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THE MALE GENITAL SYSTEM AND REPRODUCTIVE CYCLE OF *ELEPHANTULUS MYURUS JAMESONI* (CHUBB)

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[Plate 2]

CONTENTS

A study was made of the structure of the testis, epididymis, vas deferens and accessory sexual glands in a number of males of *Elephantulus myurus jamesoni* (Chubb), killed at different periods of the year.

The testes are retained in the abdominal cavity and contain very little connective tissue and interstitial cells; a mediastinum testis is absent and the rete testis is reduced and confined to a small area in the capsule.

The corpus epididymidis is abnormally elongated. The cauda epididymidis is a large body consisting of a wide and greatly coiled tube, folded on itself and located between the rectum and the urethra in a gutter formed by the dorsal prostate glands.

The testes in adults are fully active throughout the year, and no seasonal variation in the size of the testes, or change in the diameter of the seminiferous tubules, is found.

The accessory sexual organs were identified as consisting of five pairs of prostate glands situated around the proximal part of the urethra, a pair of Cowper's glands and a bilobed uterus masculinus. The prostate glands differ in epithelial structure, the amount of stroma and in the type of secretion produced.

The accessory sexual organs are in full activity from July to January. During the latter half of January and in February regression in size and in height of the epithelium takes place. The ventral prostate glands become inactive before the other four pairs of prostate glands. After a period of quiescence, the accessory sexual glands prepare for the next breeding season.

There is a definite cycle in the size of the interstitial cells. From June there is a steady increase to August and October when the cells reach their maximum size and are in the fully active secretory condition. They gradually decrease in size to reach their minimum size in April. This inactive condition persists to June when a steady growth for the next breeding season begins; the most rapid growth takes place at the end of July.

Introduction

In recent years a number of papers have appeared dealing with the male reproductive system and cycle of various small mammals. Allanson (1932) described the reproductive cycle of the ferret and in 1933 that of the grey squirrel; Miller (1939) reported on two species of bats; Rowlands (1936) described that of the bank vole. The only papers to appear on Insectivora are those of Allanson (1934) on the hedgehog, and of Brambell (1935) on the common shrew.

The work of van der Horst & Gillman (1941) and van der Horst (1946) has established that in the female *Elephantulus myurus jamesoni* the breeding season is restricted and lasts approximately from the end of July to the middle of January; during the remaining six months of the year the reproductive organs are in a state of quiescent anoestrus. The first matings occur at the end of July or the beginning of August, and by the middle of August the breeding season is in full swing with nearly all the females in complete oestrus or early pregnancy. At the beginning of the breeding season sterile ovulations were never observed, but at the end of the season they do occur frequently, and many females, at this time, have repeated ovulations before fertilization may take place (van der Horst, 1954).

In view of these facts it seemed probable that the male *Elephantulus* would also show seasonal reproductive activity, to thus account for the fact that many females at the end of the breeding season ovulate but are not always fertilized. The present investigation was undertaken in order to determine the occurrence of such a quiescent period in the male *Elephantulus* and to correlate the changes taking place in the testes with those taking place in the accessory sex organs. Since no histological studies of the testis and accessory sex glands of the Macroscelididae have been made, it was thought essential to undertake such a study in this investigation.

Material and technique

(1) *Source of material*

The organs were obtained from the material stored in the collection of *E. myurus jamesoni* (Chubb) which has been collected by the Department of Zoology over a period of years. The majority of animals was collected at Bronkhorstspruit in the Transvaal, but a few came from Alberton and Klerksdorp.

(2) *Histological technique*

The material was fixed in Bouin's fluid immediately after the animals were captured and killed, and was then transferred to 70 % ethyl alcohol, in which it was stored. Since the males were not originally collected for a specific research problem, they were fixed whole, but this method did not appear to give inferior histological results. Sections of the testis were cut at 7, 8, 10 and 12 μ, those of the accessory sex glands at 10 μ generally, although a few sections in some of the series were cut at 8, 12 and 14 μ. The circum-urethral glands were, in the majority of series, sectioned with the gland *in situ* around the urethra. A complete seasonal histological series was obtained for the circum-urethral glands and for Cowper's glands, excepting for the months of September, March and May, when apparently no male animals were collected.

The sections of the testis were stained with Heidenhain's iron-haematoxylin, some of them being counterstained with eosin. One series was stained with Hansen's haematoxylin and eosin. The accessory sex glands, epididymis and vas deferens were stained with Hansen's haematoxylin and eosin, every third slide, however, being stained with Mallory triple stain.

(3) *Measurement of organs*

Measurements were made of the diameters of seminiferous tubules, epididymis tube and vas deferens. In each animal the diameters of the organs were obtained with a micrometer eyepiece at a magnification of either 60 or 258. For each of these organs fifty tubules were measured, the least diameters being taken in order to avoid measuring oblique sections due to the coiling of the tube. Measurements of the epididymis were all taken in the posterior part of the caput and in the actual cauda, and all measurements given include the muscular layers of the tubules unless otherwise stated. Since the diameter of the vas deferens varies slightly throughout its length, the measurements were confined entirely to the middle region, where the diameter appeared to be constant for any individual. Since the vas deferens was measured in the same position in the different animals these measurements can be used for comparative purposes.

The interstitial cells of the testis were measured with a micrometer eyepiece at a magnification of 582. Twenty-five cells were measured in each testis, and great care was taken to measure only those cells located well within the section.

GENERAL MORPHOLOGY OF THE REPRODUCTIVE ORGANS

(1) *Testis*

The testis of *E. myurus jamesoni* are abdominal throughout life, lying slightly caudally to the kidneys, thus retaining their embryological position (figure 1). The anterior parts of the testes are partly covered ventrally by the kidneys. In the fully mature male the testes

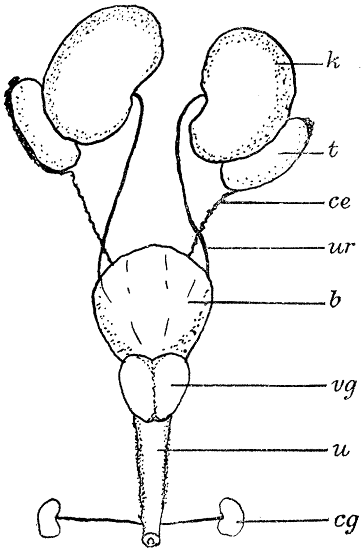


FIGURE 1. Diagram of the general morphology of the male genital system of *Elephantulus myurus jamesoni*. (Magn. × $1\frac{1}{2}$.) *b*, bladder; *ce*, corpus epididymidis; *cg*, Cowper's gland; *k*, kidney; *t*; testis; *u*, urethra; *ur*, ureter; *vg*, ventral prostate gland.

are ovoid in shape, with average measurements of 11·0 mm for length, and 4·0 mm for width. Individual variation occurs, with the length varying from 10·0 to 12·0 mm, and the width from 3·5 to 4·0 mm, these ranges being for animals killed in the same month and having approximately the same body weight.

(2) *The genital ducts*

On the medial surface, somewhat anterior to the middle of the testis, six to eight vasa efferentia arise, running dorso-medially towards the anterior part of the testis where they unite to form the epididymis. The caput epididymidis essentially consists of a greatly coiled canal, tightly packed into a form of a long, wide, flattened body attached to the lateral part of the dorsal surface of the testis and extending to its posterior surface where it passes over into the corpus epididymidis. The latter has a characteristic type of coiling in the form of a flat spiral, and is a very narrow, flattened body measuring about 24·0 mm in length from its point of junction with the corpus to that with the cauda epididymidis. It is this extremely elongated corpus epididymidis and not the vas deferens that forms the loop around the ureter where it passes down the abdominal cavity to join the cauda epididymidis. The latter is a large, greatly coiled body consisting of a wide tube folded on itself and lying with its blind end caudally, between the urethra and the rectum, in a gutter formed completely from the two posterior dorsal accessory sex glands. This gutter lies against the rectum, so that the caudae epididymides are sometimes forced to lie to the sides of the rectum. This is the position in which the caudae epididymides were generally found, but in a few animals it was observed that the left or right tube may be located to the side of the bladder, and in one individual the two tubes were found to lie criss-cross on the sides of the bladder. Since these animals had been fixed as whole animals, previously to dissection, it was difficult to determine whether these different positions occupied by the caudae epididymides were natural positions and not caused by rough handling of the material; it appears to be easy to pull them out of their normal position, since they are not fixed by connective tissue to the posterior dorsal accessory glands or the rectum.

In summary, the epididymis consists of three sections, viz. the caput epididymidis which adjoins the dorsal border of the testis, the corpus epididymidis which continues across the abdominal cavity, and the cauda epididymidis which lies dorsally to the urethra in a perfectly formed gutter. The epididymidis thus extends from the anterior tip of the testis to approximately the middle of the urethra.

Medially from the cauda epididymidis the short ductus deferens, approximately 8·0 mm in length, arises and passes anteriorly along the dorsal side of the urethra, running parallel to the distal part of the corpus epididymidis and enveloped in the same connective tissue. Both the corpus and cauda epididymidis lie in the gutter described above. The vasa deferentia enter the urethra dorsally about 1·0 mm distal to the neck of the bladder. The latter point, however, is not sharply delimited, since the bladder narrows gradually into the urethra.

(3) *The accessory glands*

Posterior to the bladder and surrounding the urethra is located a series of at least five pairs of glands (figures 2, 3). The first pair, which may be called the ventral pair, lies against the posterior ventral surface of the bladder and covers the urethra ventro-laterally;

these glands are large and in the form of flattened lobes. The second pair, which may be called the outer anterior dorsal pair, is located dorsally to the former pair, also lying against the bladder and laterally to the urethra; this pair is smaller than the first pair but also in the form of flattened lobes. The third pair, or inner anterior dorsal glands, is of similar type to the second pair and is located medially to the latter. Lying medially to the outer anterior dorsal glands, and partly covered laterally by them, is the fourth pair of glands, which may be designated as the middle dorsal glands; this pair is also flattened and lobular. The fifth pair, the posterior dorsal glands, is long and narrow and lies dorsally on either

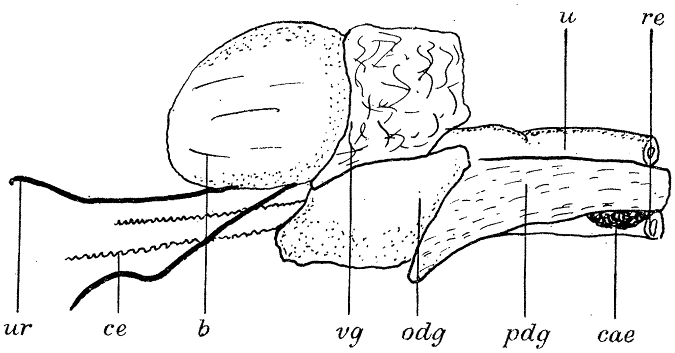


FIGURE 2. Diagram of lateral view of the prostate glands. (Magn. ×$2\frac{1}{2}$.) *b*, bladder; *cae*, cauda epididymidis; *ce*, corpus epididymidis; *pdg*, posterior dorsal prostate gland; *odg*, outer anterior dorsal prostate gland; *re*, rectum; *u*, urethra; *ur*, ureter; *vg*, ventral prostate gland.

