

The Urogenital System of the Dasyurinae and the Thylacinae (Marsupialia, Dasyuridae) (1)

by

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(WITH 14 FIGURES)

SUMMARY

The present paper deals with the female urogenital system of *Dasyurus*, *Dasyurops*, *Sarcophilus* and *Thylacinus*.

I. INTRODUCTION

It is proposed to deal with the female urogenital system of the family Dasyuridae with the exception of that of the sub-family Phascogalinae which was described in a previous paper in which *Antechinus* was used as a representative of the sub-family (Pearson and de Bavay, 1951). Where it is found necessary to make broad comparisons of the various sub-families in the course of the present discussion use will be made of the conditions already found in *Antechinus*.

The urogenital system of *Dasyurus* and *Sarcophilus* was described somewhat summarily in an earlier paper (Pearson, 1945) but the observations then made were based solely upon dissections, a method which was realized at the time to be inadequate. In particular the method failed in the assessment of the size of the pseudovaginal gap, which further researches with more precise methods have now been able to correct. Owen (1868) stated that in *Dasyurus* "The mesial culs-de-sac of the vaginae descend to the urogenital passage and are connected to it but do not communicate with it or with one another". In the first paper of this series Pearson (1945) stated that "In Australian forms [Polyprotodonts] which have achieved parity the pseudovaginal gap hardly exists . . . In young females the pseudovaginal gap is present and gradually becomes reduced as maturity approaches".

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Both these opinions need to be amended in the light of the results given in the present paper which are based upon careful examination of serial sections. These have revealed beyond a shadow of doubt that the median vaginal culs-de-sac of the Dasyuridae do not extend caudally as far as the urogenital sinus at any period of life. That is to say, a definite pseudovaginal gap is present in all members of the Dasyuridae, varying in length from 40 per cent to about 60 per cent of the antero-posterior length of the vaginal complex (Table 1). Of the five superfamilies of the Marsupialia only one, the Phalangeroidae, contains some species in which the two culs-de-sac (or a single fused cul-de-sac) reach the urogenital sinus and, in a few of the more specialized forms, may acquire an actual connexion with it.

A further point of some significance revealed by the examination of these serial sections is the true extent of the urethra, as well as the precise level at which the urethra opens into the urogenital sinus. The urethra is the median efferent tube by which the contents of the urinary bladder are conveyed to the urogenital sinus. It begins anteriorly at the level of the entry of the ureters into the neck of the bladder and terminates caudally at its connexion with the urogenital sinus. Dissections of dasyurids would give the impression that the urinary bladder opens directly into the sinus and that the urethra is almost non-existent. The measurements given in Table 1, however, show that in five specimens of *Dasyurus* and one of *Dasyurops* the relative length of the urethra in terms of the antero-posterior length of the vaginal complex varies from 28 per cent to 76 per cent with a mean relative length of 50 per cent. This rather large variability may be due to one or more causes, such as, the effects of allometric growth at different stages in the life history, or to the ordinary variability found in animals of the same species, or to the condition of the urogenital system at different oestrous stages, or even to the irregular contraction brought about by variability in fixation and preservation. By comparison the mean relative length of four specimens of *Antechinus* was 38 per cent (Pearson and de Bavay, 1951). Though it is clear that reliable conclusions can hardly be drawn from such a small sample, it is nevertheless sufficient to show that the urethra in these genera is much longer than was previously thought to be the case.

These important features of marsupial morphology could not have been revealed by recourse to ordinary dissections alone, at any rate in the Dasyuridae where the vaginal complex is so small that more refined and exact methods are required. It is for this reason that serial sections have always been used to supplement, and correct where necessary, the information previously gained by mere dissections.

II. MATERIAL AND METHODS

The results described in the present paper are based upon the examination of serial transverse sections of the following species.

Sub-family *Dasyurinae*

1. *Dasyurus quoll* (Zimmermann, 1777).
2. *Dasyurops maculatus* (Kerr, 1792).
3. *Sarcophilus harrisi* (Boitard, 1841).

Sub-family *Thylacininae*

4. *Thylacinus cynocephalus* (Harris, 1808).

The numbers given to the specimens dealt with do not refer to numbers recorded in the Tasmanian Museum register but to special numbers given to specimens which were preserved, and in many cases dissected and sectioned in the course of the present investigations. To prevent any ambiguity the preserved material, as well as the large collection of serial sections, will be kept apart and will be known as the Pearson collection. This collection of serial sections of Australian marsupial material is an important one and is perhaps one of the most comprehensive of its kind to be found in any biological institution. It is hoped that this material, which at the present time (1953) is housed in the Tasmanian Museum, will be made available to other research workers when the present work has been completed.

The sections, which were cut transversely at thicknesses varying from 10 μ to 15 μ , were stained with Ehrlich's haematoxylin and counter-stained with Eosin. Graphic reconstructions have been made from these serial sections and occasionally three-dimensional models have been made. In the case of fresh material the organs to be sectioned were dissected, and then removed and fixed in Bouin's fluid. With rare species, however, it was sometimes found necessary to make use of material which originally had been preserved in alcohol of unknown strength fifty or more years ago. This applied particularly to *Thylacinus* material which, however, in spite of this disability came through the microtome ordeal fairly well and revealed somewhat inadequately the essential structures though histological details were not revealed as clearly as might have been desired. In such cases of poorly preserved material sections were sometimes cut as thick as 20 μ .

III. DESCRIPTIONS

It will be convenient to consider the four species under examination in three separate groups, viz:—

Group 1. *Dasyurus quoll* and *Dasyurops maculatus*.

Group 2. *Sarcophilus harrisi*.

Group 3. *Thylacinus cynocephalus*.

In order to obtain a full picture of the condition of the urogenital system throughout the Dasyuridae a previous paper on *Antechinus*, representing the Phascogalinae, should be consulted (Pearson & de Bavay, 1951).

GROUP 1. *Dasyurus* and *Dasyurops* (Figs. 1, 5-8)

There are only two species of Native Cat indigenous to Tasmania. As there appear to be no essential differences between the female urogenital system of the two forms, it is proposed to consider them together.

Uteri (ut.)

An examination of figs. 1-4 shows that the uterus is built on somewhat similar lines throughout the Dasyuridae. That is to say, the two fusiform uterine bodies vary in the amount of tilt displayed towards the median line. In extreme cases they lie almost parallel to the antero-posterior axis and in the other extreme such as is shown in figures 1 and 3 the caudal ends of the two uterine bodies approach close to each other. There may

be considerable variability in this respect in different individuals of the same species. The caudal extremities of the uterine bodies are linked with the vaginae by a pair of narrow uterine necks which are clearly separated from the uteri and which in combination present a characteristic Y-shaped appearance.

It should be noted that in the measurements given in Table 1 those of the uterus have been omitted, since the dimensions of this part of the urogenital system exhibit considerable variation at different periods of the oestrous cycle and will certainly vary greatly at different stages in the life of the animal. It would be difficult, therefore, to attempt to give a reliable and helpful picture of the normal dimensions of the uteri.

Vaginal complex

The vaginal complex consists of the posterior region of the two Müllerian ducts (¹). In the simplest condition each duct has a double bend. The proximal portion of the first bend receives the os uteri and passes caudally near the median line as the *cul-de-sac (m.v.c.)*. The right and left culs-de-sac are in contact mesially but are separated by a median septum between the two chambers. In certain cases this septum may be partially or completely destroyed in mature specimens, but more often than not in the more primitive members of the Dasyuroidea the septum remains inviolate. The second section of each vagina forms the distal portion of the first bend and the proximal portion of the second bend. It is the *anterior vaginal canal (a.v.c.)* and in its simplest condition passes anteriorly and outward and links the cul-de-sac with the *lateral vagina (l.v.)*. This third element of the vaginal complex forms the distal portion of the second bend and runs caudally, veering in its course towards the median line. The two lateral vaginae open together into the urogenital sinus.

As already stated, the relative size of the vaginal complex of the Dasyuridae is surprisingly small, as can be judged from the measurements given in Table 1.

These measurements show that in seven specimens of the four genera dealt with in the present paper, the relative length of the urogenital sinus in comparison to the length of the vaginal complex varies from 224 per cent to 845 per cent with a mean of 500 per cent. These figures reveal the relatively small vagina in these genera. In four specimens of the genus *Antechinus* dealt with in a previous paper, the figures varied from 221 per cent to 298 per cent with a mean of 258 per cent. The total number of specimens examined was much too small to give a reliable result but the measurements tend to emphasize two points, first, that the vaginal complex of the Dasyuroidea is very small by comparison with the length of the urogenital sinus, and secondly that the disparity is not so great in *Antechinus* as in the four genera under consideration in the present paper. In this latter respect *Antechinus* would appear to approach more closely to the condition found in the Didelphidae. The photographs given by

(¹) This statement needs some qualification as it is generally conceded that the most caudal region of the marsupial vaginae may be composed partly or entirely of elements which are not of Müllerian origin. However there is a lack of unanimity as to what these elements are. The present investigations have thrown entirely new light upon this question and it is proposed to deal with it in a paper which is now being prepared.

