 147 f. The organs are drawn as if seen from the lateral aspect, with the outline of the right half of the pelvic girdle superimposed. For the sake of clarity, only the muscles directly associated with the reproductive tract are figured. They were found to correspond exactly with those of the male foetus described by Eales (1928), except that the urethral muscle, or compressor of Cowper's gland, was absent in the female. Cowper's gland itself is present in the female, but very small, being rudimentary in comparison with that of the male. The musculature of this region of a male foetus, somewhat older than that dissected by Eales, was examined for purposes of comparison. It will be shown below that the principal differences between male and female, with regard to the accessory reproductive organs, lie in the absence of the urethral muscle in the female, and the greater size and bulk of the corpus spongiosum in the

male. Comparison showed that the greater bulk of the intra-pelvic organs of the female, the structure of which is described in detail below, is related to the more spacious pelvic cavity and the wider pelvic girdle in that sex.

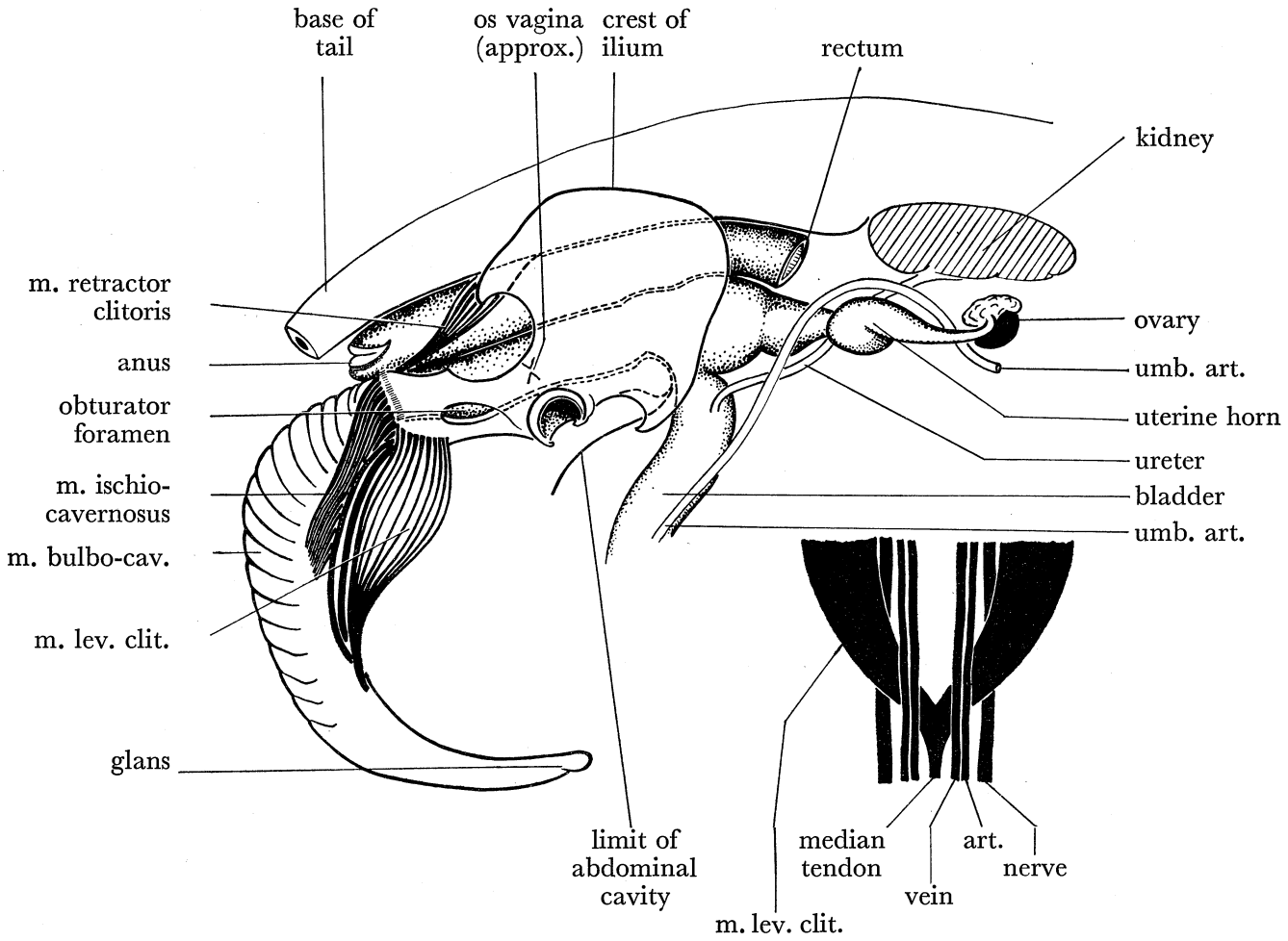


FIGURE 2. Side view of reproductive tract of mid-term female foetus, in relation to the pelvic girdle. Inset: arrangement of the dorsal artery, vein and nerve in relation to the levator clitoris muscle.

Retractor clitoris muscle

This muscle is similar in position and in size to the retractor penis of the male. It arises from the coccygeal vertebrae and passes backwards and downwards to its insertion in the strong fascial layer overlying the urogenital canal in the region of the anus, about the level of the posterior extremity of the ischium. The tapering shape of this muscle in the specimen E147f is shown in the drawing (figure 2). The retractor clitoris of the elephant occupies the position of the suspensory ligament of the anus in such an animal as the horse. In the stallion, and in the bull, the retractor penis muscle is a continuation of the suspensory ligaments of the anus. These ligaments arise on the ventral surface of the 1st and 2nd coccygeal vertebrae and pass downwards over the sides of the rectum to meet below the anus. Here there is a decussation of fibres, thus forming a sort of suspensory apparatus for the posterior part of the rectum and the anus. From the decussation the muscle proper

passes along the ventral surface of the penis to its insertion (see Sisson 1953). In the elephant this suspensory apparatus is incomplete ventrally. Laterally, the position of the ligaments of the horse is occupied by the muscle in the elephant, and that portion of the muscle of the horse which runs along the lower surface or ventrum of the penis is not represented in the elephant of either sex.

Ischio-cavernosus muscle

This muscle is again similar in size and in position in male and female. At its origin it partially envelops the tuber ischii, its true attachment being to the medial surface. Its insertion is into the fibrous tissue of the corpus cavernosum clitoris, its body enveloping the crus clitoris. The structure of the clitoris is described in some detail below; it will be shown that it is large, though smaller than the penis of the male. The corpora cavernosa of penis and clitoris are not very greatly different in size or extent in the foetal stages and the muscles inserted into them reflect their similarity.

Levator clitoris muscle

The muscle thus labelled in figures 2 and 13 and in figure 22, plate 16, was similarly named by Watson (1881) in his drawing of the reproductive tract of a young female Indian elephant. This name, analogous with that of the levator penis of the male (Camper 1802), appears to be appropriate to the function of the muscle, which is discussed below. Eales (1928) prefers the term 'compressor venae dorsalis penis' in reference to the male. She points out that this muscle 'is not usually present in ungulates, is small in the dog, and is present in rodents, *Hyrax* and Sirenia'. It is unusually well developed in the male elephant and is of something like comparable size in the female, at least in foetal stages. It takes origin from the ischium, medial to the origin of the ischio-cavernosus muscle. In figure 2 it is drawn as if displaced anteriorly to reveal underlying structures. Its insertion is into a strong tendon which almost immediately joins its fellow from the other side to form a very prominent cord, sheathed in a tough tunica, running along the dorsum clitoris to the anterior tip of the clitoris. The name compressor venae dorsalis penis (clitoris) refers to the position of this muscle in relation to the dorsal vein of the penis (clitoris) which, together with a prominent artery and a nerve, runs between the muscle and the body of the penis (clitoris) until the muscle reaches its tendon. In the specimen E147f the nerve and the vessels continued their course lateral to the clitoris, the nerve passing 'under' the tendon of its own side (i.e. between the tendon and the body of the clitoris) while the vessels crossed 'over' the tendon but continued alongside the median tendon formed by the junction of those from right and left sides (inset, figure 2).

Two muscles without skeletal attachment, the urethral and the bulbo-cavernosus, contribute to the urethral wall of the male elephant but only the latter is present in the female. It is similar in position and extent in both sexes, but is less bulky in the female. Its greater bulk in the male, together with the fact that the urogenital canal of the female is thin-walled and has a large lumen, while that of the male is thick-walled and has a narrow lumen, accounts for the different appearance of the perineum in the two sexes, as seen in figures 20 and 21, plate 15. The urethral wall is much thicker in the male by virtue of the more prominent corpus spongiosum. Thus in a transverse section of the female tract

(figure 13) there is a large cavity (the urogenital canal) within a relatively thin spongy layer, surrounded by a shallow muscle layer. The outer dimensions of the male tract in this region are similar but the corresponding transection would consist of a thick spongy layer traversed by a lumen of narrow bore and surrounded by a thick layer of muscle.