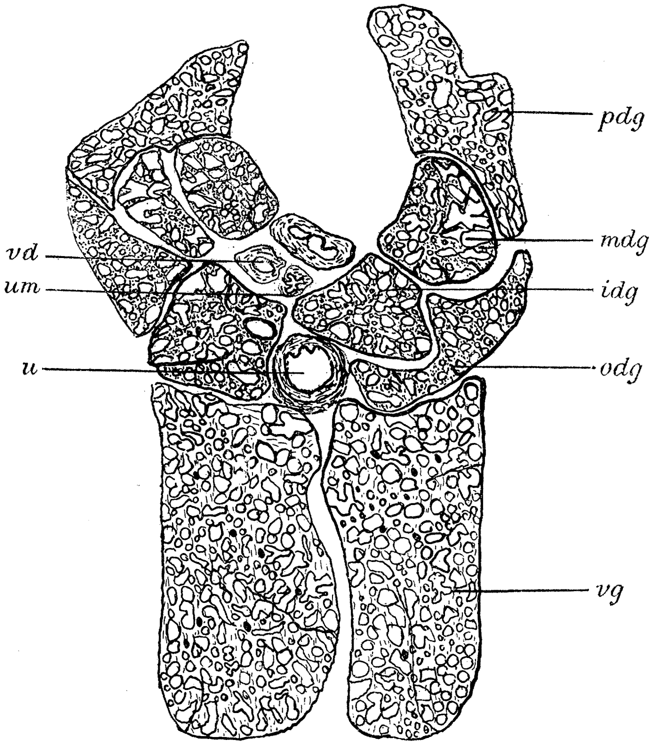


FIGURE 3. Camera lucida drawing of a transverse section of the urethra, prostate glands, vas deferens and uterus masculinus. (Magn. ×18.) *idg*, inner anterior dorsal prostate gland; *mdg*, middle dorsal prostate gland; *odg*, outer anterior dorsal prostate gland; *pgd*, posterior dorsal prostate gland; *u*, urethra; *um*, uterus masculinus; *vd*, vas deferens; *vg*, ventral prostate gland.

side against the urethra, while the anterior ends cover the remainder of the middle dorsal glands, so that the latter are completely covered laterally. The dorsal glands, since they lie dorsally to and on either side of the urethra, form a complete gutter inside which the caudae epididymidis lie. Preliminarily these five pairs of circum-urethral glands may be called the prostate mass.

There appears to be no gland consisting of a tube, coiled upon itself, and giving off numerous outpocketings, which opens into the distal part of the vas deferens and which could thus represent a seminal vesicle.

Between the vasa deferentia and lying within the anterior and middle dorsal mass of glands is a single, bilobed, blind dilation of about 1 mm in length; this is the uterus masculinus. In the majority of the specimens the double nature of the uterus masculinus can be recognized with ease; in these it appears as a single canal with two separate horns. However, in others the double nature of the uterus masculinus is obscured, the two horns or lobes being enclosed in a common sheath.

Cowper's glands are well developed, kidney-shaped and somewhat flattened dorso-ventrally; each measures approximately 5 mm in length and 3 mm in width. The two Cowper's glands lie outside the pelvis, behind the ischia on either side of the base of the tail and embedded in the fascia of the thigh. Long ducts, 8·5 mm in length, run from them to the urethral bulb where they enter by a common opening into the lumen of the urethra.

The praeputial glands, which are very large in many rodents, are apparently absent in the *Elephantulus*. Animals were examined with great care for any trace of these glands; they were, however, always found to be wanting. Since no sections of the tip of the penis were cut, it is possible that the glands, which may be extremely minute and diffuse and only discernible in sections, were overlooked. According to Brambell (1935) the glands are not conspicuous in the shrew, and Carlsson (1909) does not mention these glands in her description of *E.* (*Macroscelides*) *rozeti*.

The anterior part of the penis is folded back on itself and lies extended against the abdominal wall, covered with skin. Compared with the size of the animal the penis is very long and in the present series varies in length from 50 to 64 mm, measured from the insertion of the ischio-cavernosi muscles to the tip of the glans penis, which is situated near the umbilicus of the animal.

HISTOLOGY OF THE TESTIS AND THE ACCESSORY SEX GLANDS

(1) *Testis and genital ducts*

The histology of these organs is essentially the same as that found in other mammals; some differences, however, do occur, and these will be described in the following paragraphs.

In the majority of mammals the tunica albuginea projects at the anterior dorsal surface into the interior of the testis, forming an incomplete vertical septum, the mediastinum testis. This is not found in *Elephantulus*, there are no septa, the compartments are wanting, and a mediastinum testis, as seen in other mammals, is not present. The seminiferous tubules all appear to converge towards the medio-dorsal surface of the testis where they enter directly into the irregular anastomosing channels of the rete testis. The latter is produced and confined to a small area in the capsule, about midway down the medio-dorsal border of the testis, and has the appearance of cleft-like spaces within the white fibrous tissue. The cavities of the rete testis are generally lined by squamous epithelium, but where they pass over into the vasa efferentia they are lined by cuboidal epithelium. At the upper end of the rete testis these channels terminate in from six to eight ducts, the vasa efferentia, which run outside the tunica albuginea to the anterior tip of the testis where they converge and pass over into the epididymis. In the majority of mammals the vasa efferentia arise from the rete testis in the anterior tip of the testis where they perforate the tunica albuginea and pass straight into the epididymis. The vasa efferentia in *E. myurus jamesoni* are lined by a single row of low columnar cells. These cells have spherical nuclei, clear cytoplasm, are ciliated, and rest upon a very thin connective tissue wall of about two bundles thick. The vasa efferentia are bound together by collagenous fibres.

The anterior part of the caput epididymidis is but slightly coiled; the epithelium lining the lumen is medium columnar with rounded cells, resembling the epithelium of the vasa efferentia. The remaining and main portion of the caput is greatly coiled, the epithelium gradually becomes pseudo-stratified, consisting of tall columnar cells at the base of which lie the flattened basal cells. The cells of the epithelium are about 38μ in height, have elongated nuclei, finely granular cytoplasm and are ciliated. The cilia are long and often adhere together to form a brush border. The coils of the caput epididymidis are firmly united into a solid mass by means of the intervening collagenous fibres. In many transverse sections of the tubules a secretory product was found to be present.

The caput abruptly passes into the much less coiled and narrow corpus. The epithelium of the latter is histological similar to that of the caput, being also pseudo-stratified. The cells of the epithelium, however, are lower than those found in the caput, being approximately 31μ in height; the cilia are shorter. The epithelium lining the lumen of both the caput and corpus rests upon a very thin coat of collagenous fibres interspersed with odd muscle cells. The flat spiral coil of the corpus is bound together by a large amount of white fibrous connective tissue.

The cauda epididymidis is greatly increased in diameter as compared with the corpus and caput, and the large lumen is always packed to capacity with sperms (figure 5, plate 2). The epithelium here is also pseudo-stratified, consisting of cuboidal cells between the bases of which are wedged the flattened basal cells. The cilia are extremely short and do not adhere together to form a brush border, the nuclei are spherical filling about three-quarters of the cell, whereas those of the caput are elongated and fill only the basal third of the cell. The epithelium rests upon a relatively thick muscular wall consisting of smooth muscle fibres running in a circular manner. The coils of the cauda are held together by collagenous fibres, and where the cauda passes over into the vas deferens the coiling becomes reduced and the wall of the tubule much thicker.

Macroscopically, the diameter of the vas deferens does not appear to vary, but in sections it has been found to vary slightly throughout its whole length, being narrower towards the cauda epididymidis and wider towards the urethral end; however, there is no marked dilatation into an ampulla. The vas deferens was measured throughout its length with a micrometer eyepiece and was found to vary from 430μ at its proximal end to 500 μ

at its distal end, the main body of the vas deferens being approximately 480μ. These measurements were taken from an animal killed in July. Thus in *Elephantulus* there are no swellings either in the distal or proximal part of the vas deferens comparable to those found in *Sorex* by Brambell (1935), and in *Hylomys*, *Gymnura* and *Crocidura* by Ärnbäck-Christie-Linde (1907). These swellings have been described by the latter as glandular evaginations of the vas deferens, covered by the muscular wall of the latter, and thus it was thought that, although the vas deferens did not enlarge into a visible swelling, the glandular mass may be found surrounding the lumen. On histological examination this was not found to be the case. No glandular material of any kind was found throughout the vas deferens.

The lumen of the vas deferens is slightly irregular, it is lined by tall ciliated cells with prominent basal nuclei. The vas deferens has a very thick muscular coat of smooth muscle fibres. There are no distinct divisions into circular and longitudinal muscle-fibre layers, the fibres being interwoven very intimately with one another, and with the numerous collagenous fibres, to form a single thick layer, with numerous nuclei. On the periphery an adventitious coat of connective tissue and a few longitudinal fibres can be seen, and immediately external to the basement membrane a very thin coat of collagenous fibres can be distinguished.

The deferentia do not open directly into the lumen of the urethra, but run alongside the urethra tube within the muscular coat for some distance posterior to their entrance into the wall. On the dorsal wall of the lumen of the urethra a narrow median longitudinal evagination of the epithelium and surrounding connective tissue is formed. Into this small elevation, in the prostatic part of the urethra, the vasa deferentia open by small slit-like openings; the uterus masculinus opens by a single slit-like orifice which lies between the openings of the vasa deferentia on the summit of the elevation.