TABLE 1

Measurements of the parts of the female urogenital system of the specimens used in the preparation of the present paper.

	<i>ae</i> mm.	<i>ac</i> mm.	<i>ce</i> mm.	<i>de</i> mm.	<i>ef</i> mm.
Dasyurus, T.M. 221	2.80	1.29 (46%)	1.51 (54%)	2.15 (76.8%)	?
Dasyurus, T.M. 174	4.98	2.71 (54.4%)	2.27 (45.6%)	3.09 (62%)	?
Dasyurus, T.M. 88	18.30	9.00 (49.2%)	9.30 (50.8%)	5.53 (30.2%)	41.00 (224%)
Dasyurus, T.M. 282a	7.86	4.64 (59%)	3.22 (41%)	2.23 (28.4%)	33.70 (429%)
Dasyurus, T.M. 219	7.07	4.25 (60%)	2.82 (40%)	3.02 (42.7%)	45.36 (641%)
Dasyurops, T.M. 306	5.64	2.31 (41%)	3.33 (59%)	2.92 (51.9%)	47.66 (845%)
Sarcophilus, T.M. 267	10.70	2.52 (23.6%)	8.18 (76.4%)	5.29 (49.4%)	58.72 (548%)
Sarcophilus, T.M. 293	1.70	2.60 (15.3%)	1.44 (84.7%)	1.05 (61.7%)	?
Sarcophilus, T.M. 50	12.85	4.02 (31%)	8.83 (69%)	5.59 (43.5%)	?
Thylacinus, 292 (Melbourne)	2.31	0.28 (12.1%)	2.03 (87.9%)	1.83 (79.2%)	8.05 (350%)
Thylacinus, 199 (Sydney)	5.91	1.44 (24.4%)	4.47 (75.6%)	4.56 (77.1%)	27.00 (458%)

ae—Antero-posterior length of vaginal complex.

ac—Anterior extremity of vaginal complex to caudal end of cul-de-sac.

ce—Pseudovaginal gap.

de—Length of urethra.

ef—Length of urogenital sinus.

NOTE.—The percentages given in brackets refer to the proportionate length of each part in relation to the antero-posterior length of the vaginal complex (*ae*).

Hill and Fraser (1925, Plates I and II) present an admirable picture of the urogenital organs of various species of Didelphidae, but it is impossible to determine from them the precise point at which the vaginal complex ends and the urogenital sinus begins and it is equally difficult to be assured of the exact position of the clitoris. Nevertheless from these photographs it is possible to make a broad determination of the relative antero-posterior measurements of both vaginal complex and urogenital sinus. This as already stated, would be closer to those of *Antechinus* than to those of the remaining Dasyuroids which have been examined. This lends support to

the suggestion made by the present authors in an earlier paper that *Antechinus* is perhaps one of the most primitive of Australian marsupials if the evidence of the urogenital system may be used as a reliable criterion. If due allowance is made for the small number of specimens which have been measured it may be permissible to conclude that the greater relative length of the urogenital sinus in *Dasyurus* and the other genera dealt with in the present paper is perhaps evidence that on this single character *Dasyurus* and the associated genera may have departed from the prototypal condition, but not in the direction taken by some of the more highly specialised Australian marsupials in which the urogenital sinus becomes shorter than the antero-posterior length of the vagina.

It is interesting to compare the condition of the vaginal complex in No. 282A which is a parous specimen with that in No. 88 which, though of large size, is non-parous. In No. 88 both the anterior vaginal canals and the culs-de-sac have a very small lumen with an irregular shape when seen in transverse section (figs. 8A and B). These transverse sections reveal the fact that in No. 88 the thick muscular walls of the lateral vagina are made up of five or six well defined longitudinal ridges. The walls of each cul-de-sac have five longitudinal ridges and in each anterior vaginal canal the ridges are more numerous and more complicated. Moreover, the lumina of these three portions of the vagina are very constricted. The walls of the culs-de-sac are very thick and the right and left sides are separated by a solid mass of connective tissue which is much thicker than a normal septum. In 282A, on the contrary, the walls of both anterior vaginal canals and culs-de-sac are tenuous and the cavities are spacious and the longitudinal ridges referred to above are feebly developed and project but a short distance into the vaginal cavity. The right and left culs-de-sac are separated by a very thin wall consisting of a double layer of epithelium separated by a thin layer of connective tissue. This marked difference between the appearance of the vaginal complex in No. 88 and No. 282A would appear to be entirely due to the effects of distension in the latter specimen caused by parturition.

Culs-de-sac (m.v.c.)

In both *Dasyurus* and *Dasyurops* each uterine neck opens into the roof of the cul-de-sac near the tip of the swollen uterine papilla. The cul-de-sac ends blindly at its caudal end and at its anterior end passes imperceptibly into the anterior vaginal canal which runs forward immediately below the uterine neck.

Each cul-de-sac represents the proximal region of the vaginal complex and it is here that each os uteri opens into the vagina. In fully mature specimens each os uteri is situated near the tip of its uterine papilla. Theoretically the anterior or proximal region of each cul-de-sac is situated at the level of the os uteri but because of the growth and protrusion of the uterine papilla into the cavity of the cul-de-sac, the os uteri is carried a short distance caudally, leaving behind a very small irregular chink of the main cul-de-sac which surrounds a part or the whole of the papilla. Therefore, this almost isolated portion of the cul-de-sac represents the extreme anterior level of the cul-de-sac. Fig. 6 should serve to make this point clear. In very young specimens the uterine papillae are rudimentary or absent altogether in which case the anterior extremity of the cul-de-sac would be at the same level as the os uteri. This is the case in *Dasyurus* No. T.M. 221.

Usually in all immature and non-parous adult specimens the two culs-de-sac are completely separated from each other by a well-defined septum. In certain cases, however, the septum may be broken, a condition which has been considered to be the result of parturition. Flynn (1912) discussed this question at some length in the case of *Trichosurus* and concluded that a broken septum implied that the animal was parous. However, he was obliged to modify this view in the light of his later discovery of the presence of a thick unbroken septum in a *Trichosurus* which carried a pouch embryo. This confirmed van den Broek's observations on *Didelphis* in which one specimen with pouch young had a complete septum while another, which also carried pouch young, had a perforated septum. Flynn, therefore, suggested that in those parous females in which the septum was torn pseudovaginal parturition had taken place, while in those in which the septum was unbroken parturition had taken place through the lateral vaginae. New evidence on this point is now given in Table 2 from which it will be seen that in *Dasyurus* No. T.M. 282a, which carried four pouch young, the septum was complete, while in *Dasyurus* No. T.M. 174, a young non-parous specimen, the septum was broken, both phenomena being precisely the reverse of what had previously been regarded as the normal state of affairs.

It would appear, then, that Flynn's conclusions on this question cannot be sustained, since a broken septum does not necessarily imply that parturition has taken place. A broken septum in a non-parous female may possibly be explained as having been due to abnormal intra-vaginal fluid pressure during pseudopregnancy or during the height of the oestrous period. An unbroken septum in a parous specimen, on the other hand, may be simply due to the abnormal thickness and strength of the septum as may be seen in the Phascogalinae, and this may have been the normal condition when pseudovaginal parturition was first established in the Marsupialia. It is clear that in the most highly specialized members of the Phalangeroidea, where a permanent connexion between the cul-de-sac (median vagina) and the urogenital sinus is established, the primitive septum breaks down, as it does in the eutherian vagina, so as to afford as wide a passage as possible for the embryo on its hazardous journey to the exterior.

Anterior vaginal canals (a.v.c.)

Each cul-de-sac opens distally into the anterior vaginal canal which is second in sequence of the three sections of the vagina. The position of the anterior vaginal canal in relation to the cul-de-sac is perhaps seen in its least specialized condition in *Antechinus* (see Pearson and de Bavay, 1951). In that case the canal arises ventro-laterally from the cul-de-sac and takes a wide outward and forward sweep before making a sudden caudal turn into the lateral vagina. In *Dasyurus* and *Dasyurops*, however, the anterior vaginal canals take a somewhat different course. Each canal emerges from the anterior extremity of the cul-de-sac immediately below the base of the uterine papilla and proceeds cephalad below the uterine neck. The right and left canals run side by side as shown in fig. 7, then diverge and make a sharp turn first outward and then caudally to merge into the lateral vaginae, which veer gradually towards the middle line in their caudal progress until they meet and coalesce at their point of entrance into the roof of the anterior end of the urogenital sinus.