Attention has already been drawn to the fact that the external genitalia are superficially similar in the two sexes (p. 38) a condition which invites comparison with the hyena, where the resemblance between the sexes is even closer. In this case, the clitoris is almost identical with the penis in immature animals and forms a pendulous organ through which the copulatory canal runs (Matthews 1939). There is, however, a marked difference in the musculature; the levator clitoris is very prominent in the elephant, and the retractor clitoris does not extend along the ventrum of the clitoris, whereas in the hyena the levator clitoris appears to be absent, and the prominent muscle of the clitoris is the retractor.

The short length of the retractor penis (clitoris), which does not extend beyond the pelvis in the elephant, contrasts with the prominence of this muscle in the horse and the bull. Eales suggests that its condition in the elephant is related to the permanently extended condition of the penis. It is possible to imagine that contraction of the large levator penis (clitoris) has a different effect in male and female. It has been shown (Slade 1903) that the erected penis protrudes enormously; this is presumably brought about by contraction of the bulbo-cavernosus and ischio-cavernosus (erector penis) muscles, the maintenance of turgor being assisted by compression of the dorsal vein of the penis when the levator penis (compressor venae dorsalis) contracts. In the adult female there is little cavernous tissue in the wall of the urethra so that the clitoris is not protruded like the penis at copulation. Instead, the vulva is dragged posteriorly after the insertion of the penis, and it may be that contraction of the levator clitoris assists the process by pulling the clitoris, and with it the vulva, towards the pelvis. In the male, when the turgid penis forms a flexible rod hinged on the crura, contraction of this muscle will apparently lift the whole structure. It is therefore suggested that the corresponding muscle may act differently in male and female, because of the difference in rigidity of the corresponding organs in the two sexes. If this is the case, this muscle is truly a levator in the male but effectively a retractor in the female. As already mentioned, the levator clitoris is absent and the retractor clitoris fairly prominent in the hyena. The urethra and clitoris of this animal form a pendulous organ and in copulation the vulva is carried to the rear by the action of the retractor muscle which is inserted into the ventrum of the clitoris. The latter has a fairly well-developed corpus spongiosum and, when it is turgid, contraction of the retractor muscle causes it to pivot, hinged on its crura. This pivotal movement is not possible in the case of the female elephant, where the copulatory canal is within the integuments of the belly wall.

(*d*) *The internal structure of the reproductive tract*

The structure of the reproductive tract of the adult female has been briefly described in a previous paper (Perry 1953). The present material affords an opportunity to amplify that account considerably. Figure 23, plate 16, shows the reproductive tract of a very young calf (E119) photographed soon after its dissection from the carcass, as described

above (p. 38). Figure 3 represents a diagrammatic plan view of this tract as seen from the dorsal aspect. It serves to indicate the relations of the successive segments of the tract from the ovaries to the vulva, and also provides a key to the series of semi-diagrammatic drawings of transverse sections of the reproductive tract shown in figures 4 to 16 and that of the region of the glans clitoris, in sagittal section, figure 17. The morphological relation-

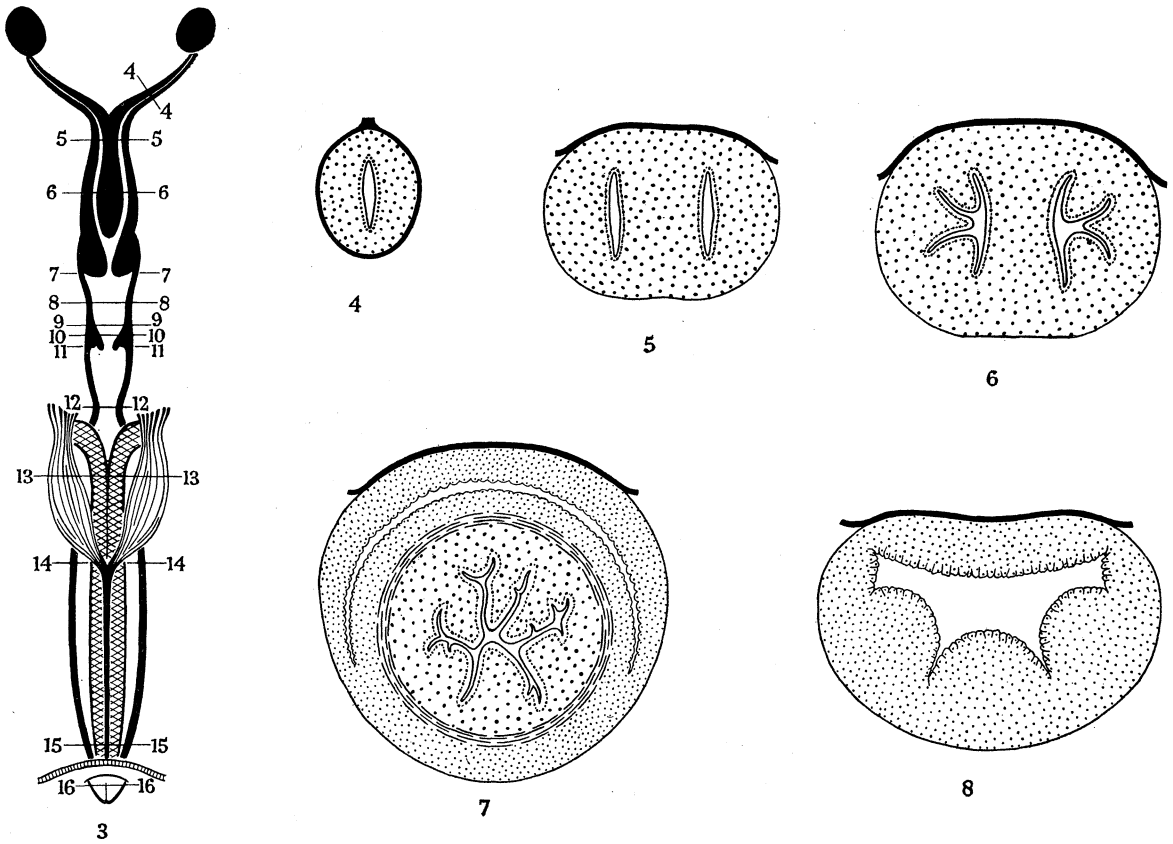
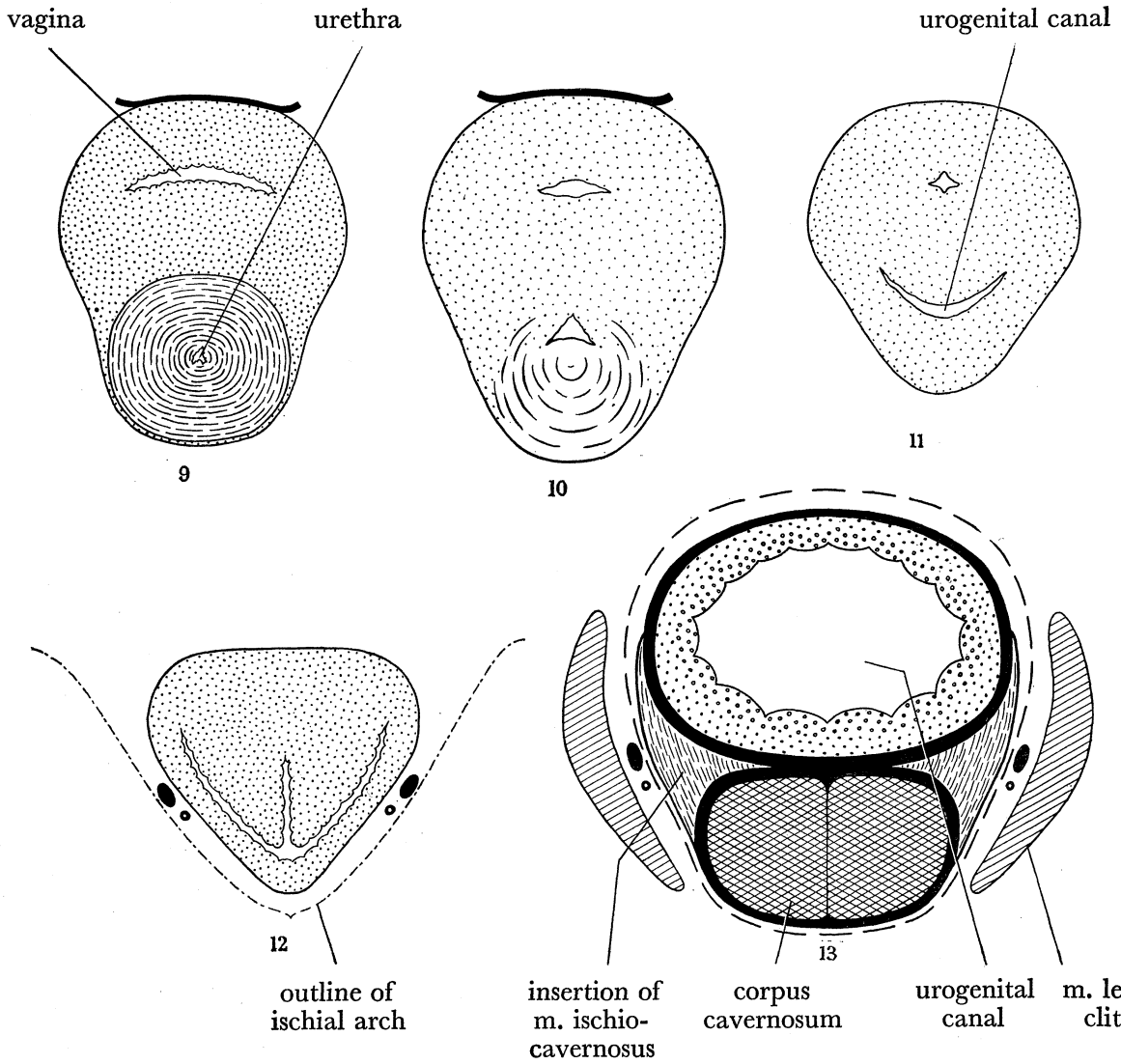


FIGURE 3. Diagrammatic plan view of the reproductive tract of a young calf (E119, see figure 23, plate 16). The lines 4–4, 5–5, etc., mark the levels of the transverse sections shown in figures 4 to 16.