(2) *The accessory glands*

(*a*) *The prostate mass*

The ventral and posterior dorsal pairs of glands of the prostate mass are similar in structure, both being of the branching tubular variety and having very little intertubular tissue. The ventral gland consists of four main lobes, the outer lobes being much larger than the inner ones which lie medially to the former and are completely covered by them. The tubules of both the ventral and posterior glands are tightly packed together and lie in a very small amount of stroma which is found merely scattered in the angular spaces between the tubules. The stroma of the gland is of loose connective tissue, consisting of strands of collagenous fibres, connective tissue cells and odd muscle fibres which can be seen scattered in the stroma. The glands are enclosed in a thin investing capsule of a similar but denser structure.

The glandular epithelium which lines the tubules of the ventral and posterior dorsal glands is generally of a simple columnar type (figures 6 and 10, plate 2). The cells are of the tall columnar variety, although in different parts of the gland the epithelium may show a great deal of variation depending on the state of activity of the tubules; where the lumina are greatly extended with secretion the epithelium appears to be medium or low columnar. The cells possess spherical nuclei which fill the basal third of the cell; the cytoplasm is finely granular. The nuclei of these glands do not stain darkly and contain a number of karyosomes. The epithelium rests upon a thin wall of connective tissue fibres. In sections, the secretion of the ventral gland forms coagulated, net-like, deeply staining masses in the lumen (figure 6). The secretion stains a deep blue colour with Mallory stain, but only a faint pink with haematoxylin and eosin. The vesicles of the posterior dorsal glands are of various sizes and contain a viscous, homogeneous, colloidal substance which stains a pale blue colour with Mallory stain. The granules of secretion which are found mostly in the distal part of the cells has a slightly different staining reaction to that of the ventral gland with Mallory stain.

The ventral glands give rise to a pair of excretory ducts which pass laterally to the urethra where they enter the prostatic portion of the latter a short distance after the vasa deferentia have entered the lumen. The posterior glands give rise, at varying intervals along their whole length, to single pairs of excretory ducts, one from each gland, which open independently into the floor of the membranous part of the urethra, thus giving rise to from twelve to eighteen excretory ducts. These ducts enter the lumen of the urethra opposite where they enter the wall. Histologically there appears to be very little difference in structure between the tubules and the excretory ducts of the posterior glands. Those of the ventral glands, however, are generally lined by a single row of low columnar or squamous epithelium.

The outer and inner dorsal pairs of glands can be grouped together, since, although they differ in the type of secretion produced, they are identical histologically. These glands differ very greatly from the ventral and the posterior dorsal glands in structure and to a lesser extent from the middle dorsal glands. Both the anterior and middle dorsal glands are, in contrast to the ventral and posterior dorsal glands, of the compound alveolo-tubular variety, the middle dorsal glands, however, appearing much more alveolar. The lobes of these glands are divided into a small number of lobules which are separated from one another by thin strands of connective tissue fibres. These glands are closely invested by a capsule of fibro-muscular tissues, which sends incomplete septa into their substance, dividing the lobules still further into masses of irregular shape and size.

The internal structure of the anterior dorsal glands is of an irregular nature, large cavities, sometimes assuming the character of cyst-like enlargements, alternating with narrow branching tubules (figure 8, plate 2). The secretory portion of the gland is lined mainly by simple columnar epithelium. The cells of the epithelium are medium columnar, very narrow, with elongated nuclei filling about two-thirds of the cells. The cytoplasm contains numerous fine secretory granules, and both the cytoplasm and the nuclei take up a much darker colour than those of the ventral gland when stained with the same stain. Whereas the secretory portions of the glands are lined by medium columnar epithelium, the tubular portions are lined by low columnar or squamous epithelium. The middle dorsal glands differ from the anterior dorsal glands in that the cells of the epithelium are wide, with spherical nuclei, whilst those of the latter are narrower with elongated nuclei which stain darker. The epithelium of both the anterior and middle dorsal glands rest upon a thickish coat of connective tissue fibres.

The secreting alveoli of the glands of the anterior and middle dorsal pairs of glands are embedded in a very dense stroma; the abundant interstitial tissue consists of dense connective tissue, strands of collagenous fibres, and many smooth muscle fibres arranged in strands of varying thickness and intimately blended with the collagenous fibres. The muscle cells form either groups or bundles of variable size, or are frequently isolated within the meshes of the connective tissue.

On the free surface of the cells of the epithelium of the anterior gland, drops or bleb-like formations appear which are cast off into the lumen. In sections the secretion appears as globules which vary considerably in size; some of these globules are minute, others are very large, measuring up to 12μ in diameter. In the outer anterior dorsal glands, the globules, the material of which appears fractured, stains a bright blue colour with Mallory stain. The globules in the pair of inner anterior dorsal glands are all homogeneous in structure but differ as regards their staining capacity, some staining a blue colour, others a bright red with Mallory stain. With haematoxylin and eosin the secretion of both glands stains a pale pink colour, but here too the fractured nature of the globules of the outer glands can distinctly be seen to differ from the homogeneous type of the inner glands. In the middle dorsal glands the lumina of the alveoli are filled with a homogeneous colloidal substance which stains readily with eosin, taking a very bright pink colour; with Mallory stain, however, it stains a pinkish mauve colour. As a rule the lumen of the alveoli is not completely filled with the colloidal mass, which is adherent to the surface of the lining epithelium by delicate thread-like processes (figure 12, plate 2). This appearance is possibly a fixation artefact and is found in all the prostate glands described here.

From the inner dorsal glands a pair of large ducts passes dorso-laterally into the urethra wall. Three small ducts arise from each outer anterior dorsal gland to enter the urethral wall in the same position as the ducts from the inner glands. Within the wall these six ducts unite to give rise to a single pair of ducts lying on either side of the urethra. The ducts from both pairs of glands run in the urethral wall and open into the lumen laterally and posteriorly to the vasa deferentia, the ducts from the inner glands opening slightly anteriorly to those from the outer glands. The excretory ducts are generally lined by low columnar epithelium, but within the wall of the urethra they are stratified; they possess a relatively thick fibro-muscular coat. From the middle dorsal pair of glands six to eight excretory ducts, three to four from each gland, which enter the floor of the urethra after the ducts of the anterior dorsal and ventral gland have opened into the lumen, arise. These ducts are generally lined by medium columnar epithelium.

During the study of the five pairs of accessory glands it became evident that, although the lining epithelium is of a simple columnar type, small areas occur where this is based on a few small cells, giving the appearance of a pseudo-stratified epithelium.

(*b*) *Uterus masculinus*

Lying between the anterior dorsal and middle dorsal glands and opening on the summit of the urethral evagination between the vasa deferentia, is the uterus masculinus. It is not merely a vestigial organ without any function, but is an accessory gland of the male sex organs. The vesicles are lined by a mucous membrane with many folds and with numerous glandular invaginations (figure 14, plate 2). The latter lie very close to one another and are only separated by thin strands of connective tissue. The epithelium of the glandular invaginations consists of tall columnar cells with spherical nuclei lying in the basal parts of the cells. The lumen of the vesicles is wide and very irregular and filled with a thick homogeneous secretion which stains a deep pink colour with eosin.

Surrounding the vesicles is a thick smooth muscle coat consisting of longitudinal and circular fibres intimately interwoven and not arranged into distinct layers. On the periphery numerous blood vessels lie within a layer of connective tissue. In sections it has been observed that the two horns of the uterus masculinus, although retaining their own muscular wall, may be enclosed in a common connective tissue sheath, thus macroscopically appearing as a single blind vesicle. In the majority of cases, the horns are not enclosed in a common sheath but are completely separate. Where the horns fuse to form the single tube the epithelium is still simple but later when the tube becomes the excretory duct it becomes stratified and very narrow.

(*c*) *Cowper's glands*

The only glands remaining to be described are the large Cowper's glands. These glands appear to be very alveolar and consist of irregular cavities which anastomose freely with one another at their terminal portion (figure 15, plate 2). Surrounding the gland is a thick muscular capsule consisting of striated muscle fibres which run longitudinally in parts and in a circular fashion in others. From the capsule strands of muscle fibres penetrate the interior, dividing the gland into a number of lobules of varying size. Within the lobules the enlarged alveoli are separated from one another by connective tissue bundles of varying thickness. The interstitial tissue consists of loose connective tissue, collagenous fibres and odd smooth and striated muscle fibres and appears to form a fair portion of the material of the gland. The stroma is richly supplied with blood vessels.

In the secretory acini the structure of the epithelium is subject to great variation. Some of the smaller alveoli are lined by tall columnar epithelium, with spherical nuclei occupying the basal third of the cells, and with granular cytoplasm. The enlarged alveoli are, however, lined by cuboidal or squamous epithelium. The secretion generally is invisible microscopically, but sometimes a highly dispersed material, which stains a faint pink colour with eosin, is found within the lumen.

Within the gland the interlobular and the smaller intralobular ducts are lined by a single layer of low columnar cells. From each gland a single long duct arises. These excretory ducts have a very irregular lumen which is lined by tall columnar cells with elongated nuclei, alternating with low columnar cells containing spherical nuclei. A thin coat surrounds the ducts.

Seasonal variation in the reproductive organs

(1) *Testis*

(*a*) *Gross size*

The testes were measured for the various months of the year, and it was found that there was no appreciable difference between the size of the testes of animals killed during the breeding season and those of animals killed during the non-breeding season. For the breeding season the testes varied in length from 10·0 to 12·0 mm and 3·5 to 4·0 mm in width, whilst the testes of animals killed in April varied in length from 9·5 to 10·5 mm and in width from 3·1 to 3·7 mm. The latter animals, although spermatogenically active, were smaller in size, which may account for the small difference in size found between the testes of animals killed during the breeding season, and those killed during the non-breeding period. From the data of the histological study it was felt that the testes of individual animals would not show any great seasonal variation in weight; the size for the various seasons apparently falls within the limits of individual variation, and thus the testes were not weighed. In other animals which have an anoestrous period very large seasonal differences in size are found. In *Sorex vulgaris* the breeding season testis is 8·0 mm long and 5·0 mm wide, whilst the anoestrous testis is only 2·0 mm long and 1·5 mm wide (Ärnbäck-Christie-Linde 1907). In the ferret, the active testis reaches over ten times its anoestrous weight (Allanson 1932); in the common shrew the increase may be over three times (Brambell 1935), and in the hedgehog, which does not show such a marked seasonal variation, the increase is only about twice its anoestrous weight (Allanson 1934).