Lateral vaginae (l.v.)

This region of the vaginal complex calls for special comment in two important respects and the following remarks may be said to apply equally to all four genera dealt with in this paper.

(a) *Periodic occlusion of the lateral vaginae.* In some cases occlusions in the lateral vaginae occur near their caudal ends (see Table 2). Such occlusions are well known throughout the Marsupialia and have been referred to by various authors. (e.g., Hartman, 1923). The occlusions appear and disappear at intervals during the lifetime of an individual and this variability is probably due to changes in the oestrous condition. The lateral vaginae functioned as the birth passage in the prototypal marsupials but at a later stage in the evolution of the Marsupialia the development of the characteristic double kink probably made these ducts unsuitable for parturition. In recent marsupials parturition takes place almost invariably by way of the median pseudovaginal passage, a method which provides one of the most amazing stories in the history of mammalian embryology. In consequence of this change the lateral vaginae now have only one main function, that of storing the spermatozoa received during oestrus. These improvised spermathecae become more efficient if they are provided with plugs at their caudal extremities and the periodic occlusions serve this purpose. When the full story is known it will probably be found that these vaginal occlusions develop immediately after oestrus and last through the metoestrus stage and in exceptional circumstances perhaps through the anoestrous stage. Normally, however, the lateral vaginae are probably patent throughout the anoestrous and prooestrous stages. It is not unlikely that in certain of the more specialized marsupials such as the Kangaroos, a single supply of spermatozoa may be retained in the spermathecae for a relatively long period and in such circumstances would be available to fertilize two different sets of ova (see Wood Jones, 1923, p. 74).

This phenomenon of occlusion was observed by Flynn (1911) in an adult female specimen of *Sarcophilus* with three pouch young. He concluded that this "obliteration" of the caudal region of the cavity in each lateral vagina was caused by the mechanical action of compression or actual tearing due to the passage of the embryos down the pseudovagina, which lies medial to the lateral vaginae and in close proximity to them. This single example of occlusion observed by Flynn was confirmed by Hill and Fraser (1925) in several species of the family Didelphidae and has also been found in the course of the present investigations in the genera *Dasyurus*, *Dasyurops*, *Sarcophilus* and *Thylacinus* as well as in other marsupials. Table 2 records the incidence of occlusion in these four genera as observed during the present inquiry. Seven out of the eleven specimens examined showed occlusion of the lateral vaginae and of these seven specimens with occlusions four were definitely immature and non-parous and another was doubtfully non-parous. This evidence very clearly disposes of Flynn's contention that the occlusions are caused by the effect of pseudovaginal parturition.

(b) *Vestigial Wolffian ducts (W. d.).* The second important feature of the posterior region of the lateral vagina is the occasional persistence of the caudal remnant of the Wolffian duct, which after ceasing to function as the duct of the mesonephros undergoes degeneration in the female.

TABLE 2

Information regarding specimens of the Dasyuridae used in the preparation of the present paper.

	Maturity	Head & Body (D.C.L.)	Parity	Condition of lateral vagina	Vestigial Wolffian duct	Septum between culs-de-sac
Dasyurus T.M. 221	immature, $\frac{1}{4}$ grown pouch young	23.5 cm.	non-parous	occluded	present	complete
Dasyurus T.M. 174	immature	32.2 cm.	non-parous	occluded	present	broken
Dasyurus T.M. 88	fully grown but apparently non-parous	35 cm.	non-parous	patent	present	complete
Dasyurus T.M. 282A	was carrying 4 pouch young	33 cm.	parous	patent	present	complete
Dasyurus T.M. 219	was carrying 3 pouch young	?	parous	occluded	present	broken
Dasyurops T.M. 306	one nipple of pouch very large. Rest small	?	parous	occluded	present	complete
Sarcophilus T.M. 267	young adult	?	non-parous	occluded	present	complete
Sarcophilus T.M. 293	pouch embryo	11.7 cm.	non-parous	patent	present	complete
Sarcophilus T.M. 50	adult	60.5 cm.	probably parous	occluded	present	complete
Thylacinus 292 (Melbourne)	pouch young	13.1 cm.	non parous	occluded	present	complete
Thylacinus 199 (Sydney)	advanced pouch young	21.2 cm.	non parous	patent	present	complete

Van den Broek (1906) showed that the middle part of the Wolffian duct disappears while the cranial and caudal sections remain. In some instances it is probable that the Wolffian ducts disappear completely in the adult. On the other hand in the course of the present investigations one of us (de Bavay, 1951) has recorded the presence of a persistent Wolffian duct in an adult female specimen of *Tarsipes*. This was undoubtedly an abnormality. As already mentioned briefly in a previous paper (Pearson and de Bavay, 1951) a Wolffian remnant is present in the Dasyuroidea and an examination of Table 2 reveals that in all eleven specimens upon which the conclusions of the present paper are based a Wolffian vestige was present. Both the specimens of *Thylacinus* were pouch young and, as mentioned later, no knowledge whatsoever of the condition of the urogenital system in mature specimens of this rare form has been made known to the world, so that it is not possible to say whether the Wolffian remnant persists in adults of *Thylacinus*, but it can be stated without a shadow of doubt that in the adult females of the genera *Dasyurus*, *Dasyurops* and *Sarcophilus* the Wolffian duct is recognizable as a component of the caudal portion of the lateral vaginal. On the other hand in *Antechinus* only one out of five specimens examined by serial sections showed signs of the Wolffian remnant. (Pearson and de Bavay, 1951). It is of interest to note that in their exhaustive examination of several species of the Didelphidae, Hill and Fraser (1925) made no mention of the presence of this vestige, and the single female specimen of *Didelphis virginiana* examined by the present authors also showed no signs of the Wolffian remnant. This interesting problem is under consideration at present and a preliminary note, as yet unpublished, was submitted to Section D of the Australian and New Zealand Association for the Advancement of Science at the Sydney meeting in 1952.

Urethra (Ureth.)

This has already been discussed above. It is a median tube which runs in a caudal direction from the neck of the bladder immediately ventral to the culs-de-sac and the "pseudovagina". Its caudal limit may be regarded as the point of confluence of the two dorso-laterally placed lateral vaginae and the three ducts thus join to form the urogenital sinus. As already seen the length of the urethra is variable but normally may be said to be about one half of the antero-posterior length of the vaginal complex.

Urogenital Sinus (u.g.s.)

As already seen, the sinus is very long in the two genera now being considered (see Table 1). The clitoris is arbitrarily regarded in these studies as the posterior limit of the urogenital sinus, but in *Dasyurus* and *Dasyurops* the clitoris is not so clearly defined as it is in most marsupials. Immediately posterior to the clitoris the urogenital sinus passes into the cloaca.

GROUP 2. *Sarcophilus* (Figs. 2, 9-11)

It is proposed to deal only with those anatomical features in which *Sarcophilus* departs from the usual dasyure arrangement.

Uteri (Ut.)

It will be seen from fig. 2 that the two fusiform uterine bodies are connected with the vaginae by means of the Y-shaped uterine neck which

have two proximal convergent arms of abnormal length and a very short distal portion consisting of right and left elements which run side by side to open into the vaginae by means of the ora uterorum. This abnormally long uterine neck obviously puzzled Mackenzie (1919) who regarded it as the proximal portion of the vaginal system. This interpretation can be refuted on at least three grounds:—

1. The nature of the epithelium of the uterine necks.
2. The position of the ora uterorum on the swollen uterine papillae at the distal extremities of the uterine necks.
3. The evidence provided by a comparative study of the urogenital system of the Marsupialia.

Vaginal Complex

This consists on each side of the usual three sections, first the cul-de-sac which is the most proximal portion of the vagina. In this region the right and left sides meet in the middle line though separated by a septum. This is followed by the anterior vaginal canal which, in *Sarcophilus*, is not easily recognizable and last the lateral vagina which proximally is connected with the anterior vaginal canal and opens distally into the urogenital sinus along with its counterpart from the other side.

Culs-de-sac (m.v.c.)

Flynn (1911) has given a detailed account of the proximal portion of the vaginal complex. His description, however, is difficult to follow owing to the absence of drawings reconstructed from his serial sections. In the present paper this omission has been made good and it is hoped that the description which follows, combined with figs. 9, 10 and 11, will clarify this matter.