FIGURES 4–16. Diagrammatic transverse sections of the reproductive tract at successive levels as indicated on the plan, figure 3. Morphologically dorsal portion uppermost.

ship of dorsal and ventral components of the reproductive tract has been retained in the diagrams of transverse sections so that each is shown as if it were made through a specimen arranged like that in figure 23, plate 16. Figure 4 represents a transverse section through one of the uterine horns about half way from the ovarian end of the horn to its junction with its fellow of the opposite side. The corresponding position in the foetal uterus would be immediately above the ram's horn flexure. The diameter of the uterine lumen does not increase proportionately with the thickness of the uterine horn and in the adult the free part of the horn is 3 to 4 in. in diameter at its base whereas the lumen is only about $\frac{1}{2}$ in. in bore. Linear measurements of the uterus as seen at autopsy are very deceptive as they vary very greatly with the degree of contraction of the muscles, but the figures quoted serve to give some indication of the massiveness of the uterine wall in relation to the lumen.

The uterine horn of the adult becomes progressively more slender towards the ovary, its external diameter being reduced by about a half. The diameter of its lumen is reduced to a much more marked extent so that it is minute in the upper part of the uterine horn. The lining of the uterine lumen is not greatly folded or richly vascularized. In the fresh condition it has a smooth creamy-white surface.



FIGURES 9 to 13. For legend see p. 44.

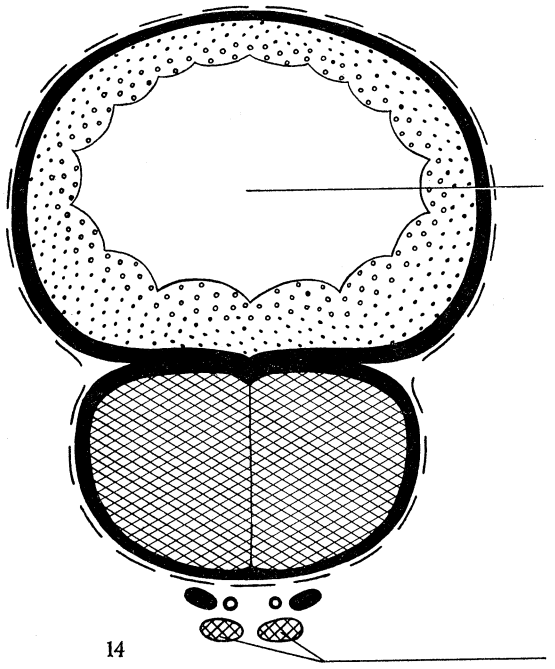
Figures 5 and 6 represent transverse sections of the next region of the uterine tract, where the two horns are fused but the lumina remain distinct. The level of the section shown in figure 5 is just below the point where the right and left horns unite, and that of the section in figure 6 is just above the point where the two canals join to form a single lumen. This part of the uterine tract is relatively longer in the foetus than in the adult. As the diagrams indicate, the area of the uterine lining is somewhat increased by a greater degree of folding as the separate lumina approach their junction with the corpus uteri proper. In the adults examined in the fresh condition, the uterine lining of this segment of the uterus, like that of the separate uterine horns, was remarkably little folded, but in the

foetus and the young calf the organs were more contracted by the action of preservatives. The confluence of the two lumina is quite simple, with no valvular structures. In the adult the lumen of the corpus uteri is comparatively spacious and its walls, though thick, are extensible. When this cavity is opened, the openings of the paired lumina are seen, an inch or two apart. A finger can be inserted into them, but they are not easily distended, their course lying through a massive structure of muscle and connective tissue. The lining of the paired canals is slightly more vascularized than that of the rest of the uterus, and in non-pregnant parous animals the scars of former implantation sites were usually found in this part of the tract. The youngest examined, however, was implanted in the upper part of the uterine horn (see Amoroso & Perry 1964).

The relative proportions of the successive segments of the uterine tract are different in foetal and adult stages. The body of the uterus is marked externally in the foetus by a subspherical swelling, as seen in figure 2 and figure 22, plate 16. Almost the whole of it is occupied by a thickening of the wall which forms a relatively massive hemispherical papilla pierced by a narrowed lumen, opening at the os uteri, as indicated in figure 2. Thus the uterus is joined to the vagina by a sort of massive and blunt intussusception. This is shown in transverse section in figure 7 where the lumen of the uterus and that of the vagina are seen in the same plane; for an appreciable distance such a section would show the vaginal lumen as a complete circle around the papilla which surrounds the os uteri. As indicated in the diagram, the uterine lumen within this papilla is surrounded by a distinct band of circular muscle, presumably with a sphincter action. The circular muscle is not yet visible as a distinct band in transections of the uterine horns of the foetus or the young calf. The developmental history of the papilla of the os uteri is one of continuous reduction relative to the adjacent structures, and in the adult the os uteri is not particularly strongly guarded. It is marked by an annular thickening of the wall containing the sphincter muscle, and by the sudden transition from the thick muscular wall of the uterus to the thin extensible wall of the vagina.

The os uteri is just within the pubic rim of the pelvic girdle and the vagina occupies about two-thirds of the distance to the ischial rim. For most of its length it is a simple tube (figure 8). Its floor is complicated posteriorly by the urethra's junction with it. The urethral canal runs within a large sphincter muscle (figure 9). Posteriorly, the lumen of the foetal vagina was found to narrow abruptly, becoming minute in diameter. The somewhat complicated structure of the wall of the reproductive tract in the region of the os vaginae was studied in detail in the foetal specimen (E15f) shown in figure 18, plate 15, to which the following description applies. As the vaginal canal narrows, the urethral canal emerges from its sphincter muscle (figure 10) and opens into the extremity of the urogenital canal (figure 11). The vaginal canal ends blindly. The dorsal wall of the extremity of the urogenital canal is thickened to form a cushion-like projection into the lumen, and in this cushion there is a deep longitudinal groove (figure 12). Nearer to the vagina, this groove is closed over, so that its anterior extremity is a short tube. The extremity of the urogenital canal is therefore divided into two compartments, a ventral part below the dorsal papilla, and a dorsal tube which continues the line of the deep groove in the dorsal papilla. The two compartments respectively carry reproductive and urinary products. The tube within the dorsal papilla will later unite with the vagina and the point of junction will in fact be

the os vaginae, slightly posterior to the urethral opening. Immediately anterior to the closure of the groove to form this tube, two lateral branches leave it to run forwards for some little distance alongside the posterior extremity of the vaginal canal. These lateral canals presumably represent the canals of Gaertner. They were identified in the young



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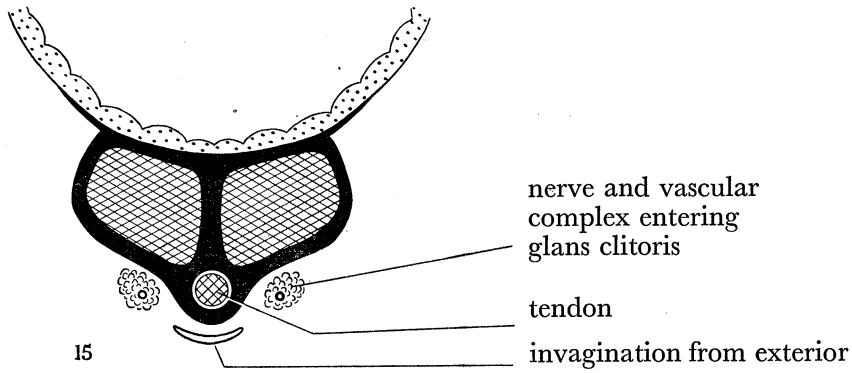