(*b*) *Diameter of the seminiferous tubules*

In animals with a typical anoestrous period the size of the seminiferous tubules varies with the degree of activity of the germinal epithelium. In *Elephantulus myurus jamesoni* the germinal epithelium of the seminiferous tubules is active throughout the year, and a lumen of more or less constant size is always present. The diameters of the seminiferous tubules were, however, measured to see whether there was any seasonal variation in spite of the fact that the testes were spermatogenically active throughout the year. The diameter of the seminiferous tubules for August was found to have a mean of $196 \pm 1{\cdot}6\mu$, while for April a mean diameter of $186 \pm 1{\cdot}4\mu$ was found, which varies significantly from that for August with $t = 4{\cdot}1$ for 38 degrees of freedom. Too few individuals, however, were examined to be able properly to evaluate these deviations and to separate them from individual variations. For example, on comparing two individuals, one killed in August and the other in April, the average diameter of the tubules of the former was found to be $194 \pm 2{\cdot}1\mu$ and for the latter $190 \pm 2{\cdot}1\mu$, which gives a $t = 1{\cdot}4$ for 38 degrees of freedom and evidently not a significant difference. On the other hand, an individual killed in January was found to have a mean tubule diameter of $182 \pm 2{\cdot}1\mu$, which when compared with the above-mentioned diameter for August shows a $t = 4{\cdot}04$ for 38 degrees of freedom, which is significant. It seems certain, therefore, that the seminiferous tubules do not show marked seasonal variation in diameter and that the differences found are probably due to individual variation. The extreme limit of variation, in *E. myurus jamesoni*, would be an increase of only 0·07 time during the breeding season. In the ferret, where there is a marked seasonal variation, the diameter of the tubules varies from 70 to 80μ during the non-breeding season to 150 to 190μ during the breeding period, so that during the latter period they may be about twice their anoestrous size (Allanson 1934).

(*c*) *Spermatogenesis*

The occurrence of the various stages of spermatogenesis was studied for the different seasons of the year and the following facts emerged.

During the breeding season spermatogonial divisions are fairly common. All stages of mitosis are found, but the stage most commonly seen is that of interphase after the last division which appears to be a stage of long duration. The anaphase and metaphase stages of mitosis are found near the basement membrane. All the seminiferous tubules contain a large number of meiotic divisions in all stages of division, the most common stage being the pachytene stage of prophase. This stage appears to last for a considerable time. Occurring in patches in several sections of the seminiferous tubules are the metaphase and anaphase stages of the first meiotic division. The second meiotic division is of very short duration, and only a few spermatocytes have been observed in metaphase and anaphase. In nearly all sections of the seminiferous tubules large numbers of spermatids are found. From July to January over 75 % of the sections of the seminiferous tubules contain sperms in various stages of spermiogenesis; many sections having spermatozoa with their tails projecting into the lumen (figure 4).

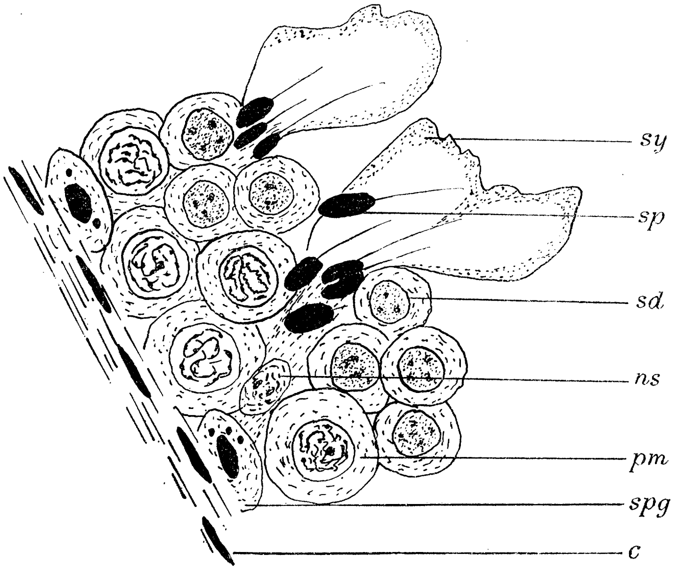


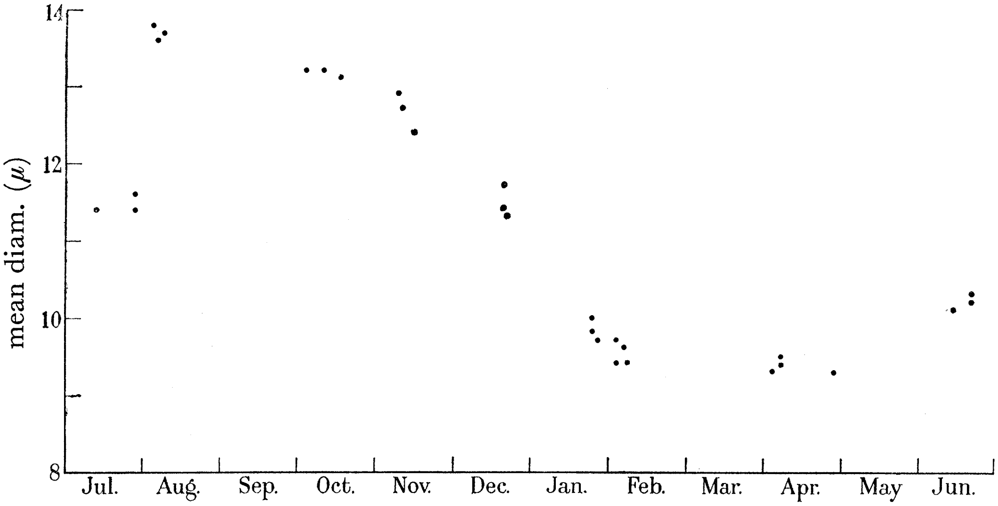
FIGURE 4. Camera lucida drawing of part of a transverse section of a seminiferous tubule. (Magn. × 750). *c*, connective tissue capsule; *ns*, Sertoli cell nucleus; *pm*, primary spermatocyte; *sd*, spermatid; *sp*, sperm; *spg*, spermatogonium; *sy*, cytoplasm of spermatids.

At the end of the breeding season, i.e. towards the end of January, the production of spermatozoa slows down and about 60 % of the sections of the seminiferous tubules contain sperms. Spermatozoa with tails projecting into the lumen occur in about 30 % of the sections. During this period mitotic divisions are fairly common, more being seen during February than at any other time of the year, but meiotic divisions are relatively scarce, and those that do occur are mostly in the pachytene stage. However, at no time during the year do we find the production of spermatozoa ceasing. During February and April large numbers of spermatids are found in the sections, but the process of spermiogenesis is slowed down. By the middle of June spermatozoa are being formed at a similar rate to that found during the breeding season.

(*d*) *Interstitial cells*

In *E. myurus jamesoni* the interstitial tissue of the testis appears to undergo cyclic variation. Throughout the year the interstitial cells occur in small masses located in the angular spaces formed between the seminiferous tubules. Owing to the difficulty of estimating the amount of interstitial tissue and the fact that microscopically there appears to be no difference in the number of cells seen during the breeding season and that seen during the non-breeding period, no attempt was made to determine whether their volume varies for *Elephantulus*. The diameters of the interstitial cells were, however, measured in each of several animals for the various seasons, and were taken as a measure of cell size; these data are given in graph 1.

It is clearly evident from the data given that the individual variation in the size of the interstitial cells for any particular month is not significant. On the other hand, highly significant differences in interstitial cell size are seen in the comparison of individuals killed in one month with individuals killed in another month. The mean diameters for animals killed in August, November and April were respectively 13·7 ± 0·139, 12·7 ± 0·136 and 9·4 ± 0·124 μ. For 48 degrees of freedom the *t* for the difference between August and November is 5·1, for August and April it is 23·1, and for November and April it is 17·9. Thus the difference in interstitial cell size of animals killed during the early part of the breeding season and those killed in April is highly significant.



seasonal variation in diam. interstitial cells

GRAPH 1

From August to October the interstitial cells are at their maximum size. Both the nucleus and cytoplasm of the cells are large, and in sections appear to be spherical in shape. The nuclei of these cells are centrally located and exhibit a definite variation in staining capacity. Some of the cells are almost achromatic, only the varying number of karyosomes staining clearly; other cells, however, take a very intense stain, and here the karyosome cannot easily be distinguished from the surrounding karyoplasm. During the remainder of the breeding season the cells of the interstitial tissue decrease steadily in size. The nuclei of these cells, however, exhibit a similar variation in staining capacity. At the end of the breeding season the interstitial cells reach their minimum size and remain small throughout April (graph 1). The cytoplasm of these cells is very small in amount, and the exact shape of the cells is not easily discernible. The nuclei do not appear to vary greatly in size, and the decrease in cell size in April is due mainly to decrease in the amount of cytoplasm. From about mid-June there is a steady increase in cell size until July, when the increase becomes much more rapid to reach the maximum size in August (graph 1). The nuclei of the cells in February, April and in some animals in June, are oval or spherical in shape and assume a more uniform staining capacity. There appears to be a close correlation between the staining capacity of the nuclei and the size of the cells. During the breeding season when the cytoplasm increases to its maximum size, due partly to the accumulation of the products of secretion, the nuclei exhibit definite variations in staining capacity as described above. When the cytoplasm reaches its maximum size, however, the nuclei all stain uniformly. Miller (1939) remarked on the variation in staining capacity in the nuclei of the interstitial cells of bats killed during the summer. No other authors have remarked on differences in staining capacity of the nuclei of the interstitial cells.

The interstitial tissue was examined very carefully for mitosis, but at no period of the year were any figures seen, although a few binucleated cells were found. These facts have also been observed in the ferret by Allanson (1932) and in bats by Miller (1939).

Pigment occurs in the interstitial cells of the testis of the ferret (Allanson 1932), of the grey squirrel (Allanson 1933) and of a number of other animals. It is not found in the interstitial cells of the hedgehog (Allanson 1934). In *Elephantulus* only a few of the testes examined contained pigment in the interstitial cells, and those testes which possessed pigment showed great individual variation. In some, many interstitial cells contain pigment, in others a few interstitial cells only were found to contain pigment. The pigment is in the form of irregular masses of coarse granules which appear yellow and refractive in sections. Pigment was found in the interstitial cells of the testes of animals during the breeding and non-breeding seasons, and thus appears to show no cyclic variations. These observations support the view expressed by other workers, viz. that the pigment is a degeneration product of the interstitial cells (review in Rasmussen 1917).