The right and left culs-de-sac lie side by side and are separated by a well-developed median septum. Mackenzie (1919) stated that the septum is broken in some specimens but no such instance has been noted in the course of the present inquiry, and in the case of the parous adult specimen of *Sarcophilus* described by Flynn (1911) the septum was intact. However, the variability of the septum in *Dasyurus* justifies the assumption that *Sarcophilus* and *Dasyurus* may be similar in this respect and thus lend support to Mackenzie's statement.

Each cul-de-sac consists of two portions, a proximal tubular chamber into which the os uteri opens and a larger distal portion, connected with the former by a narrow opening. This distal portion which may be regarded as the cul-de-sac proper expands into a relatively large and irregularly shaped chamber which ends blindly at its caudal extremity and in its ventro-lateral region passes imperceptibly into the lateral vagina.

The proximal chamber of the cul-de-sac was designated by Flynn, the "median vaginal neck" which according to him, "is seemingly quite distinct . . . from the median vaginal cul-de-sac". It is difficult to understand this statement as there would appear to be no doubt that the median vaginal neck is part of the cul-de-sac and actually opens into it. Throughout the present series of papers each cul-de-sac is regarded as that part of the vaginal system which is situated medially and lies immediately caudal to the os uteri. In those cases where the os uteri is situated near the tip of the uterine papilla the anterior limit of the cul-de-sac is regarded as being at the base of the papilla. The right and left culs-de-sac lie

apposed to each other and, in the specimens given in Table 2, are completely separated from each other by a median septum. This consists of the epithelium of each cul-de-sac, and an intervening layer of connective tissue of variable thickness.

Anterior vaginal canal (a.v.c.)

In an earlier paper one of us (Pearson, 1950) traced the variation in the disposition of the three sections of the marsupial vagina, viz., cul-de-sac, anterior vaginal canal and lateral vagina. Hill (1899) first coined the term "anterior vaginal canal" for a specialized narrow duct which linked each vaginal caecum with the common cul-de-sac in *Perameles*. In *Antechinus*, *Dasyurus* and *Thylacinus* Hill's anterior vaginal canal forms the proximal arm of the loop which is so characteristic of the more typical marsupials. In this respect *Sarcophilus* is not typical and it requires an effort of the imagination to locate this part of the vaginal complex. This difficulty may be resolved, however, if one defines the canal as being that part of the vagina which links the cul-de-sac with the lateral vagina.

Lateral vaginae (l.v.)

This portion of the vaginal complex calls for no special comment. But the generalized remarks made in the case of *Dasyurus* and *Dasyurops* as regards the spermathecal function of the lateral vaginae, as well as the presence of occlusions at certain stages in the oestrous cycle, and also the retention of a Wolffian remnant throughout life apply equally in the case of *Sarcophilus*.

Urogenital sinus (u.g.s.)

It has already been mentioned that *Sarcophilus* and the other members of the Dasyuroidea are characterized by the presence of a relatively long urogenital sinus. It is probably true that by comparison with the antero-posterior length of the vaginal complex the urogenital sinus of the Dasyurinae, represented by *Dasyurus*, *Dasyurops* and *Sarcophilus* is longer than in the Phasogalinae, represented by *Antechinus*. In this respect the latter sub-family would seem to conform with the members of the primitive super-family Didelphoidea. However, the few measurements dealing with this question given in Table 1 are obviously inadequate and perhaps too much should not be made of this, but it is our view based upon the condition found in primitive genera such as *Didelphis* and *Antechinus* that the prototypal marsupial had a urogenital sinus which was of considerable length though perhaps not so long as in *Dasyurus* and *Sarcophilus*. It is found that the least specialised members of the Phalangeroidea have a relatively long sinus which becomes shorter in the Macropodidae and still shorter in the Potoroidae. In one of his papers on *Sarcophilus* Flynn (1910), dealing with the long urogenital sinus present in that genus, stated that this was one of the points in which "the genital organs of *Sarcophilus* are relatively more advanced than those of *Perameles*" (where the sinus is almost non-existent). In earlier papers Hill (1899, 1900) had also expressed the view that the short sinus was a primitive condition, but there is abundant evidence to claim that the exact opposite is probably true, namely, that the very short urogenital sinus of *Perameles* is one of several characters in that genus which show that the bandicoots are an aberrant group and not primitive, as Hill and Flynn claimed. (see Pearson, 1945, pp. 76-80).

GROUP 3. *Thylacinus* (Figs. 3, 12-14)

This interesting marsupial is confined to Tasmania though it once lived on the Australian mainland. It is now, unfortunately, very rare and almost extinct. So far as is known a specimen has not been captured for at least twenty-five years though from time to time reports come in of specimens having been seen. Perhaps a dozen such reports have been received at the Tasmanian Museum in the last twenty years, many of them being most unreliable. However, until about 1920 *Thylacinus* was occasionally killed or captured and there can be no doubt that in the early settlement days in Tasmania, it was fairly common, so common in fact that it proved to be a menace as a sheep-slayer and a price was actually placed upon its head. Looking back, it is amazing to contemplate that no Australian zoologists took advantage of the presence of this rare form to make a serious study of its anatomy while specimens were readily procurable. The result has been that no account of the female urogenital system has hitherto been published. The only account of its internal anatomy was made by Professor D. J. Cunningham (father of Admiral of the Fleet Viscount Cunningham) from material collected by the "Challenger" Expedition. Unfortunately Cunningham's admirable paper dealt with a male specimen. The present account loses much of its value since it is based upon the examination of immature specimens, one a fairly advanced pouch young, No. 199, having a dorsal contour length (head and body without a tail) of 31.2 cm. This specimen was kindly lent by the authorities of the Australian Museum, Sydney. Another specimen, a pouch young, No. 292, having a D.C.L. of 13.1 cm. (head and body, minus tail) was placed at our disposal through the kindness of the authorities of the National Museum, Melbourne. These specimens had been preserved in spirit without any special process of fixation and as they are about fifty years old it was not to be expected that the serial sections would be very revealing. However, it was found that the sections proved to be sufficiently informative to enable a reasonable interpretation to be made of the condition of the urogenital system. But such an interpretation being based upon immature material loses much of its value and we are still ignorant of the precise arrangement of the mature female urogenital system of *Thylacinus*.

The condition of the female urogenital system in the two pouch embryos which have been examined does not disclose any striking features. It can be said that both specimens show a general arrangement of the urogenital system as might be seen in most marsupials at some early stage in their development. Fig. 3 shows the general design which calls for no special observations. In figs. 12 and 13 the vaginal region is shown in greater detail and this is further elaborated in the diagrams given in fig. 14. These diagrams are not as satisfactory as might have been desired but the poor condition of the specimens precluded the use of detailed drawings.

Uteri (ut.)

The general arrangement is disclosed in fig. 3. The two uteri are splayed outward from their distal extremities which meet in the middle line. Here each uterine body passes sharply into the uterine neck, the right

and left necks running side by side in a caudal direction for a distance equal to one-half the length of each uterine body. At their distal ends the two uterine necks pass imperceptibly into their respective culs-de-sac. It is noteworthy that the ora uterorum are not situated on uterine papillae. No significance should be attached to this feature which may be regarded as common to all marsupials in the immature condition.

Vaginal Complex

The general disposition of the vaginal region follows the simple conventional double loop arrangement which forms the basis of the vaginal plan of all marsupials. That is to say, the proximal portion, the culs-de-sac (right and left, separated by a septum in the median line) which end as blind sacs at their caudal extremities; a second portion, the two anterior vaginal canals which pass forward and outward from each cul-de-sac; and a distal portion at each side continuous with the anterior vaginal canal which turns sharply in a caudal direction to form the lateral vagina.

Culs-de-sac (m.v.c.)