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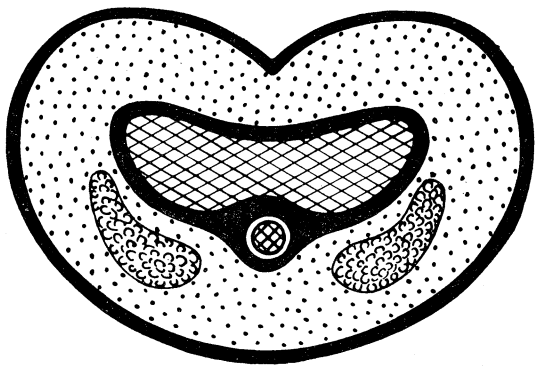

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FIGURES 14 to 16. For legend see p. 44.

calf, E119, after their nature had been discovered by study of the foetus. In the young calf they are discernible as lateral diverticula about 4 mm long. Their occurrence in a young female Indian elephant was described by Watson (1881). His specimen was abnormal in possessing a duplex form of uterus and vagina, so that there were in fact two ora vaginae. Figure 29, plate 18, shows a transverse section through the region where the canals of Gaertner lie alongside the vaginal canal. Although the vaginal canal ended blindly in E15f, a strand of epithelial tissue was found to connect its tip with one of the two canals of Gaertner. This presumably marks the line of the opening which would subsequently have been formed, perhaps with the eventual obliteration of the canals of Gaertner. It is evident that the development of the elephant reproductive tract involves progressively less obstruction between its successive segments. It has been suggested (Perry 1953) that failure at some stage of this process may account for a number of aberrations which have been described in the literature (Neuville 1937). This is perhaps borne out by evidence, within the present material, of a degree of individual variation in the sequence of events leading to the development of the os vagina. The description given above applies to a 2 kg foetus (E15f). In a 6 kg foetus (E138f), the passage was open although extremely narrow, but in one much later foetus of about 96 kg (E84f) the hymen was intact. This was a specimen in which the ovaries were greatly enlarged, probably by the action of maternal hormones (Perry 1953), and it is conceivable that the same influence had brought about temporary changes in the wall of the reproductive tract, though it seems unlikely that such changes would involve the re-closure of the os vagina. In the young calf, E119, the os vagina was clearly patent.

The os vagina is within the pelvic girdle, as already described. It opens into the very prolonged vestibular portion known as the urogenital canal, and this is narrowest near the point where it debouches from the pelvic girdle. It is roughly triangular in section (figure 12) where it passes between the floor of the rectum and the V-shaped ischial arch. Immediately after leaving the pelvic girdle the urogenital canal abruptly changes direction (figure 2) and thereafter continues along the curve of the abdominal wall to the vulva, just posterior to the umbilicus. For most of its length its roof is reinforced by the skeletal nature of the clitoris, in particular that of the corpora cavernosa. The flexure of the canal of course brings the morphologically ventral clitoris to a position above the canal and adjacent to the belly wall. The corpora cavernosa take origin from the crura clitorides which are attached to the ischial tuberosities. The following description of the clitoris and associated structures is based on a study of the reproductive tract of the young calf, E119 (figure 23, plate 16), measurements of which formed the basis for the diagram in figure 3, the actual dimensions being as follows:

	cm
from tip of left uterine horn to junction with right	9·5
from tip of right uterine horn to junction with left	11·0
part of uterus with two separate lumina	10·0
part of uterus with single lumen	3·0
length of vagina (os uteri to os vagina)	5·0
Gaertner's canals	0·4
os vagina to junction of crura clitorides	12·0

	cm
junction of crura to openings of Cowper's glands	2·5
ducts of Cowper's glands (approximately)	6·0
corpus spongiosum extends above crura for approximately	7·5
from junction of R. and L. tendons of levator clitoris muscle to insertion of common tendon in glans clitoris	14·0

As indicated in figures 13 to 16, a prominent feature of the body of the clitoris and the wall of the urogenital canal adjoining it is the stiffening provided by the tough tunica which covers the corpora cavernosa and extends around the canal below them. At this point attention must be drawn to the presence of a fairly well-developed corpus spongiosum (or corpus cavernosus urethrae) in the female elephant (figures 13 and 14 and figure 30, plate 18). In the young calf, E119, it extended along the wall of the urogenital canal

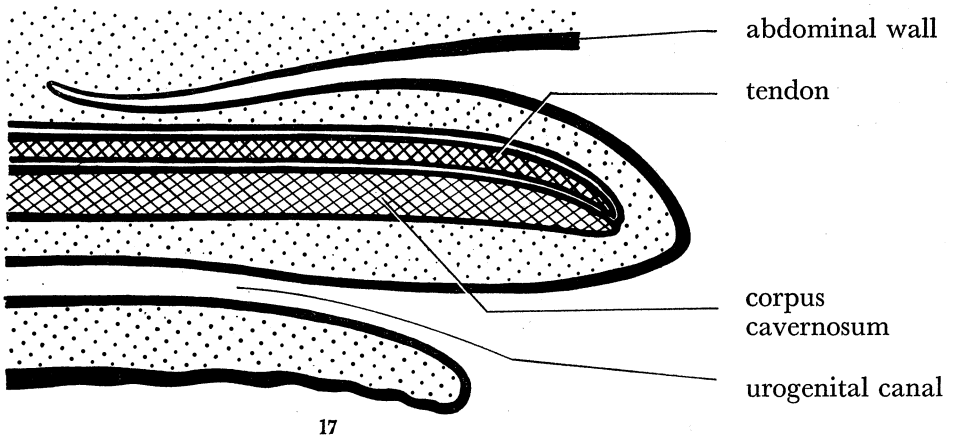

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FIGURE 17. Diagrammatic sagittal section through the glans clitoris; cf. figures 15 and 16.

above the junction of the crura clitorides for about 7·5 cm, so that it reached almost to the pelvic portion of the tract. Towards the vulva its limit was less clearly seen, but on macroscopic examination it appeared not to reach the glans. Further study of foetal material showed that its condition in the female is fundamentally similar to that in the male as described by Schulte (1937, and see below). It was relatively conspicuous in the foetus E15f, and figure 30, plate 18 is a photograph of a transverse section of the urogenital canal of this animal about the middle of the body of the clitoris. The specimen was considerably distorted during fixation and storage (cf. figure 13) but the extent of the blood-laden spongiose tissue surrounding the urogenital canal is clearly seen. The structure of the corpus cavernosum is also illustrated by this section, and by that shown in figure 31, plate 18, through a portion of the clitoris of E119 (the young calf).

The corpus cavernosum, as seen in cross-section, changes very little between the levels represented in figures 14 and 15, indicated on the plan view in figure 3. The insertion of the ischio-cavernosus muscle, however, is no longer seen at the lower of these levels, and the bulbo-cavernosus muscle is reduced to a thin investing layer. The levator clitoris muscle of each side (figure 13) inserts into a short stout tendon (figure 14) which soon joins its fellow of the opposite side. The resulting median tendon is incorporated into the elastic sheath of the corpora cavernosa (figure 15). It continues thus to the tip of the clitoris, and

as development proceeds its extremity becomes cartilaginous. There is no baculum in either penis or clitoris.

The openings of the ducts of Cowper's glands, in the young calf E119, were about 10 mm apart in the floor of the urogenital canal, about 25 mm below the junction of the crura clitorides. Each was a simple opening about 2 mm in diameter and the ducts, of about the same diameter, ran directly backwards just below the lining of the floor of the canal for 4 to 5 cm. They diverged only slightly from each other in that distance and then became more widely separated and narrower in bore as they followed a slightly tortuous route deeper into the connective tissue. They led from ovoid glands about 10 mm long, the tubules of which (see figure 32, plate 18) converged to form a small antrum or reservoir within the capsule of the gland near its posterior end. These glands are considerably smaller than the corresponding glands of the male at a similar stage of development and, as already mentioned, they are not invested by a urethral muscle, described in the male by Eales (1928) and seen by the present writer in a very similar specimen.