The fat content of the interstitial cells was not studied as no fresh material was available for fixation in Flemming's solution, and thus it was impossible to verify that the vacuoles seen in the eosin-stained material contained fat.

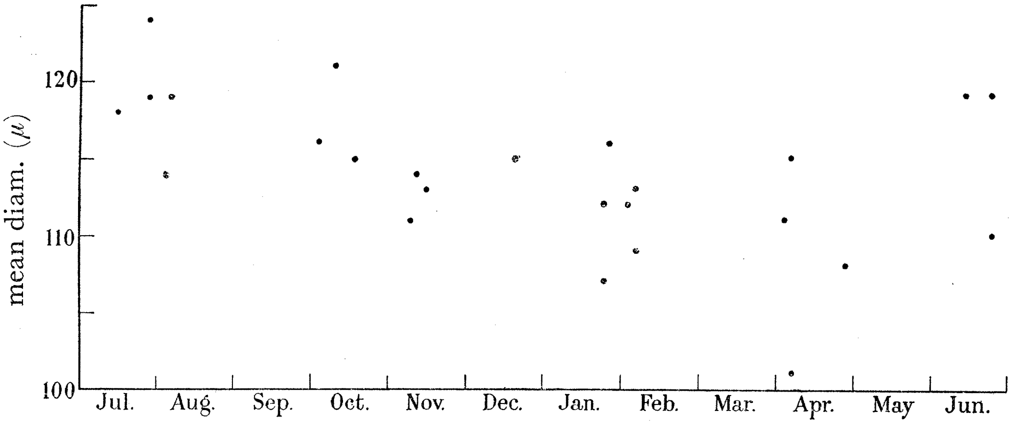
(2) *The genital ducts*

(*a*) *Caput epididymidis*

Specimens of the epididymis of *Elephantulus* collected throughout the year were examined macroscopically and histologically for any seasonal variation. Macroscopically no difference could be found between the epididymides of animals killed during the height of the season and those killed in April.

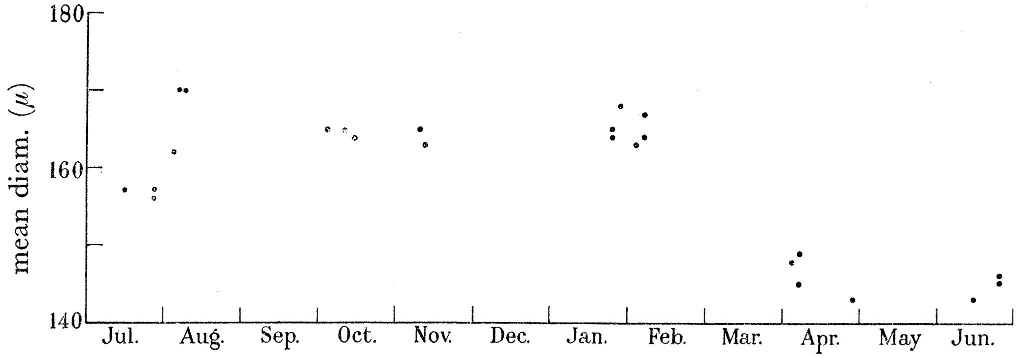
Graph 2 gives the diameter of the tube of the caput epididymidis throughout the year. From the data given it can be seen that there is no seasonal variation in the diameter of the tube and such variation as is found is apparently individual variation. The mean diameter of the tube of the caput epididymidis of animals killed during the breeding season is 116μ against 111μ for animals killed during the non-breeding season. Comparing the differences found for the two seasons with that found between two individuals killed in the same month, it is seen that the variation between the two individuals is either larger or approximately the same as that found for the breeding and non-breeding seasons.

Throughout the year the lumen of the caput epididymidis is wide, the connective tissue coat narrow, and the amount of interspersed connective tissue constant. During all the months of the year spermatozoa in large quantities are found lying in the lumen of the main body of the caput epididymidis. The height of the epithelium of the tube appears to remain constant throughout the year, and secretion in varying amounts is found in the lumen during any month of the year. Further, there is no regression of the cilia of the epithelial cells. All these data seem to indicate that the epithelial cells of the caput epididymidis are in a state of active secretion throughout the year.



mean diam. of the tube of the caput epididymidis

Graph 2



mean diam. of the tube of the cauda epididymidis

Graph 3

(*b*) *Cauda epididymidis*

In measuring the diameter of the tube of the cauda epididymidis the muscle coat was not included. The diameter of the tube varies from 156 to 170μ from July to February, and from April to the end of June it varies from 143μ to 149μ (graph 3). From the data given it seems that there is no marked seasonal variation in the diameter of the tube of the cauda epididymidis, though on comparing an August animal with a mean diameter of $162 \pm 2{\cdot}5\mu$, with an April animal with a mean diameter of $145 \pm 3{\cdot}1\mu$, a significant difference with $t = 4{\cdot}5$ for 18 degrees of freedom is found. The epithelium lining the tube increases in height at the onset of the breeding season and measures 17 to 20μ from July to February, while from April to June it decreases to 11 to 12μ. The cilia, which are very short in the breeding season, are present in the non-breeding season but are difficult to distinguish, as they lie against the surface of the cells. This part of the epididymidis thus appears to undergo a secretory cycle typical of that which has been found to occur in the whole epididymidis of the ferret (Allanson 1932). However, the caput epididymidis has been found to contain enormous quantities of spermatozoa in the lumen throughout the year, and furthermore no decrease is found in the amount of spermatozoa occurring in the lumen of the cauda epididymidis during April or June.

(*c*) *Vas deferens*

In *Elephantulus*, the diameter of the vas deferens, including the muscular coat, is 400 to 440μ in April and June, while in the breeding season it increases to 462 to 490μ. Thus the diameter of the vas deferens does not show such a marked seasonal increase as has been observed in some animals. In the ferret it increases from 240 to 280μ during the winter months to 420 to 480μ in the breeding season (Allanson 1932). By contrast, the epithelium lining the tube shows a great variation in height during the various seasons, increasing from 19 to 22μ in April and June to 38 to 40μ in the breeding season. The cilia of the epithelial cells are about 8μ in length during the breeding season but decrease to about half their length in April and June. The lumen of the vas deferens, however, was filled to capacity with sperms throughout the year. The vas deferens is known to be a region of intense secretory activity and under the direct control of the hormone of the testis. In *E. myurus jamesoni* the interstitial cells of the testis appear to be responsible for the hormone effecting the growth of the epithelial cells of the vas deferens. Apparently the secretory activity of the cells is not completely stopped, since secretion has been observed within the lumen of the vas deferens in April.

(3) *The accessory glands*

The accessory glands of *Elephantulus* collected in April and June are small, and only with difficulty can the various lobes be identified. By the middle of July and during the breeding season the glands reach a relatively large size, attaining their maximum size early in August. Through the early and midsummer months the glands remain large, and it is only at the end of January, which corresponds to the end of the breeding season, that the glands appear to decrease in size. However, it was noted that animals killed during January and February showed great individual variation in the size of their accessory glands. In the majority of males killed during this period there is a small but discernible reduction in the size of the accessory glands. In a few animals, however, a larger reduction is found, and in some males there appears to be no decrease in size at all.

A general description of the glands as seen during the breeding season has been given in detail in the section dealing with the histology of the glands. Here it will suffice to give a short summary of the appearance of the glands during full activity.

(*a*) *Ventral glands*

In July the diameter of the tubules is large and the lumina greatly distended with secretion. The tubules are separated from each other by an extremely small amount of connective tissue (figure 6, plate 2). The cells of the epithelium lining the lumina are tall columnar, with spherical nuclei near the bases, and contain varying amounts of secretory granules. Throughout the months of August to December the tubules are expanded, the lumina large and filled with large amounts of secretion.

Running parallel with the decrease in size of the glands are the histological changes. In January and February a sudden decrease in the size of the tubules, which are separated by larger amounts of connective tissue, is found. The epithelial cells are medium or low columnar and appear to contain small numbers of secretory granules in their cytoplasm. Although a definite decrease in secretory activity is to be found in animals killed during the months of January and February, the ventral glands are not in complete quiescence at this time. Furthermore, the animals examined showed large individual variation, not only in the size of these glands but also in their secretory activity. In some animals the epithelium is but slightly decreased, in others the decrease is enormous and secretory granules are almost totally absent in the cytoplasm of the cells. The amount of secretion found in the lumina also varies, from large amounts to hardly any secretion at all.

All animals killed in April possess glands which are in a state of complete quiescence. The tubules are greatly decreased in size and are separated by large amounts of intertubular tissue (figure 7, plate 2). The increase in the stroma is mainly due to the large increase of the cellular elements of the connective tissue and partly to the increase in collagenous fibres. There is no apparent increase in the thickness of the walls of the tubules which are lined by cuboidal epithelium. The cells of the epithelium contain small spherical nuclei which fill nearly the whole cell, the nucleus being spherical and the cell cuboidal. A tremendous shrinkage is found in the size of the lumina which are generally devoid of secretion, although here and there a cross-section of a tubule can be seen to contain a very small amount of secretion. This inactive state of the ventral glands persists to approximately the end of June, when an increase in the size of the glands is noted. This increase in size is accompanied by an increase in the epithelial height and an accumulation of secretion in the lumina of the glands.

(*b*) *Anterior dorsal glands*

During the breeding season the lumina of the alveoli are large and filled with enormous quantities of secretion. The alveoli are separated by broad bands of stroma which appear to form a background in which the alveoli are embedded. The epithelial cells lining the alveoli are medium columnar with elongated nuclei (figure 8, plate 2). In January the ventral gland shows signs of reduced secretory activity and the lumina are practically devoid of secretion. The dorsal glands, although showing signs of reduced secretory activity, have large amounts of secretion in their lumina which are slightly decreased in size. The alveoli are lined with a layer of low columnar epithelium whose cells contain spherical or ovoid nuclei which fill nearly the whole cell. Small numbers of degenerating cells are seen in the lumina of the alveoli which are separated from each other by increased amounts of stroma. The excretory ducts of the glands are filled with secretion.