These are well defined and have a length equal to about one-fifth of the antero-posterior length of the vaginal complex. The two culs-de-sac are separated by a well developed septum. As stated earlier, the anterior limit of each cul-de-sac is at the level of the os uteri when the uterine papillae are absent. It is important to note that even in these extremely immature specimens the culs-de-sac have reached a higher stage of development than that found in mature specimens of *Antechinus*. This might be taken to indicate that the mature females of the genus *Thylacinus* may possess a more highly developed type of urogenital system than that known to occur in the phascogales. This is a justifiable assumption as the experience gained in the course of the present intensive investigation indicates that the nature of the female urogenital system serves as a valuable pointer in the somewhat difficult question of marsupial phylogeny. Tate (1947) has suggested that *Thylacinus* and the small New Guinea phascogale *Murexia* are the survivors of a very old line, and accordingly has placed the former genus in the sub-family Phascogalinae alongside *Murexia*, which may startle some systematists. But he has been careful to point out that if *Thylacinus* is descended from a small generalized *Murexia* both the modern representatives are now far removed from their primitive ancestor and from each other, though both retain certain cranial features in common. Both have travelled a long way and to a great extent in different directions. Fundamentally there is nothing startling in this concept as most biologists have been brought up on the dictum that all marsupials have been derived from small arboreal ancestors. However, the evidence of a mature female *Thylacinus* might well show that the vaginal system of that form is sufficiently advanced to justify placing *Thylacinus* in its own separate sub-family, as is generally accepted by systematists on other grounds.

Anterior vaginal canals (a.v.c.)

Each canal leaves the antero-lateral region of the cul-de-sac and passes forward and outward lying on the outer side of the uterine neck. The cavity of the canal is laterally compressed. At its most anterior region it is confluent with the lateral vagina.

Lateral vaginae (l.v.)

Each lateral vagina passes caudally in the normal manner and approaches nearer to the middle line as it pursues its course.

In specimen No. 292 the cavity of the canal is occluded near its caudal end. In No. 199 the entire cavity remains patent. In both specimens the vestiges of the Wolffian duct can be recognized (fig. 13, w.d.).

The two canals open together into the dorso-lateral wall of the urogenital sinus. The ventrally placed urethra opens into the sinus at the same level.

Urogenital sinus (u.g.s.)

As was mentioned earlier, the urogenital sinus follows the general dasyure plan in that it is much longer than the antero-posterior measurement of the vaginal complex. This is clearly shown in fig. 3 and in Table 1.

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REFERENCES TO FIGURES

<i>a.v.c.</i> —Anterior vaginal canal	<i>r.ur.</i> —Right ureter
<i>bl.</i> —Bladder	<i>sept.</i> —Septum between r. & l. culs-de-sac
<i>cl.</i> —Clitoris	<i>s.h.</i> —sinus horn
<i>lev. ur. p.</i> —Level of the ureteric papillae (¹)	<i>u.g.s.</i> —Urogenital sinus
<i>l.v.</i> —Lateral vagina	<i>ur.</i> —Ureter
<i>M.d.</i> —Müllerian duct	<i>ureth.</i> —Opening of the Urethra into the urogenital sinus
<i>m.v.c.</i> —Median vaginal cul-de-sac	<i>ut.</i> —Uterus
<i>m.v.n.</i> —Median vaginal neck	<i>ut.n.</i> —Uterine neck
<i>occ.M.d.</i> —Occluded Müllerian duct	<i>ut.p.</i> —Uterine papillae
<i>occ.W.d.</i> —Occluded Wolffian duct	<i>W.d.</i> —Wolffian duct
<i>os. ut.</i> —Os uteri	

(¹) Also shown by the posterior pair of crosses in Fig. 7 and by the single pair of crosses in Figs. 10 and 13.

EXPLANATION OF FIGURES (1)

- FIG. 1.—Dorsal view of the female urogenital system of *Dasyurus*, No. 88 x $\frac{3}{4}$.
- FIG. 2.—Dorsal view of the urogenital system of *Sarcophilus* (No. 50) x 1.
- FIG. 3.—Dorsal view of the urogenital system of *Thylacinus* (No. 199) x 3.
- FIG. 4.—Dorsal view of the urogenital system of *Antechinus* (No. 291) x 5.
- FIG. 5.—*Dasyurus*, No. 88 x 5. Vertical paramedial section through the vaginal region. (The uterine neck, urethra and urogenital sinus are only partly shown).
- FIG. 6.—*Dasyurus*, No. 88 x 5. Horizontal section showing the uterine necks opening into the right and left culs-de-sac.
- FIG. 7.—*Dasyurus*, No. 88 x 5. Horizontal section through the same region. The positions of the ora uterorum are indicated by the two small crosses and those of the openings of the two ureters into the bladder by the two larger crosses.

NOTE.—If a tracing of fig. 6 is made on transparent paper and applied to the appropriate part of fig. 7, the relative positions of the uterine necks and the anterior vaginal canals will be more readily understood. A, B, C and D mark the levels of the four transverse sections illustrated in fig. 8.

- FIG. 8.—*Dasyurus*, No. 88 x 5. Four transverse sections, A, B, C and D taken through the four levels indicated in figs. 5 and 7.
- FIG. A.—T.S. through the region of the uterine necks and the anterior vaginal canal.
- FIG. B.—T.S. through the region of the culs-de-sac.
- FIG. C.—T.S. taken at the level of the openings of the ureters into the neck of the bladder. The urethra may be regarded as starting at this point.
- FIG. D.—T.S. taken slightly anterior to the opening of the lateral vaginae with the urogenital sinus.
- FIG. 9.—*Sarcophilus*, No. 50 x 9. Vertical paramedial section through the vaginal region. (The uterine neck, urethra and urogenital sinus are only partly shown).
- FIG. 10.—*Sarcophilus*, No. 50 x 9. Horizontal section through the same region as in fig. 9. The two crosses indicate the position of the openings of the ureters into the neck of the bladder.
- A, B, C, D, E, F and G indicate the respective levels at which the transverse sections, shown in fig. 11, are cut.
- FIG. 11.—*Sarcophilus*, No. 50 x 9. Seven transverse sections taken through the seven levels A-G indicated in figs. 9 and 10.
- FIG. A.—T.S. through the region of the ora uterorum.
- FIG. B.—T.S. showing the right and left median vaginal necks (*m.v.n.*) and the anterior extremities of the anterior vaginal canals (*a.v.c.*).
- FIG. C.—T.S. showing the connexions between the median vaginal necks and the main body of the cul-de-sac.

(1) In figs. 1-7, 9, 10, 12 and 13 the urinary bladder and urethra are not shown. However the level at which the ureters enter the neck of the bladder (*lev.ur.p.*) and the opening of the caudal end of the urethra with the urogenital sinus (*ureth.*) are indicated.

FIG. D.—Transverse section showing the confluence of the cul-de-sac and the anterior vaginal canal (*a.v.c.*).

FIG. E.—Transverse section showing the connexion between the anterior vaginal canal and the lateral vagina (*l.v.*).

FIG. F.—Transverse section through the level at which the ureters (*ur.*) open into the neck of the bladder (anterior extremity of the urethra, *ureth.*).

FIG. G.—Transverse section through the occluded portion of the lateral vagina, showing the vestige of the Wolffian duct (*occ. W.d.*) at the level at which it joins the Müllerian duct (*occ. M.d.*).

FIG. 12.—Lateral view of the female urogenital system of *Thylacinus* juv. x 20.

FIG. 13.—Dorsal view of the female urogenital system of *Thylacinus* juv. x 20.

FIG. 14.—*Thylacinus* juv. x 20.

A.—T.S. through A in fig. 13.