The dorsal artery and vein of the clitoris, and the large nerve which runs in close association with them, follow the course of the levator clitoris muscle of each side, and continue lateral to the median tendon in the lower part of the clitoris. They give off branches to the more prominent part of the corpus spongiosum in the body of the clitoris and after passing through a region in which such branches are very few they break up into a network in the region of the tip of the clitoris, in a prominent mass of spongy tissue which extends laterally around the urogenital canal and is thickest in the upper (morphologically ventral) part of the glans, as shown diagrammatically in figure 16. It is clear from Schulte's account that the corpus spongiosum of the male is similarly attenuated in the region of the body of the penis in the adult, with lateral expansions around the outside of the corpora cavernosa near the tip of the penis. This author regards the term 'glans penis' as being by definition confined to the swollen extremity of the corpus spongiosum, and as the latter does not invest the extremity of the penis he distinguishes between the tip of the penis and its glans. This distinction is not made by, for instance, Watson or Eales. Serial sections have been prepared of parts of the clitoris, including the tip, of the foetal specimens E138f and E147f by means of which this structure was elucidated. The lateral and distal portions of the spongiose tissue become bound into part of the tunica and thus have a much more definite form than the corresponding tissue in the region of the body of the clitoris. The connexion between the two prominent parts of the corpus spongiosum is extremely tenuous but quite definite, as shown in the photograph in figure 31, plate 18. The vessels have the form characteristic of the corpus spongiosum, in that the veins as well as the arteries are thick-walled. Besides being bound into the tunica, the corpus spongiosum of the glans is much more heavily innervated than that of the body of the clitoris, for although the dorsal nerve has given off a number of fine branches in its passage down the body of the clitoris, it is not greatly reduced in diameter when it reaches the glans, where it divides into a complex system interlaced with the blood channels. In dissecting part of the reproductive tract of a 5 kg male foetus it was noticed that the branches of the dorsal nerve supplying the urethral wall (and the relatively massive corpus spongiosum) were much more prominent than were the corresponding nerves in the female. Apart from this the nerve was of comparable size in male and female specimens at similar foetal stages.

The cavity of the urogenital canal widens gradually as it approaches the vulva and in figure 15 only its 'roof' is included. The body wall, which is thin in the immediate region of the vulva, is tucked in to form a pouch above the glans clitoris and the extremity of the invagination is seen in this cross-section (cf. figure 17). The skin which lines it is only very slightly pigmented. The tip of the clitoris in the young calf E119 projected some 2·5 cm beyond the lower rim of the vulva. It was bluntly pointed and slightly flattened and retained the ventral groove seen in the foetal specimen (figure 24, plate 16), but the groove had become relatively much shallower. At the level of the lower rim of the vulva the glans was about 3·5 cm broad. The extremity of the clitoris is shown diagrammatically in longitudinal section in figure 17, orientated as in the intact animal, with the clitoris above the urogenital canal.

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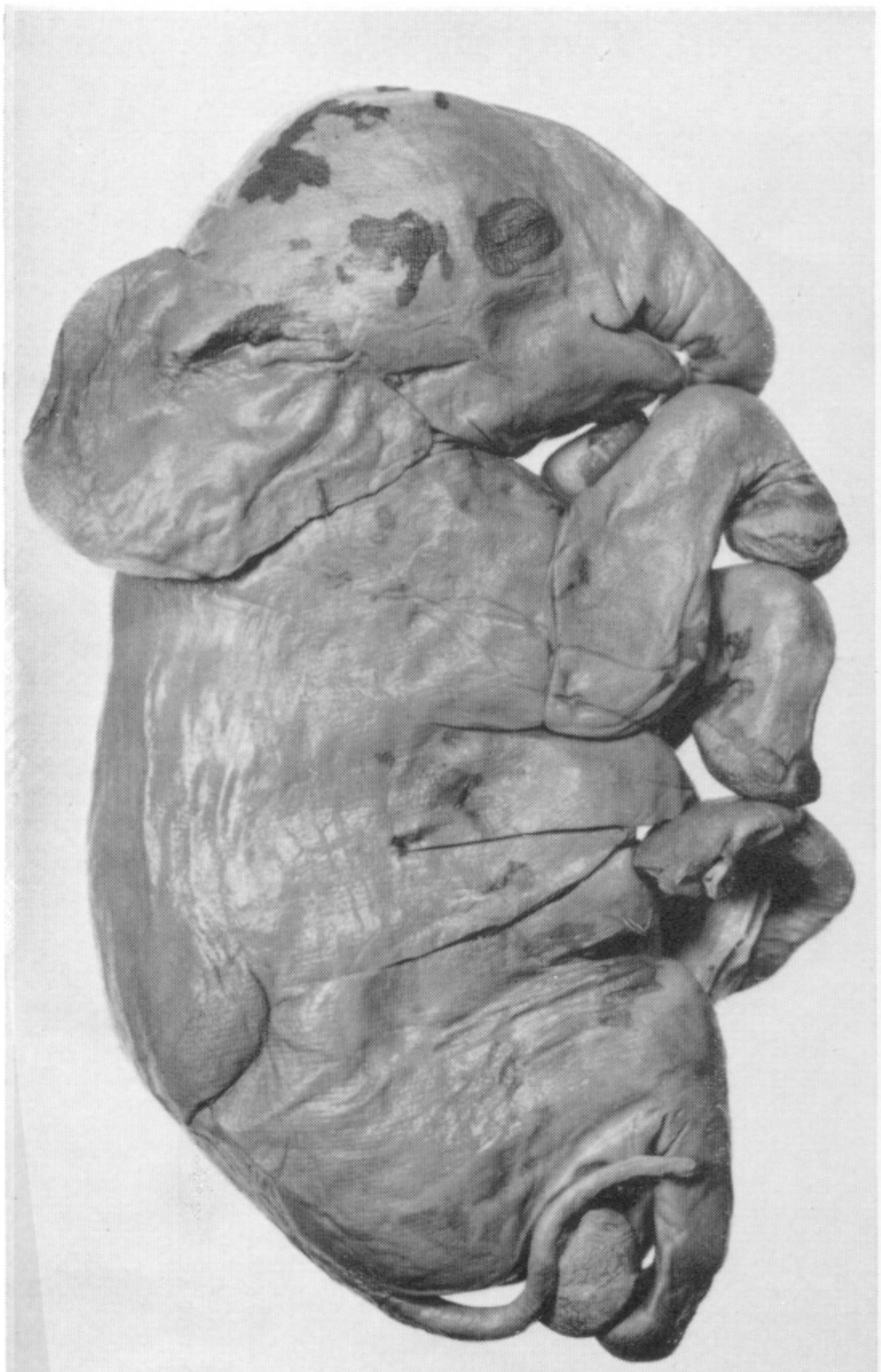

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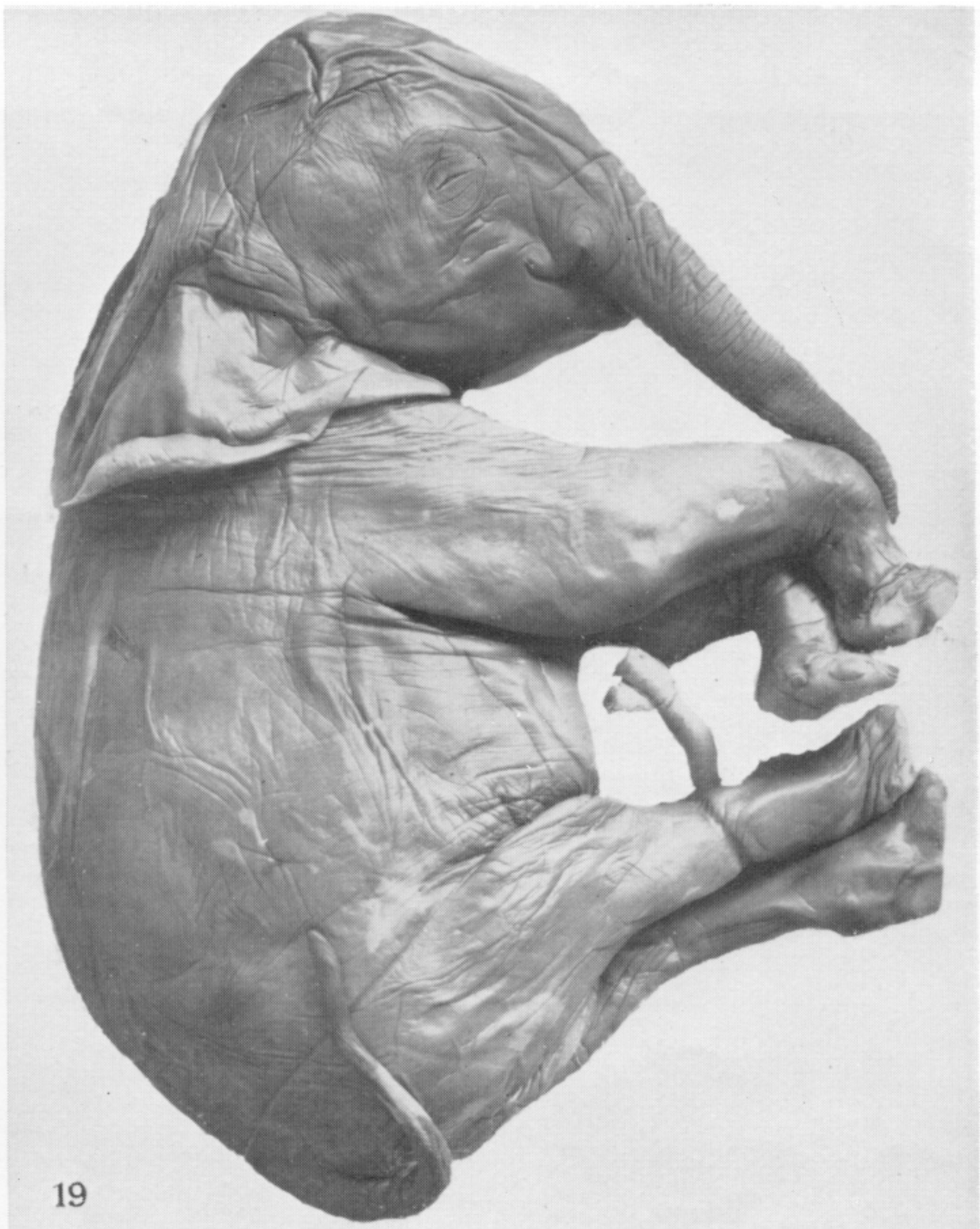