In February there is a further reduction in the size of the glands. The lumina of the alveoli are distinct but greatly decreased. The cells of the epithelium lining the alveoli are universally cuboidal, with spherical or ovoid nuclei filling the whole cell. The small amount of cytoplasm that can be seen in the cells is clear and devoid of secretory granules. The reduction in the alveoli results in a relative increase of the connective and muscular tissue of the stroma which is consequently much more conspicuous. That the increase of the stroma is due not only to the decrease in size of the alveoli and the consequent relaxation of the collagenous and muscular fibres can be seen in the fact that there is a large increase in the cellular elements of the connective tissue. Although the epithelium of the alveoli is in an inactive state, the lumina are filled with secretion.

In the remaining months of the non-breeding season the glands are very small and are in the least active state (figure 9, plate 2). The stroma is greatly increased, the largest increase being found in the cellular elements of the connective tissue. Embedded in the stroma are the tubular alveoli which are very small and are lined with a single layer of epithelium consisting of closely packed low columnar cells. The cells are so small that their nuclei, which are spherical or ovoid, fill the greater part of them. Consequently the nuclei appear to be crowded together. The cytoplasm of the cells is free of secretory granules. The lumina of the alveoli are distinct but greatly reduced in size. Secretion in small amounts is always present, and the lumina often contain varying amounts of degenerating cells. Small amounts of secretion are seen in the excretory ducts. The inactive state described here persists to the end of June, when a steady increase in the size of the lumina and height of the epithelium of the glands is observed.

(*c*) *Posterior dorsal glands*

Seasonal changes in these glands were observed, but the changes are not as marked as those found in the ventral glands and the quiescent period appears to commence some time after that of the ventral glands.

During the breeding season these glands are large and the tubules greatly expanded with conspicuous lumina. The latter are lined by tall columnar cells whose spherical nuclei lie in the basal third of the cell. The cells are filled with a large quantity of minute granules. The intertubular stroma is very scanty. Throughout the breeding season the glands remain large and highly active (figure 10, plate 2).

In February the glands as a whole have decreased and the tubules and lumina have shrunk considerably. The intertubular tissue has increased in amount, especially in their cellular elements. The cells of the epithelium of the tubules have decreased in height from approximately 27 to 16μ, and their spherical nuclei fill the basal halves of the cells. The cytoplasm of the cells is still packed with minute secretory granules, and the lumina are filled with quite large amounts of secretion.

For the remaining months of the non-breeding period the glands do not secrete actively (figure 11, plate 2). The tubules are further decreased and are separated by narrow bands of very loose connective tissue. There is a further decrease in the height of the cells of the epithelium which now measure approximately 6μ. The cells appear to be low columnar with small spherical nuclei filling the basal two-thirds of the cells. Fine granules can be seen in the cytoplasm of the cells, but they no longer fill the cell to capacity. The secretion is greatly reduced in amount; all the lumina, however, contain small quantities. The excretory ducts have been observed to contain small amounts of secretion. From these observations it appears that the posterior dorsal glands are not completely inactive during the non-breeding season.

(*d*) *Middle dorsal glands*

In these glands the alveoli are large and have conspicuous lumina during the breeding season (figure 12, plate 2). Large amounts of stroma separate the numerous alveoli, which are lined by medium or low columnar cells whose spherical nuclei lie in the basal part of the cell. Large quantities of secretion fill the lumina.

At the end of the breeding season regression of the epithelium of the alveoli takes place. The cells are no longer medium but are very low columnar with spherical nuclei filling the whole cell. A small increase is found in the cellular elements of the intervening stroma. The lumina of the alveoli are large and filled with large amounts of secretion. Individuals killed within the same week, however, show a great amount of individual variation. An animal killed in early February showed no reduction in the size of the alveoli and appeared to be secreting actively. This same animal, however, possessed ventral glands which were in quiescence and practically devoid of any secretion in the lumina.

In April the glands are much smaller, the alveoli are very much less numerous, and in consequence the connective and muscular tissue is very much increased (figure 13, plate 2). The increase is largely due to the increase of the cellular elements and the collagenous fibres of the connective tissue, through which run the widely scattered alveoli. The latter are small and the lumina reduced considerably. In parts they appear to be mere slits lying within the stroma. The epithelium of the alveoli forms a flattened row of cells, whose irregular-shaped nuclei fill the whole cell. Large amounts of degenerating epithelial cells are seen in the lumina of the alveoli, which still contain varying amounts of secretion. Although the secretory epithelium of the glands becomes inactive during the non-breeding season, the lumina are never completely devoid of all secretion.

In general it may be said of all the circum-urethral glands that they regress during the non-breeding season; the tubules and alveoli shrink and the secretory epithelium becomes inactive. The ventral glands show the greatest change in height of the secretory epithelium and in size of the tubules, and the posterior dorsal glands the least.

(*e*) *Uterus masculinus*

During the breeding season the epithelial lining of this tube is much folded, and tubular crypts are formed in it, so that the irregular wide lumen is surrounded by a broad zone of glandular tissue, made up of these tubular crypts with thin partitions of connective tissue between them. The changes taking place in the non-breeding animal consist chiefly in a decreased folding of the epithelial lining and a regression of the tubular crypts opening into it. This results in a decrease in the diameter of the vesicles, and the lumen becomes simpler. The epithelial folds are shallow and the crypts are not only reduced in extent but fewer in numbers. This change is accompanied by a decrease in the height of the epithelial cells which are now cuboidal instead of tall columnar. The decrease in cell size is confined to the cytoplasm which thus appears less abundant with the nuclei more crowded together. The cuboidal cells are clear and devoid of secretory granules. The reduction in the size of the tubular invaginations results in a relative increase of the connective tissue stroma which is consequently much more conspicuous in sections.

Throughout the breeding season the vesicles of the uterus masculinus are filled with large amounts of secretion. In April the secretion is largely reduced, but traces of it can be found within the lumina of the crypts.

(*f*) *Cowper's glands*

These glands also change in size between the non-breeding and the breeding season; during the latter the alveoli enlarge and contain secretion. In the non-breeding season the alveoli are narrower and the epithelium is only half as high as during the breeding season. The stroma is greatly increased in the non-breeding season, due chiefly to increase in the cellular elements and collagenous fibres of the connective tissue. Traces of secretion are observed in the lumina of the alveoli during the non-breeding season.

The urethra was examined for sperm content and also for the amounts of secretion present in it for all the months of the year. It was observed that enormous quantities of sperm were present in the urethra during the breeding and non-breeding season. The secretion, however, was present in large quantities only during the breeding season.

Discussion

(1) *Testes and accessory ducts*

From the literature on the Insectivora it appears that the position of the testes may vary greatly. The position may vary from one extreme, where the testes are retained in the abdominal cavity in the vicinity of the kidneys, to the other, where they are placed in scrotal sacs. In the Chrysochloridae, Centetidae, *Petrodromus* and *Macroscelides* the testes are found lying near the kidneys, so that the left testis lies more caudally than the right one. In *Elephantulus myurus jamesoni* the testes are retained in their approximate embryological position near the kidneys. According to Kaudern (1911) the majority of Insectivora, excluding those mentioned above, possess testes which are located in cremaster sacs, *Tupaia* being the only known insectivore to possess a scrotal sac.

The structure of the testis and accessory ducts of *Elephantulus* is essentially the same as that found in the typical mammalian condition. The rete testis, however, is greatly reduced and confined to a small area in the capsule of the testis, where it is supported by the white fibrous connective tissue of the tunica albuginea. A mediastinum testis and the septa radiating from it to the capsule to form numerous compartments are completely lacking. Unlike the single vas efferens found in the marsupials (Chase 1939), *Elephantulus* has six to eight vasa efferentia which are straight and long; the epithelium consists only of low columnar cells, as is found to be the case in the marsupials, and not of two types of cells characteristic of the typical mammalian condition. No detailed references could be found regarding the histology of the testis and accessory ducts of insectivores, marsupials and monotremes, and thus it is impossible to compare the differences found in *Elephantulus* from what may be termed the typical mammalian condition, with that of the so-called primitive groups of mammals. Whether these differences are primitive features or not is thus impossible to state.

The observations on the epididymis of *E. myurus jamesoni* do not differ essentially from those made by Carlsson (1909) and Kaudern (1911) on *E.* (*Macroscelides*) *rozeti*. In the latter, as well as in *E. myurus jamesoni*, the epididymis is well developed and distinctly divided into three regions. According to Kaudern (1911) the cauda epididymidis of *E. rozeti* is abnormally elongated and forms in the inguinal region the lobus minor, which then in turn passes into the vas deferens. He describes the lobus minor as consisting of two parts, viz. the cauda epididymidis, which has a fairly narrow lumen, ciliated epithelium and a thin wall, and the vas deferens which has a thick wall and wide lumen and enters the urethra. According to him the lobus minor is mainly formed by the cauda epididymidis and not, as was supposed by Carlsson (1909), formed completely by the vas deferens, which according to her was coiled and stretched from the testis to the urethra. From observations on the histology of the epididymis it appears that in *E. myurus jamesoni* it is the corpus and not the cauda epididymidis which is abnormally elongated. The lumen of the elongated portion of the epididymis is narrow and lined by tall columnar cells at the bases of which are found the basal cells; the coat is thin. The corpus is histologically very similar to that part of the epididymis which is called the caput in this work, but has a slightly lower epithelium, shorter cilia and is much less coiled. It differs, however, very greatly from the cauda. The latter is homologous to the lobus minor of Kaudern; it is greatly coiled, has a relatively thick muscular wall and wide lumen which is lined by a pseudo-stratified epithelium consisting of cuboidal cells and small basal cells. Very short cilia are found. Thus histologically there is a large difference between the elongated portion of the epididymis and the cauda, and a small but definite difference between the first-named and the caput. Miller (1939), in a description of the histology of the cauda of the bat, and many other workers on other animals, have described the cauda as characteristically possessing low columnar or cuboidal epithelium. From these observations it appears that the elongated portion of the epididymis may better be called the corpus and not part of the cauda. From the literature it appears that *E. rozeti* is the only animal belonging to the family Macroscelididae known to possess a cauda epididymidis which is situated at a distance from the testis in the inguinal region. Peters (see Kaudern 1911) described *Petrodromus tetradactyles* and *Rhynchocyon cirnei*, and mentioned that they possess long vasa deferentia which are coiled but do not form lobi minor in the inguinal region. Judging from the position of the caudae in the inguinal region it appears that in *Elephantulus rozeti* and *E. myurus jamesoni* the testes have made an attempt at descension, the caudae being the only part of the testes and its accessory ducts to descend into a position normally occupied by the complete testes of the Oryzorictinae.