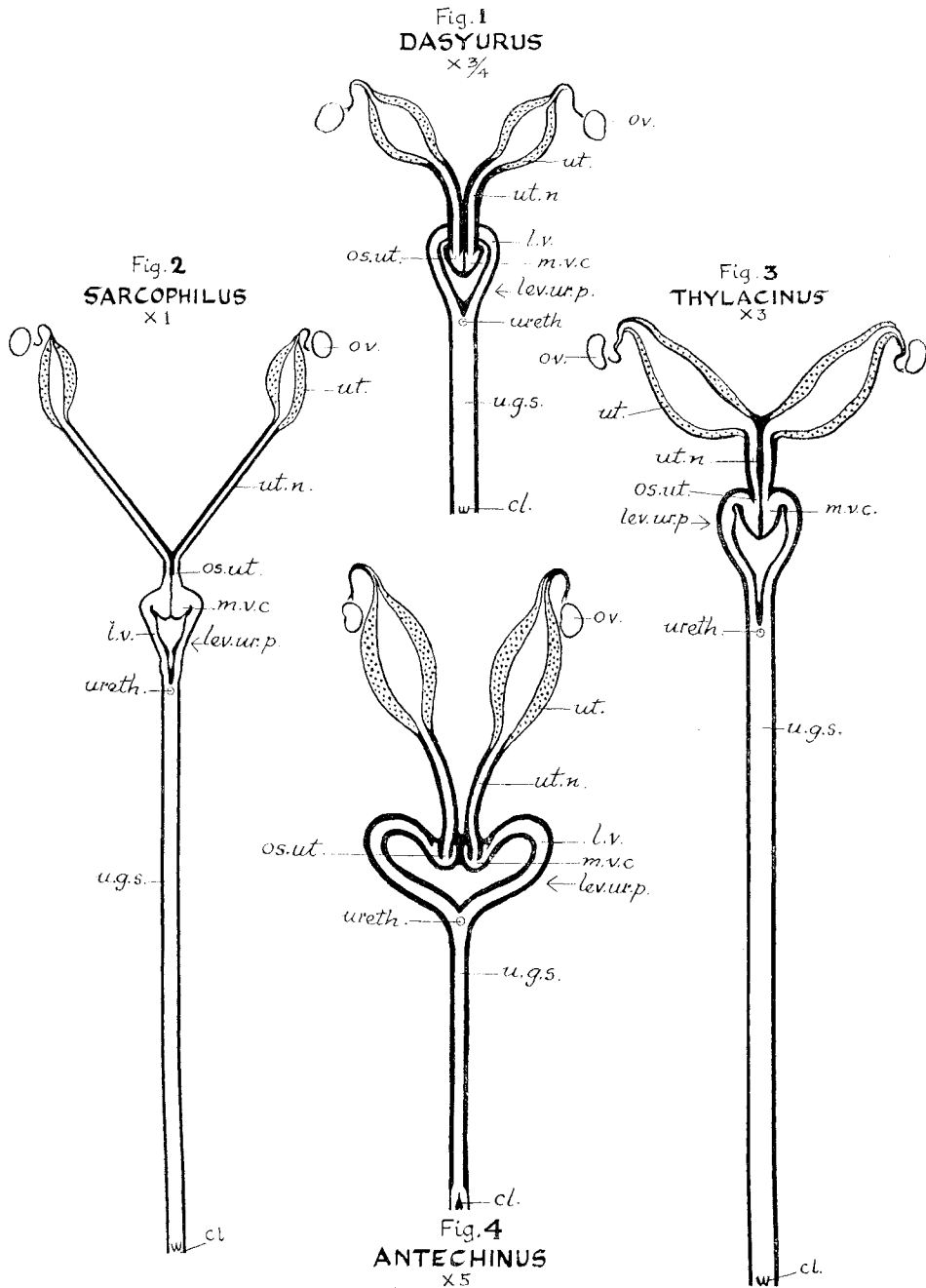
B.—T.S. through B in fig. 13.

C.—T.S. through C in fig. 13.

D.—T.S. through D in fig. 13.

E.—T.S. through E in fig. 13.

NOTE.—*l.v.* in fig. E should more correctly be termed sinus horn. The two sinus horns constitute the caudal sections of the lateral vaginae (*l.v.*) and are antero-dorsal outgrowths of the urogenital sinus.



FIGS. 1-4.—Horizontal sections of *Dasyurus*, *Sarcophilus*, *Thylacinus* (juv.) and *Antechinus* respectively.

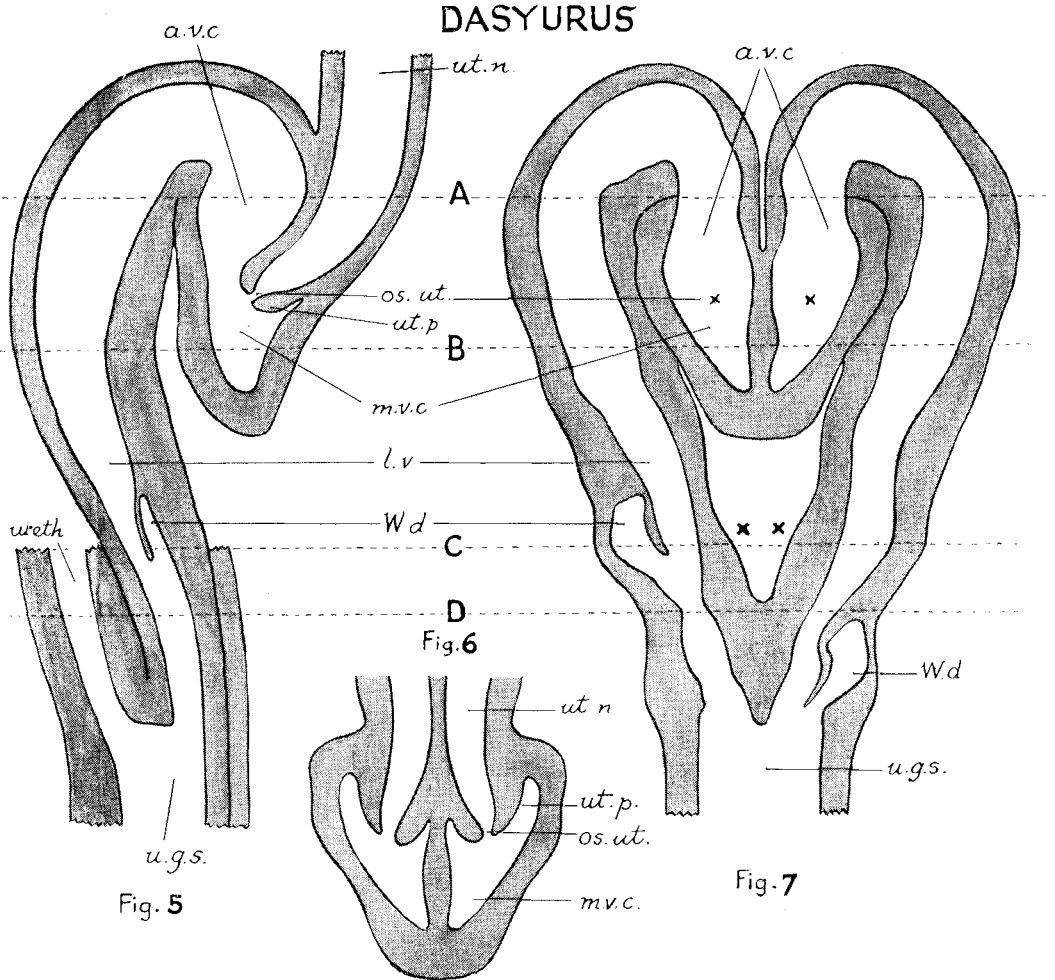


FIG. 5.—Paramedial section through vaginal region (*Dasyurus*) x 5.

FIG. 6.—Horizontal section showing connexions between the uterine necks and the culs-de-sac (*Dasyurus*) x 5.

FIG. 7.—Horizontal section of vaginal region (*Dasyurus*) x 5.