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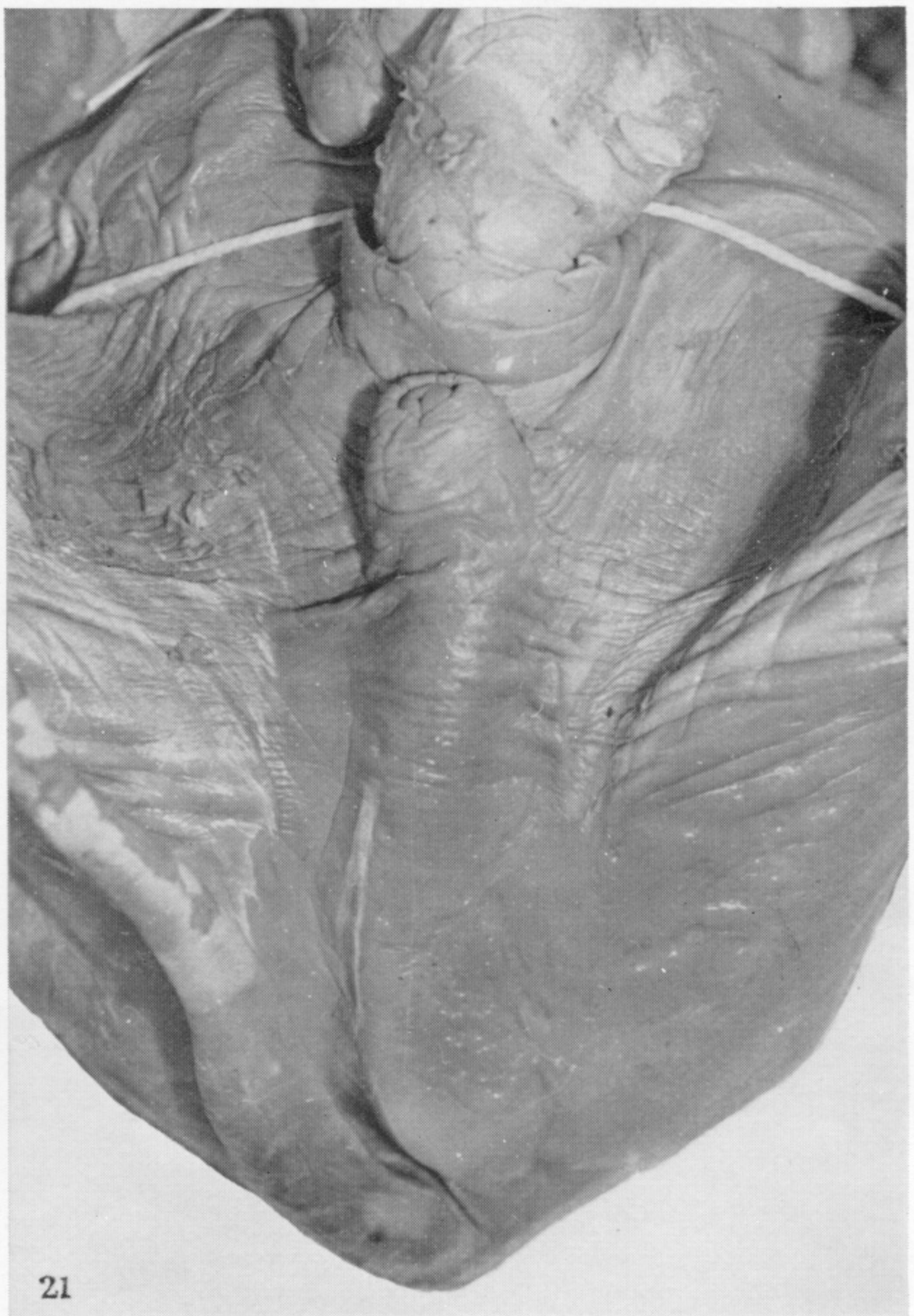

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FIGURES 18, 19. Two of the female foetuses referred to in the text. E15f (figure 18) weighed about 2 kg. E147f (figure 19) weighed about 3 kg. Both to same scale (× approx. $\frac{1}{3}$).

FIGURE 20. The perineal region of the specimen shown in figure 19 (slightly reduced).

FIGURE 21. The perineal region of a male foetus (E60f) weighing about 3·5 kg. Scale as figure 20.

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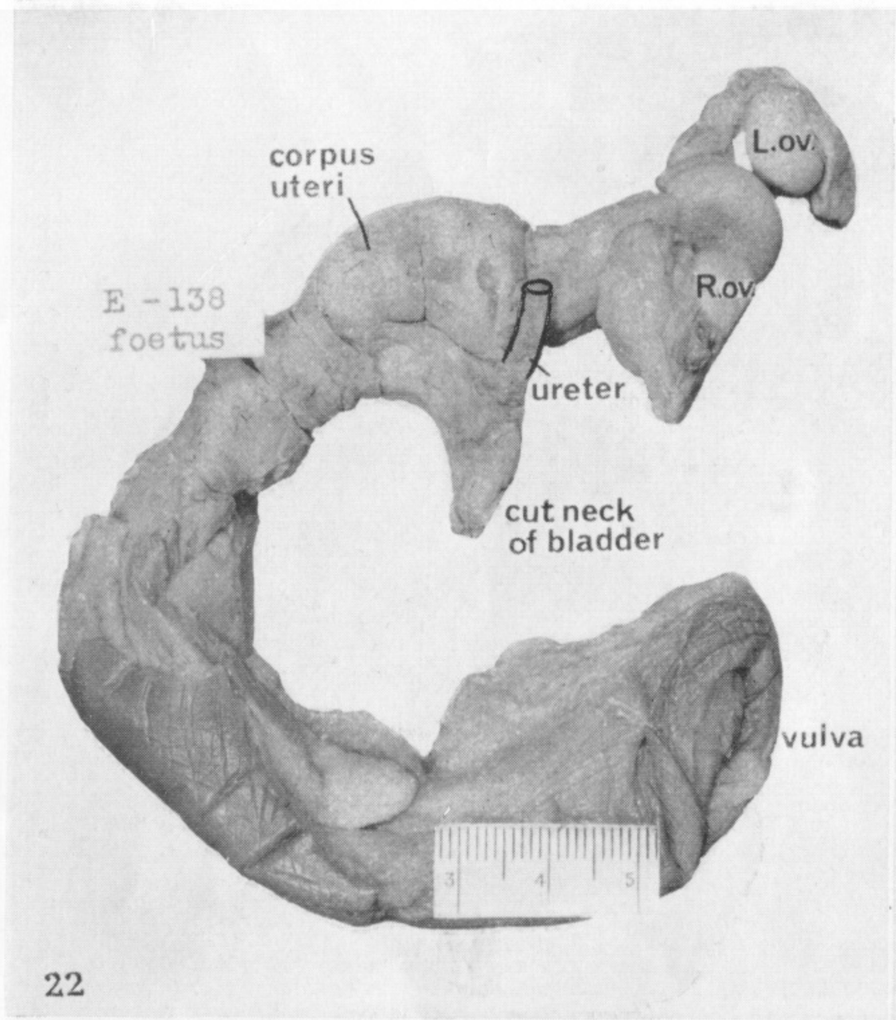

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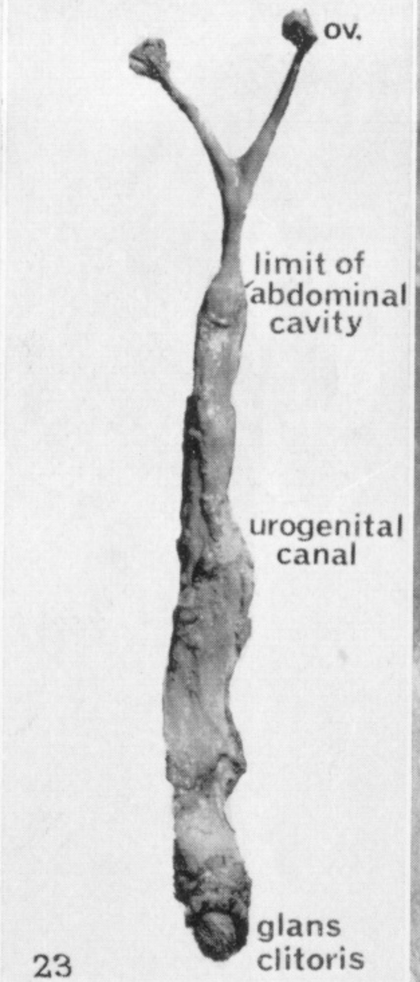