(2) *Accessory glands*

The accessory glands of this group of mammals are of particularly great interest, in that the glands show various grades of development, from the most primitive type as is found in the marsupials to the highly specialized type found in the higher Primates. Kaudern (1911), in a paper on the male genital system of insectivores and lemurs, pointed out the difficulty of drawing homologies between the prostate masses found in the different families of insectivores. These glands not only differ in their position, number and structure, but also in the number and position of the orifices of the ducts. Many workers regard the Centetidae to be the most primitive type of insectivore. One group, the Oryzorictinae, possesses only urethral glands; this type of gland is very commonly found in the Marsupialia, and at one time it was thought that these glands were the only type found in the latter. Another group, the Centetinae, however, possesses well-developed urethral glands and prostate glands. In *Sorex* and *Talpa* urethral glands are present but are reduced to small, single glands, and are generally replaced by prostate glands. *Elephantulus* and the Chrysochloridae are the only insectivores in which the urethral glands are completely absent; the glands surrounding the urethra are all prostate glands. From the literature it appears possible that the insectivora were derived from mammals which possessed only urethral glands and which have in the course of development been completely replaced by the prostate glands in *Elephantulus* and Chrysochloridae. Further more, it appears that these prostatic masses have evolved totally independently in the various groups.

In *E. rozeti* there are, according to Carlsson (1909), three pairs of prostate glands, and according to Kaudern two pairs of which one pair is divided into four lobes. In *E. myurus jamesoni* there are five pairs of glands surrounding the proximal part of the urethra. These glands have been designated as prostate glands, since they open directly into the urethra and are located in the position in which the prostate glands are generally found. Furthermore, their general structure and histology closely resemble the prostate glands of other mammals. They lie lateral to the wall of the urethra, their capsule is not formed by the muscles of the urethra and they have their own specific ducts leading into the lumen of the urethra and thus do not resemble the urethral glands found in other insectivores. No urethral glands of any description were found in *E. myurus jamesoni*. The possibility that one pair of the glands may be vesiculae seminales, has not been completely discarded, since the question could only be answered with satisfaction if their embryological development had been studied to give a final decision whether any of these glands are evaginations of the vasa deferentia which had lost their connexion with the latter, to open independently into the urethra. In the hedgehog multiple ducts from the paired seminal vesicles open directly into the urethra (Allanson 1934). Seminal vesicles are not found in *E. rozeti* (Carlsson 1909; Kaudern 1911), and they appear to be present in only a few insectivores.

Five different types of prostate glands are found in *E. myurus jamesoni*, each with a distinct type of epithelium, secretion and general structure, and each occupying a definite region of the urethra; they all possess their own specific ducts which differ in number in the various glands. The ventral and posterior pairs of glands are similar in structure, both being of the branched tubular variety and having very little intertubular tissue; both are lined by tall columnar epithelia which, however, differ in their staining capacity. The secretions of both glands are homogeneous but also differ in their staining capacity. *E. rozeti* does not appear to possess glands corresponding to these. The middle and anterior dorsal glands do not only differ in structure from each other, but differ very greatly from the ventral and posterior glands. They are, in contrast to the latter, of the alveolo-tubular variety and embedded in larger amounts of stroma. The epithelium is generally lower than that of the ventral and posterior glands. The middle dorsal glands differ from the anterior glands in that the stroma is slightly less in amount, the cells of the epithelium are wide, with spherical nuclei, whilst those of the anterior glands are narrower with elongated nuclei. The anterior dorsal glands contain a globular secretion, whilst the middle dorsal glands have a homogeneous secretion which, however, differs in staining capacity from that of the ventral and posterior dorsal glands. The outer and inner anterior dorsal glands, although very similar histologically, possess distinctly different secretions. Both the glands have a globular secretion, but the outer gland has a fractured type of globule, whilst the inner gland contains a homogeneous globule. It would appear from the description that the outer and inner anterior dorsal glands of *E. myurus jamesoni* are homologous to the anterior and more ventral pair of glands of *E. rozeti* described by Kaudern (1911). These glands, according to him, consist of four different lobes all having an epithelium slightly lower than that of the posterior pair of glands and containing a secretion which consists of masses of small globules or droplets. It is possible that Kaudern did not observe the difference in structure between the globules of the outer two and inner two glands, and thus grouped all four lobes together as one single pair of glands. From the fragmentary description of the posterior gland of *E. rozeti* it is difficult to find a homology between it and one of the glands of *E. myurus jamesoni*. However, from the description of the position, epithelium, the number of ducts and homogeneous type of secretion of the glands of *E. rozeti* it is possible that the middle dorsal glands of *E. myurus jamesoni* correspond to the posterior glands of *E. rozeti*.

In addition to the glands described above, *E. myurus jamesoni* possesses only Cowper's glands. As in *E. rozeti* they are well developed. The glands are absent in those insectivores which are adapted to a life in water and also in Erinaceidae (Kaudern 1911).

According to the literature glands of the vas deferens appear, as a rule, to be totally lacking in Insectivora, and *E. myurus jamesoni* is no exception. They are, however, present in the Soricidae, Erinaceidae, Tupaiidae and Chrysochloridae (Carlsson 1909; Kaudern 1911), where they appear in the majority of cases in the form of one or more ampullae.

Carlsson (1909) described the single, small blind vesicle lying in the prostatic mass and opening between the vasa deferentia into the lumen of the urethra as a uterus masculinus in *E. rozeti*, and considered it to be homologous to the similarly named organ in *Tupaia javanica*. Kaudern (1911) found this vesicle to be present in *Talpa*, *Erinaceus*, *Elephantulus rozeti* and *Tupaia*, but considered that it should be designated as a prostate gland and not as a vagina or uterus masculinus until embryological evidence is obtained that it is derived from the remnants of the Mullerian ducts. In *Elephantulus myurus jamesoni* the blind vesicle lies within the prostatic mass of glands and opens between the orifices of the vasa deferentia into the lumen of the urethra. This position corresponds to that occupied by the uterus masculinus of the mouse and other mammals. Furthermore, the structure of the uterus masculinus in *Elephantulus*, with its folded mucosa and glandular crypts and thick muscular coat, is very similar to that of other mammals. The vesicle consists of a single canal with two lateral horns whose appearance indicates its development from the semi-fusion of two ducts. The argument put forward by Kaudern (1911), that it is highly improbable that the blind vesicle, which is a functional sex gland and not merely a vestigial organ, has arisen from the remnants of the Müllerian ducts, which according to him must have undergone a tremendous modification from two rudimentary ducts to a single functional gland, does not seem to hold. It has been proved by many workers that the uterus masculinus is derived from the remnants of the Müllerian ducts and has been modified to form a functional gland in many other mammals. It thus appears that the uterus masculinus of *E. myurus jamesoni* is homologous to a similar organ found in *E. rozeti*, *Talpa*, *Erinaceus* and probably corresponds to one or both blind vesicles found to be present in *Tupaia*.

There has been great controversy whether the Macroscelididae are more nearly related to the Tupaiidae, Erinaceidae, Soricidae or Talpidae. Kaudern (1911) compared the sex organs of *Elephantulus* with those of the four mentioned families of insectivores, and came to the conclusion that as far as the glands were concerned they were nearer to the Soricidae and Talpidae than to the Tupaiidae or Erinaceidae. Comparing the accessory glands of *E. myurus jamesoni* with those of the former two families it becomes even more difficult to analyze the relationship of the former to the latter. The prostatic mass of *E. myurus jamesoni* appears to be more highly specialized and not homologous to that of the Soricidae or

Talpidae. More work on the histology of the glands of all insectivores is needed before a homology can be drawn with certainty between the glands of the various families.

(3) *Seasonal variation*

From the literature on the reproductive cycle of various small mammals it appears that in those mammals with a limited sexual season the period of male reproductive activity, as a general rule, roughly corresponds to that of the female. In most cyclic breeding mammals such as the ferret (Allanson 1932), hedgehog (Allanson 1934), common shrew (Brambell 1935) and vole (Rowlands 1936), a male anoestrous period roughly corresponding to that of the female is found. However, this is not always the case. In the grey squirrel (Allanson 1933) the males of the species may be in more or less continuous reproductive activity, while all the females are in anoestrus for 6 months of the year. In some of the larger animals, such as the camel, the condition is reversed; the female experiences a continuous series of reproductive cycles and is capable of conception throughout the year, while the male experiences only a short season of rut (Zuckerman, 1932).

In *E. myurus jamesoni* a limited sexual season is found, which lasts for approximately 6 months of the year; during the remaining time the female reproductive organs and accessory glands are in a state of quiescent anoestrus (van der Horst & Gillman 1941; van der Horst 1946). The males, however, exhibit obvious peculiarities of reproductive behaviour. The observations recorded for the male show that the testis is actively producing spermatozoa throughout the year, while the accessory sexual organs are in a state of incomplete anoestrus for approximately 5 months of the year. It has been generally accepted that the extent of the breeding season in the male may be judged by the occurrence of mature spermatozoa in the testes. Using this criterion, it is apparent that the breeding season extends throughout the year, but if, in addition, the state of the accessory glands is considered, this does not hold completely. As has been mentioned the testis is spermatogenically active throughout the year, and large quantities of sperm are found in the caput, corpus and cauda epididymidis, vas deferens and urethra at all times. Correlated with the observations that the testis is spermatogenically active throughout the year is the fact that the seminiferous tubules apparently do not decrease in size as is the case in the ferret, where a cessation of spermatogenesis takes place during the anoestrous period (Allanson 1932). No seminiferous tubules were found in which the lumen has been obliterated and there is no actual decrease in the size of the testis. It follows that if the testis is highly active the genital ducts would likewise be in a state of activity throughout the year. From observations it is apparent that there is no decrease in size of the tube of the caput or corpus epididymidis, and that the epithelium is in a state of active secretion throughout the year. The cauda epididymidis and vas deferens, although showing very little seasonal variation in the size of their tubules, do undergo a secretory cycle. The epithelium height decreases to approximately half that of the breeding season, and the cilia, although present, are greatly reduced in length. It must be remarked, however, that the production of secretion does not appear to cease completely, since secretion has been observed in the lumen of the vas deferens in April.