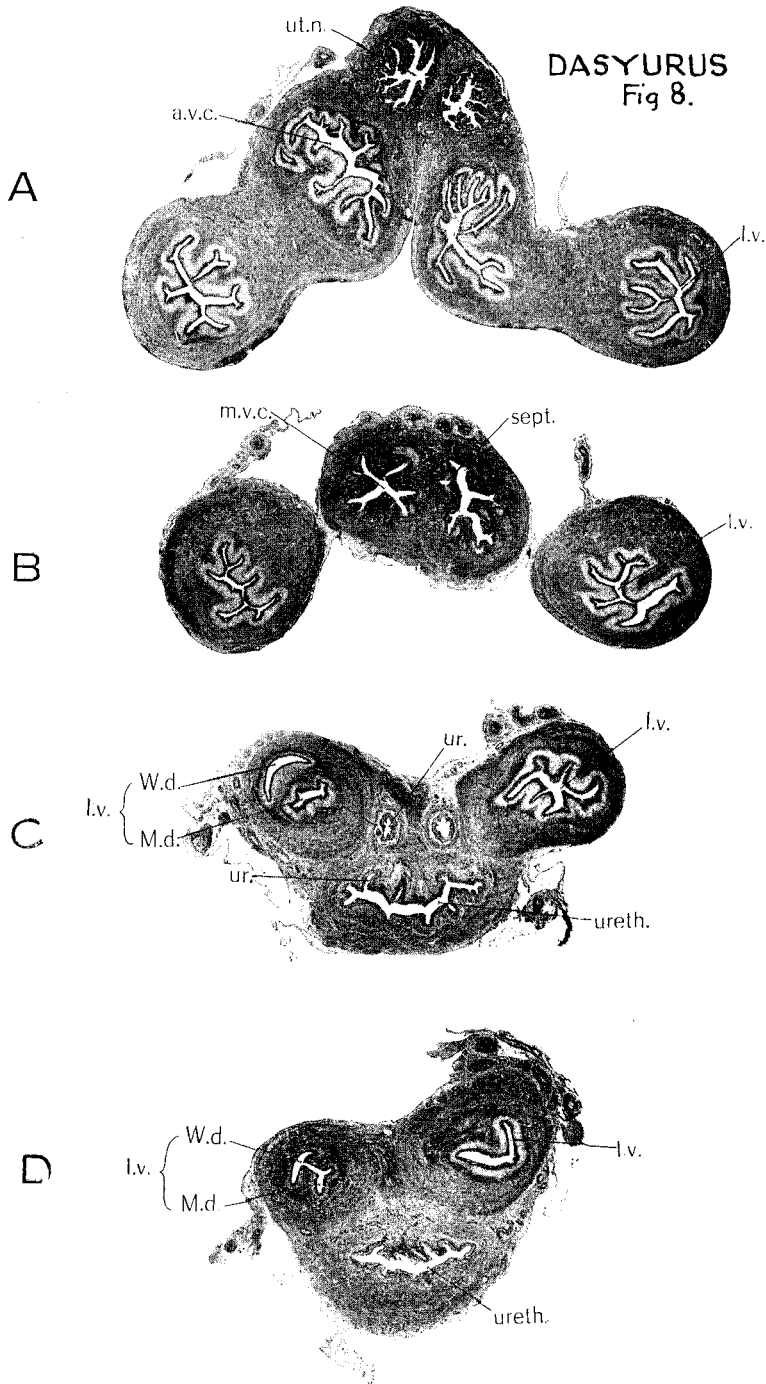


FIG. 8.—Four transverse sections through figs. 5 and 7 (*Dasyurus*) x 5.

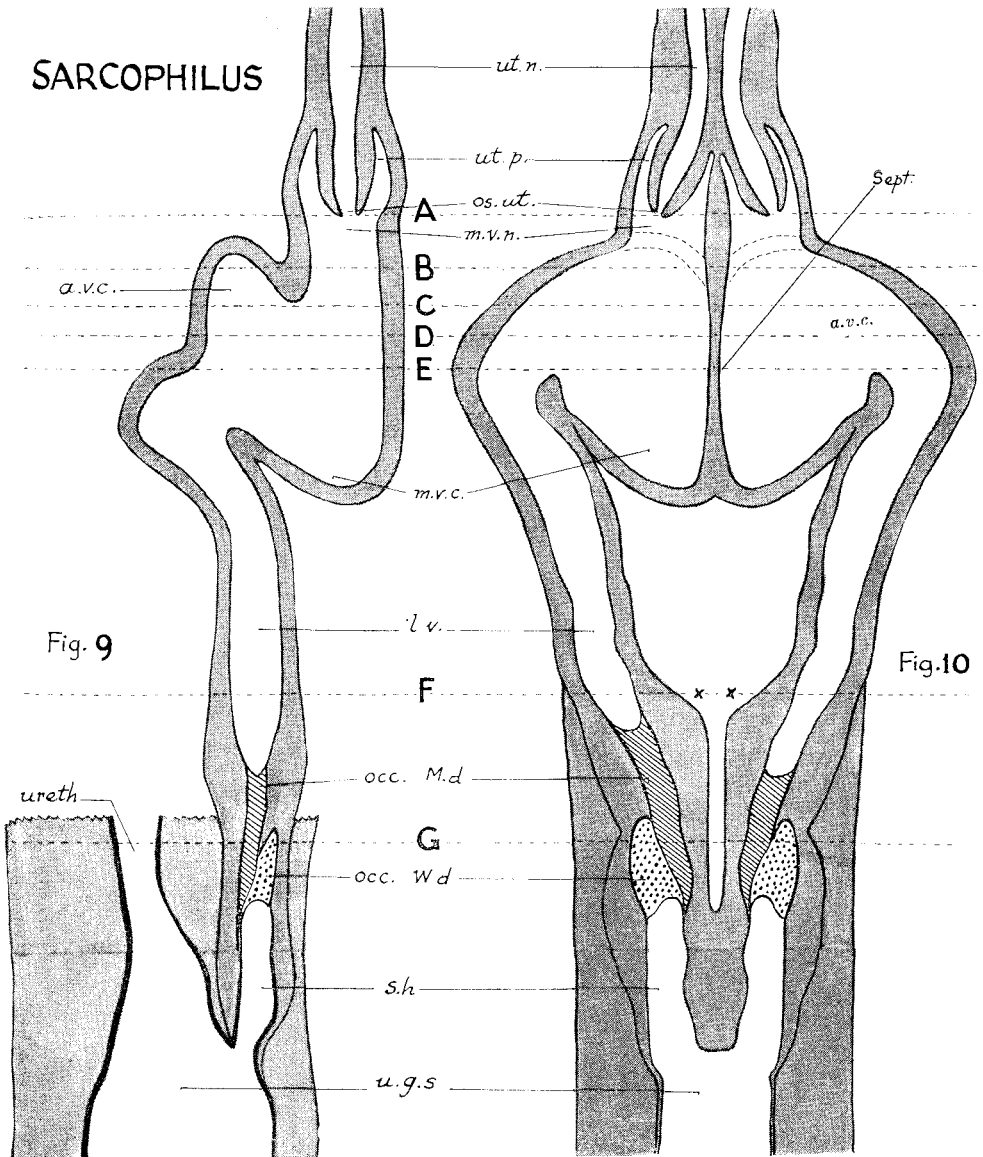


FIG. 9.—Paramedial section through vaginal region (*Sarcophilus*) x 9.

FIG. 10.—Horizontal section through same region as in fig. 9. (*Sarcophilus*) x 9.

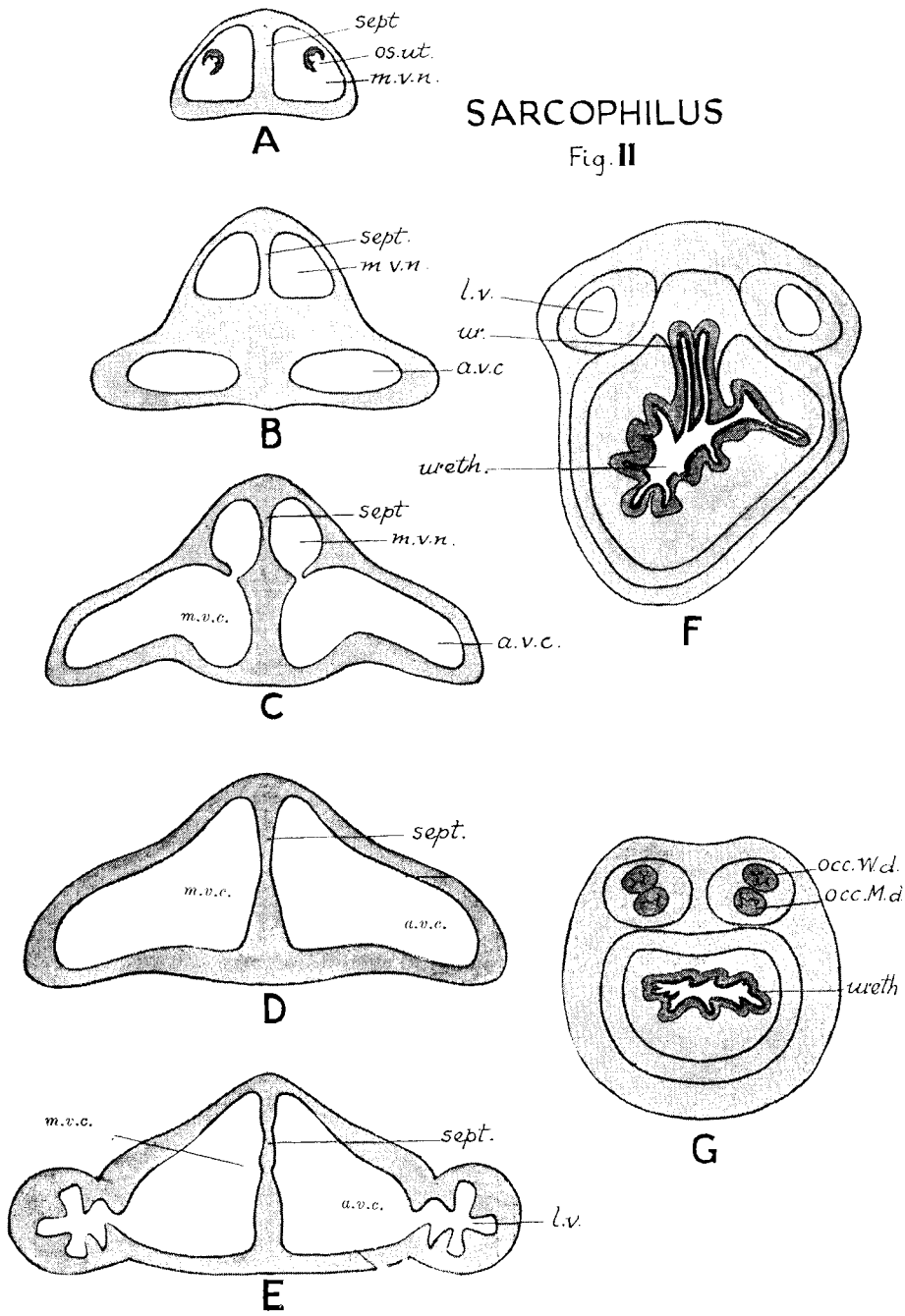


FIG. 11.—Transverse sections through fig. 10. (*Sarcophilus*) x 9.