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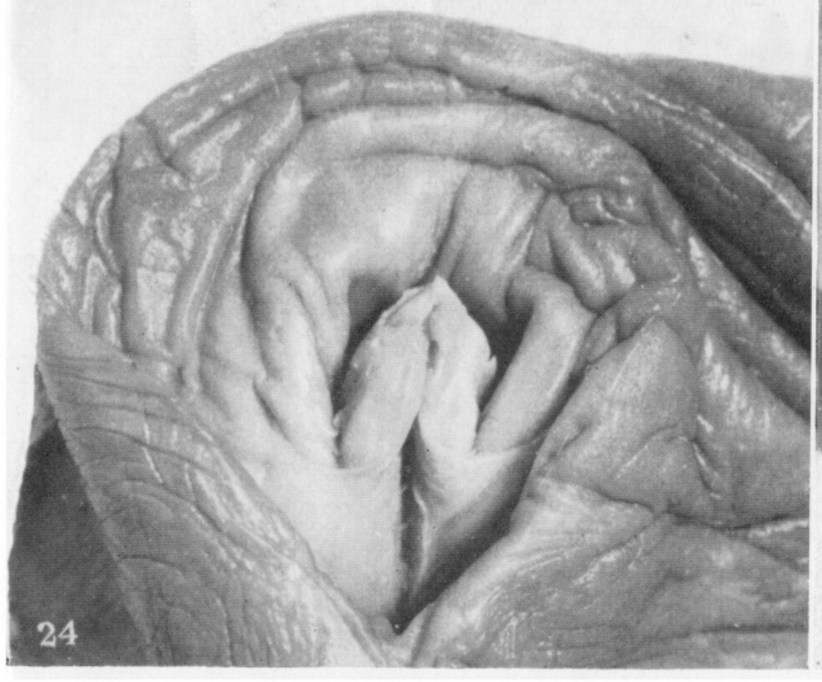

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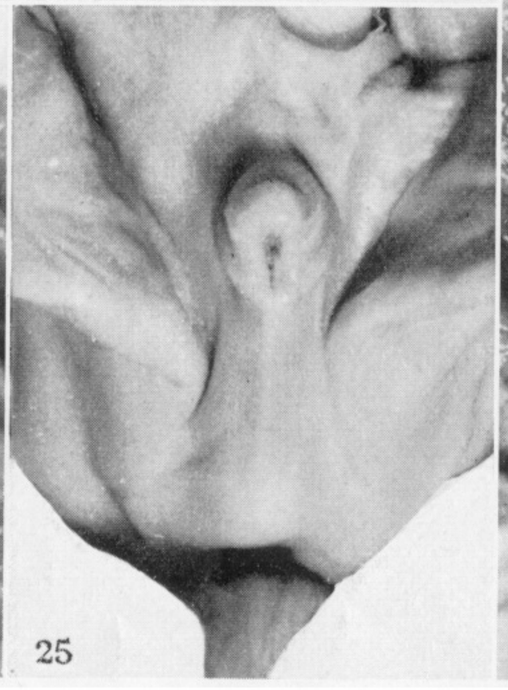

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FIGURE 22. Reproductive tract of a female foetus (E 138f) from the right lateral aspect. ($\times \frac{4}{5}$.)

FIGURE 23. Reproductive tract of a young calf (E119) photographed from the dorsal aspect after dissection in the field. The diagrammatic drawings in figures 3 to 17 are from this specimen. Measurements are given in the text. ($\times \frac{1}{9}$ approx.)

FIGURE 24. Vulval region of a 6 kg female foetus (E138f) ($\times 3$ approx.).

FIGURE 25. Perineal region of a male foetus (E20f) of about 50 g. (Scale as figure 24.)

FIGURE 26. The 'ram's horn' flexure in the uterine horns (E147f), showing the 'mesometrial lappets'. ($\times \frac{1}{3}$.)

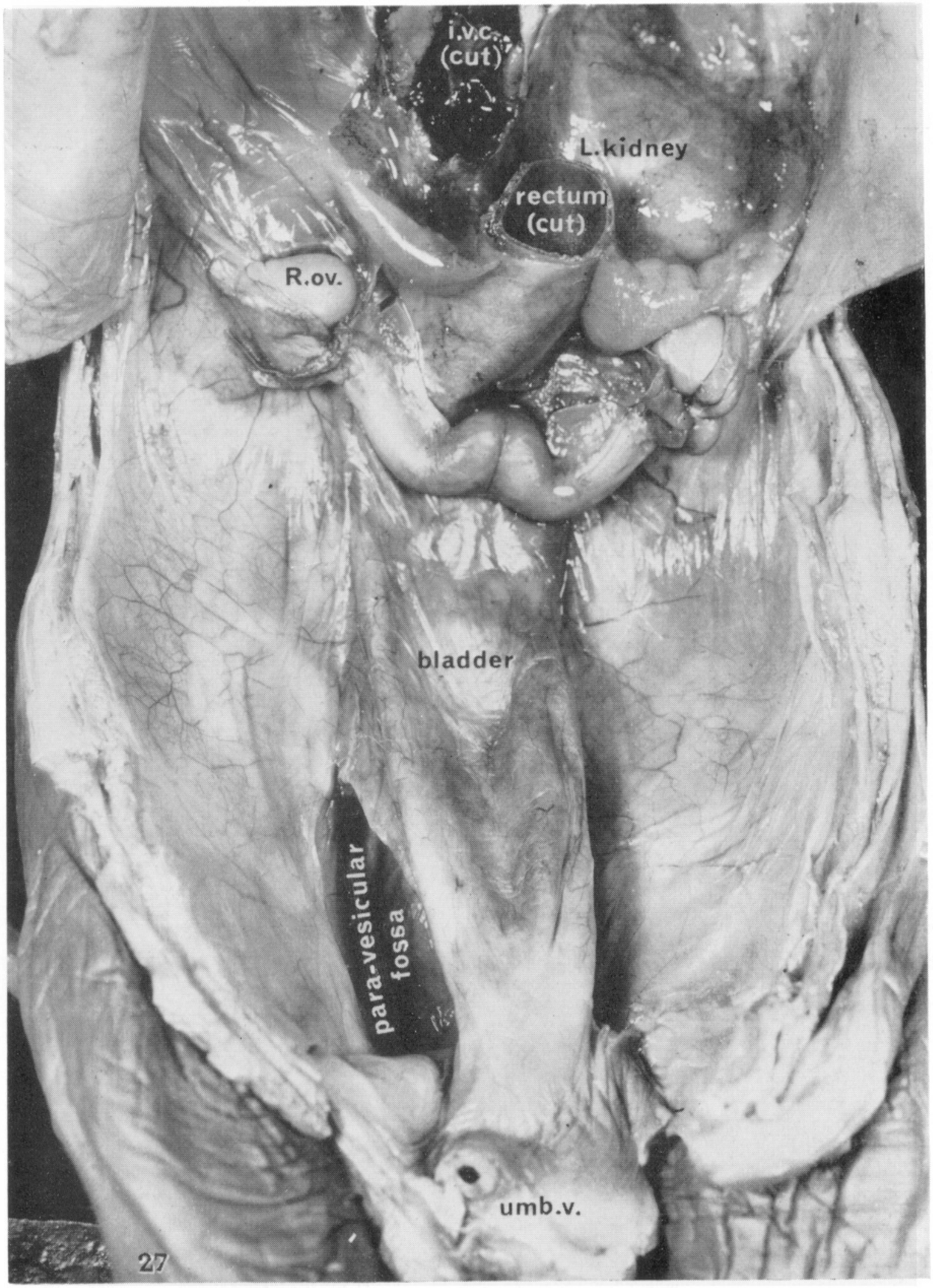
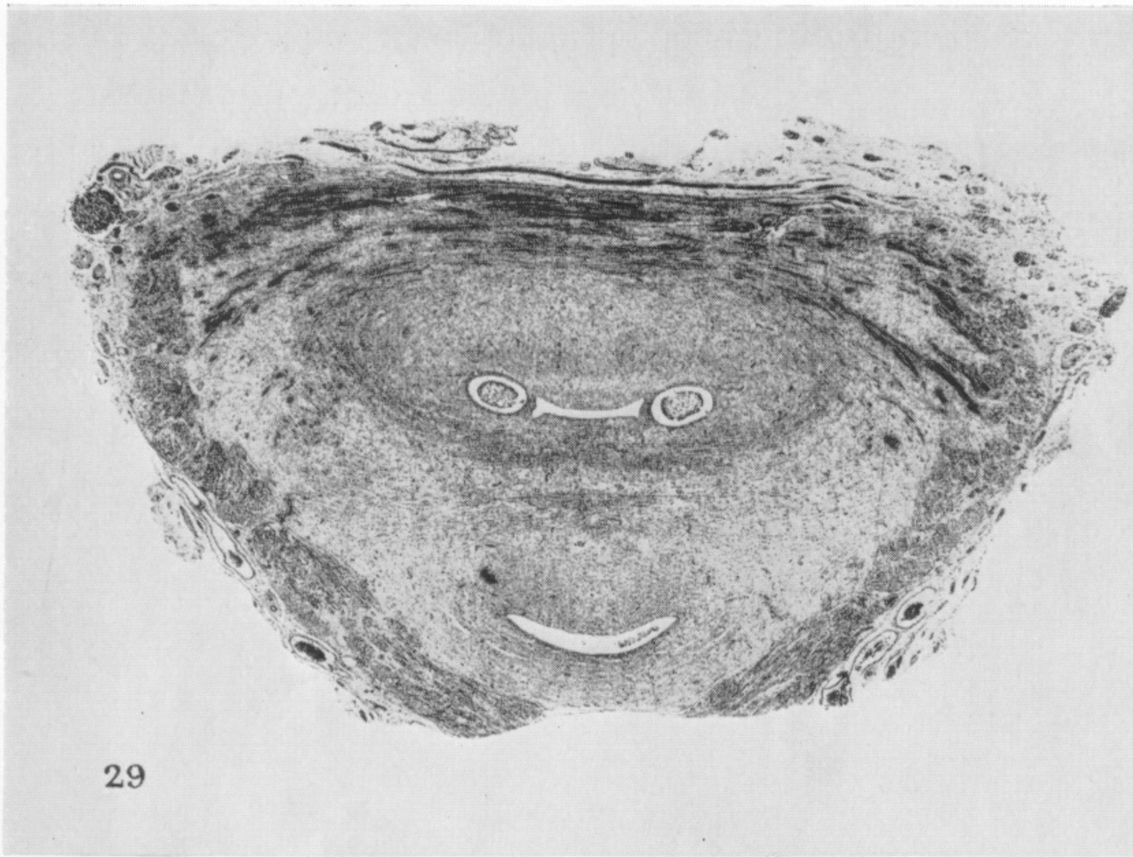


FIGURE 27. Abdominal cavity of a female foetus (E147f) opened in front of the umbilicus. Rectum cut across; liver and alimentary canal removed. (Approx. actual size; see text.)

FIGURE 28. Further dissection of the foetus shown in figure 27. The dorsal ligament has been cut and the umbilical stalk turned aside. Cf. figure 1. ($\times 1\frac{1}{2}$ approx.)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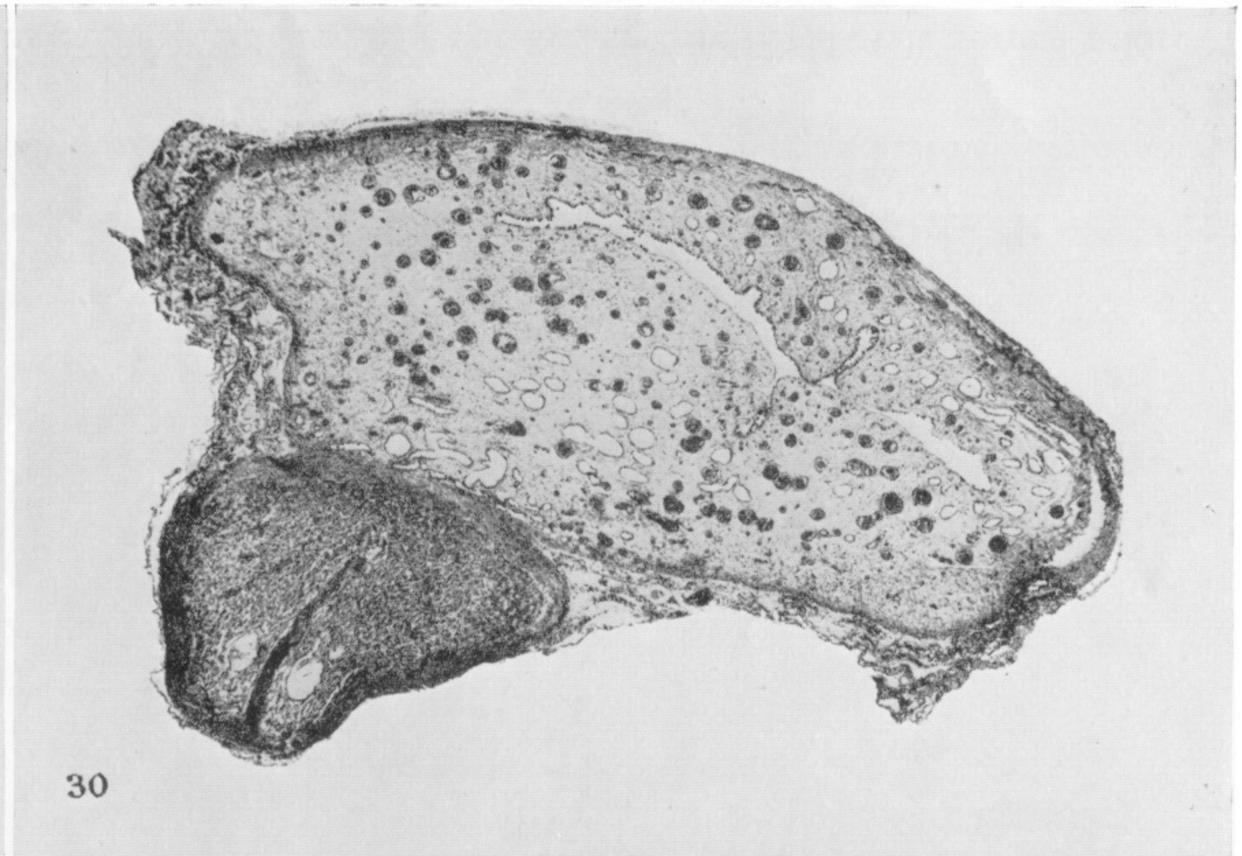
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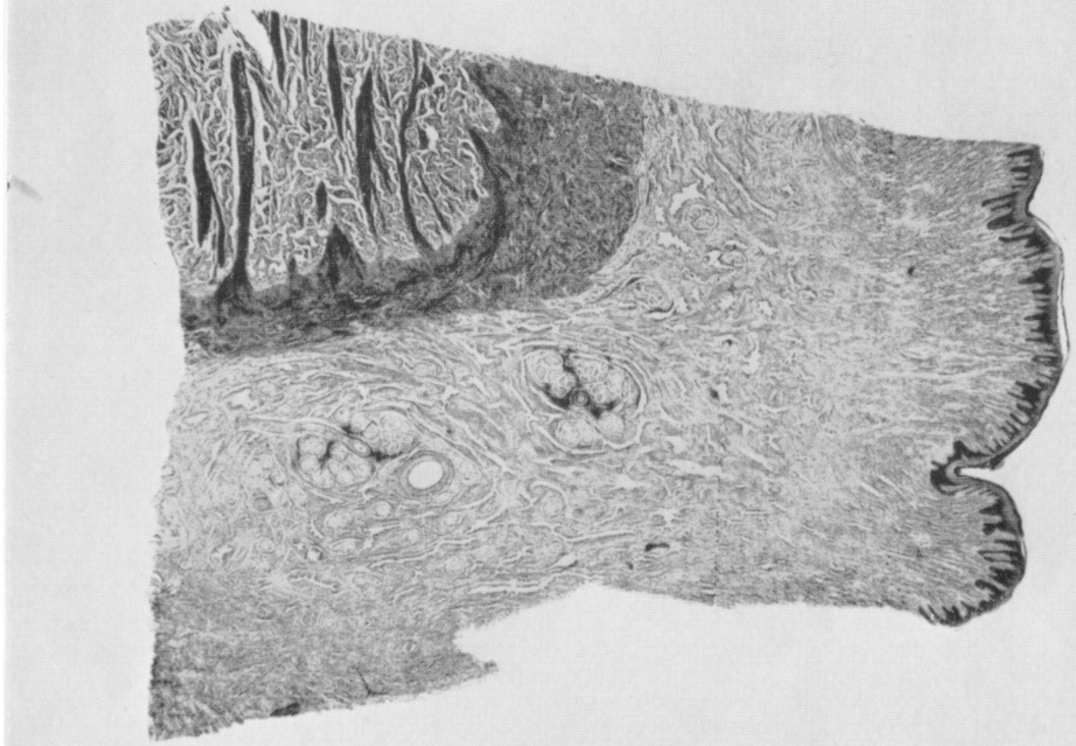
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FIGURE 29. Transverse section of the reproductive tract of the foetus shown in figure 18, in the region of the os vagina. (× 10.)
FIGURE 30. Transverse section at about the middle of the body of the clitoris of the foetus shown in figure 18. (× 15.)
FIGURE 31. Transverse section through the clitoris of a young calf (E119) shown in figure 23. (× 7.)
FIGURE 32. Transverse section of part of Cowper's gland of a young calf (E119). (× 27.)