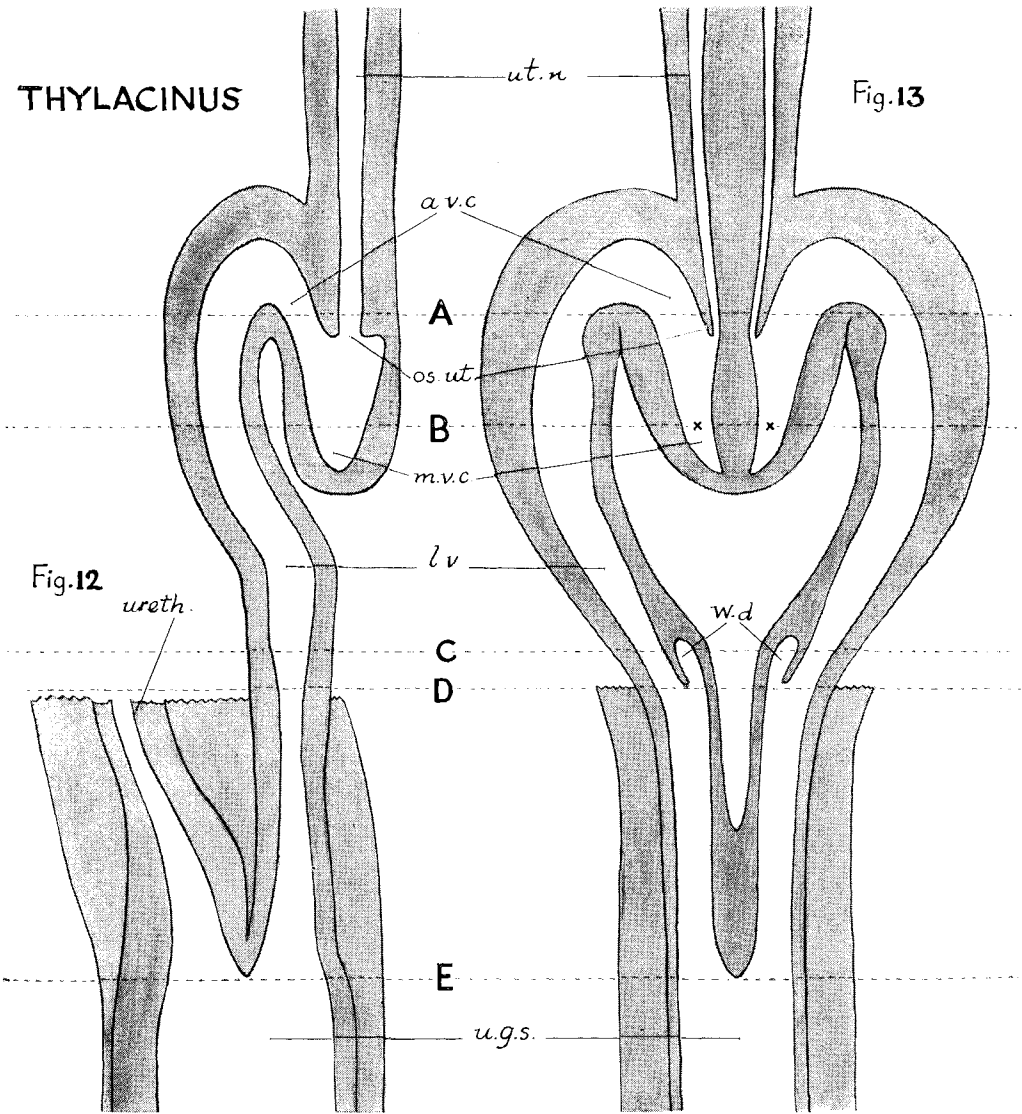


FIG. 12.—Paramedial section through the vaginal region (*Thylacinus* juv.) x 15.

FIG. 13.—Horizontal section through the same region as fig. 12. (*Thylacinus* juv.) x 15.

THYLACINUS

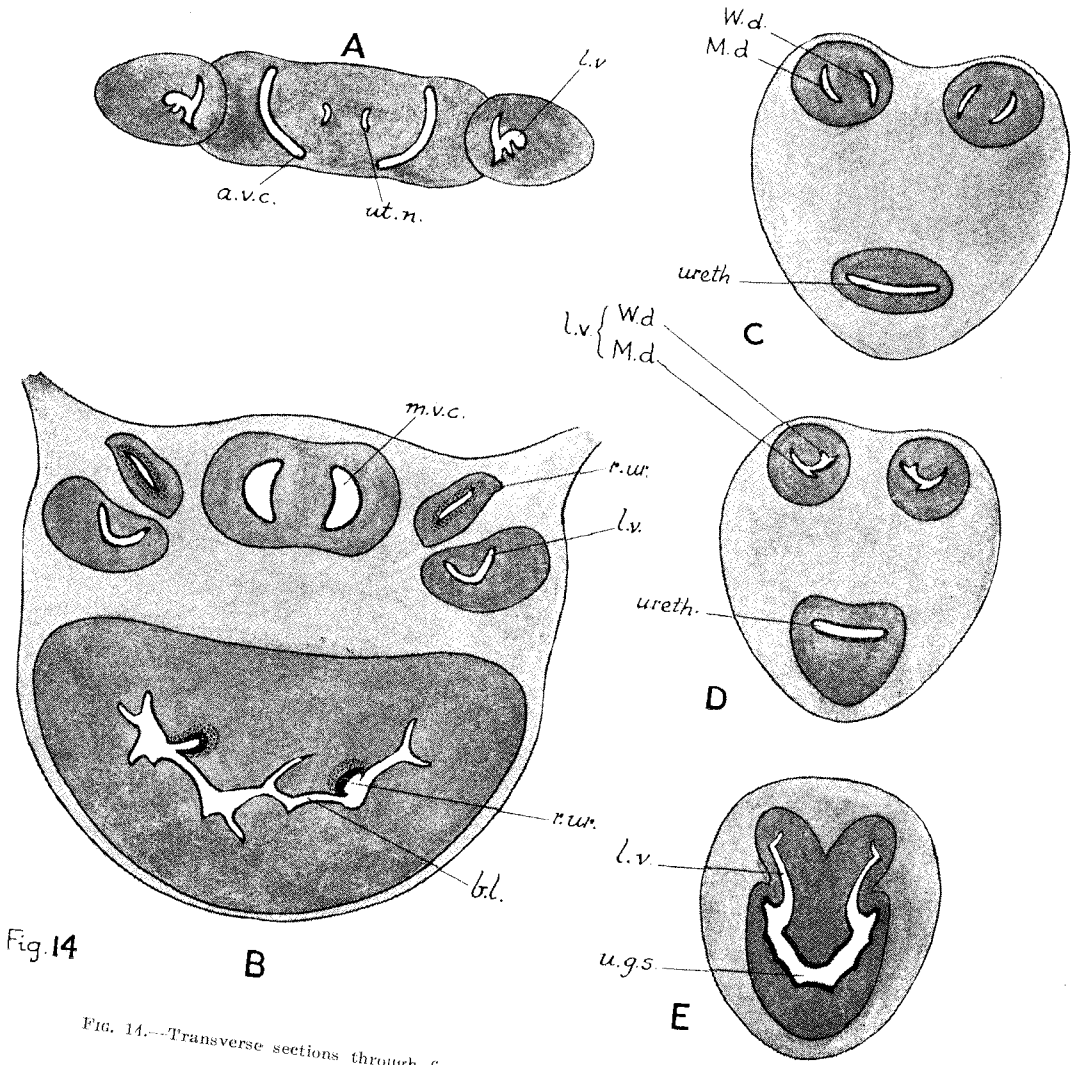


Fig. 14

FIG. 14.—Transverse sections through figs. 12 and 13. (*Thylacinus* juv.) x 15.