In the ferret (Allanson 1932), hedgehog (Allanson 1934), stoat (Deanesly 1935), common shrew (Brambell 1935) and vole (Rowlands 1936) the quiescent period of the accessory glands is approximately of the same duration as in the testis. In the male *Elephantulus* the spermatogenic activity of the testis is not correlated with the state of the accessory glands. The accessory glands, which are quite small during the non-breeding period, begin their activity in the latter part of winter and attain their greatest size in August. When the maximum size is reached, the epithelium of the glands is highly active, and the lumina of the glands are filled with secretion. It appears, therefore, that the factors which regulate the activities of the seminiferous tubules are separate from those influencing the accessory glands.

From observations on the accessory glands it appears that the ventral gland undergoes regression before any of the other prostate glands. The ventral glands are as a general rule not in complete quiescence in the early part of the non-breeding season but are, however, in a state of complete quiescence in April. The anterior dorsal glands also regress towards the end of the breeding season, but the changes are more gradual and secretion in small amounts is found in the lumina in April. In the posterior and middle dorsal glands the quiescent period commences sometime after that of the ventral gland and is never as complete, since secretion is always present in April although in greatly reduced amounts. From these observations it appears that in the male the prostate glands all regress during the non-breeding season but at different rates and to a different extent.

According to van der Horst (1954) many of the females at the end of the breeding season, previous to going into anoestrus, have repeated ovulations before fertilization may take place. He accounts for this fact by assuming that there are less active males at this period. Since only the ventral glands are at this time in an incomplete quiescent state it is possible that these glands secrete a substance which affects the motility of the sperm. There is sufficient secretion from the other glands to form a medium in which the sperms, which are continuously present in the lumen of the urethra, can travel.

The other accessory glands, viz. Cowper's glands and the uterus masculinus, also undergo a secretory cycle and are practically in complete anoestrus in April.

The reproductive cycle of the male *E. myurus jamesoni*, therefore, is of a type not hitherto described, in which the testis is spermatogenically highly active throughout the year and the accessory glands are in anoestrus for approximately 5 months of the year. It is possible that the grey squirrel described by Allanson (1933) will show a similar condition. The author did not investigate seasonal changes of the accessory glands after establishing that the testis is spermatogenically active throughout the year.

Most authors consider that the interstitial cells produce a secretion controlling the development of the accessory sexual organs. According to Rasmussen (1917), Allanson (1932) and Miller (1939) the interstitial cells are undoubtedly connected with a cyclic production of secretion in animals with seasonal reproductive activity. In *E. myurus jamesoni* the cycle in the interstitial cells follows very closely the cycle in the accessory glands. Both the interstitial cells and the accessory glands reach their maximum differentiation during the breeding season. The interstitial cells reach their greatest diameter in August when the accessory glands have reached their maximum size. During the remaining months of the breeding season the accessory glands remain large and highly active, but the interstitial cells show regression of their size towards the end of August. By the end of the breeding season when the accessory glands begin to regress the interstitial cells are nearly at their minimum size. The size of the interstitial cells begins to increase towards the middle of June and thus precedes the development of the glands by a short time. In *E. myurus jamesoni* the accessory glands are thus maintained in a functional condition for quite a long period after retrogression of the interstitial tissue has begun.

Several attempts have been made to correlate cyclic variation of the interstitial tissue with differentiation of the accessory glands (Rasmussen 1917, in the woodchuck; Allanson 1932, in the ferret and 1934, in the hedgehog; Miller, 1939, in bats). From observations it seems to be apparent that there is a close correlation between the size of the interstitial cells which may be taken as a measure of their secretory activity, and the accessory glands in *E. myurus jamesoni*. In animals such as the grey squirrel, where the reproductive system is active throughout the year in the male, there is no cyclic variation of the interstitial tissue (Allanson 1933).

The interstitial cells appear to have little, if any, effect on the epithelium of the caput epididymidis but probably affect the secretory activity of the cauda epididymidis and vas deferens.

In summary, it appears as if the seminiferous tubules and interstitial cells are under the control of two different hormones and that the interstitial cells undergo a cycle of secretory activity. The secretion produced by these cells apparently has a direct influence on the accessory ducts of the testis as well as controlling the secretory activity of the accessory glands. The secretion produced by the interstitial cells appears to affect the various accessory sexual glands to a varying extent.

I wish to express my gratitude to all who supplied material or otherwise helped in this investigation, and especially to Dr D. J. Nolte, of the Department of Zoology, for his generous and unstinted help and guidance during the course of this research. My thanks are also due to the late Professor C. J. van der Horst for supplying the material of *Elephantulus myurus jamesoni* and for reading the paper.

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Description of Plate 2

Photomicrographs of transverse sections of the genital tubules and accessory glands, stained with Heidenhain's iron-haematoxylin and eosin, and photographed through a Wratten no. 11 green filter. (Magn. × 100.)

Figure 5. Near the union of the corpus and the cauda epididymides, the former with higher columnar cells.

Figure 6. The ventral prostate gland during the breeding season.

Figure 7. The ventral prostate gland during the non-breeding season.

Figure 8. The inner anterior dorsal prostate gland during the breeding season.

Figure 9. The inner anterior dorsal prostate gland during the non-breeding season.

Figure 10. The posterior dorsal prostate gland during the breeding season.

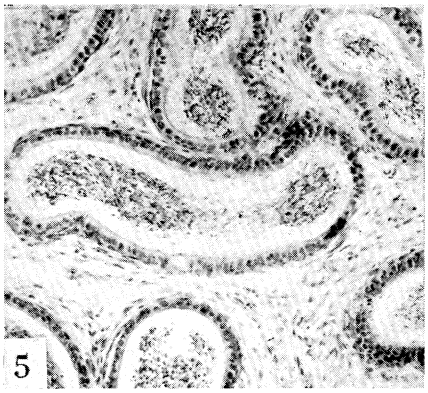
Figure 11. The posterior dorsal prostate gland during the non-breeding season.

Figure 12. The middle dorsal prostate gland during the breeding season.

Figure 13. The middle dorsal prostate gland during the non-breeding season.

Figure 14. The uterus masculinus during the breeding season.

Figure 15. Cowper's gland with its striated muscle capsule, during the breeding season.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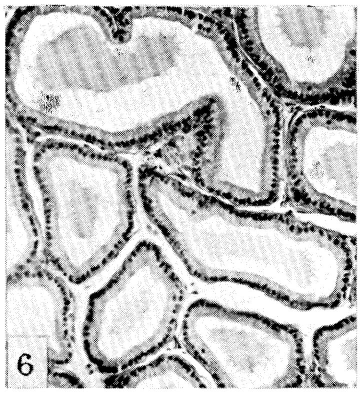
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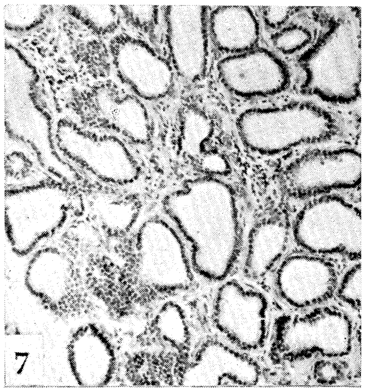
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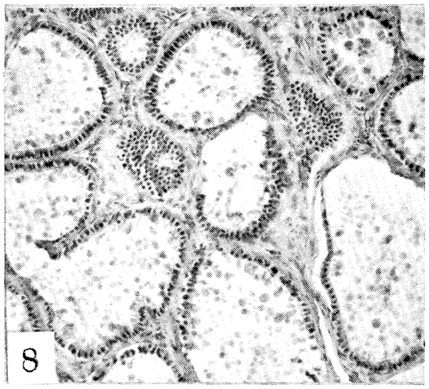
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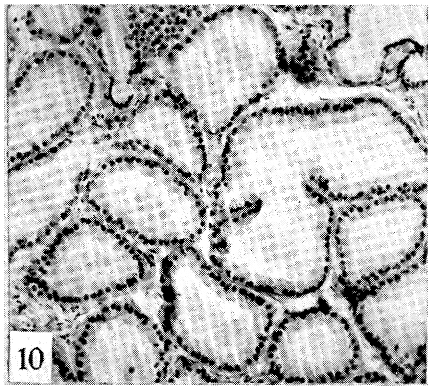
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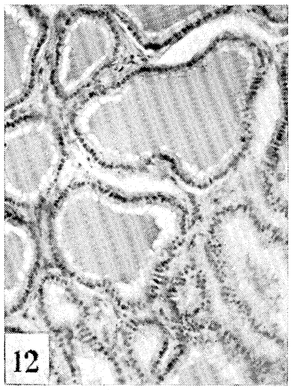
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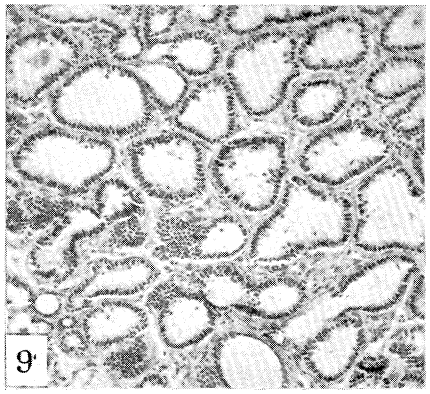
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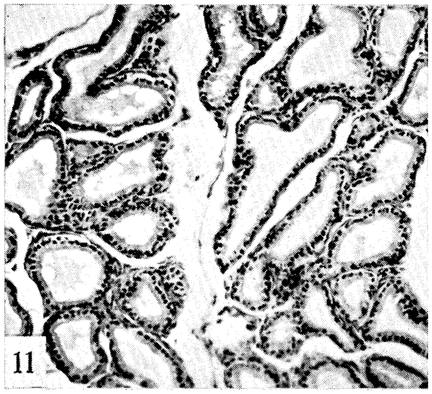
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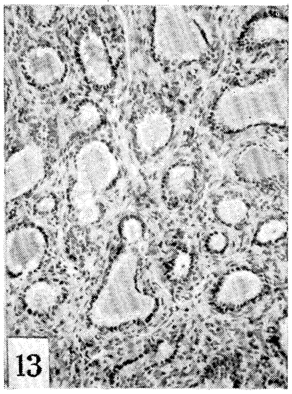
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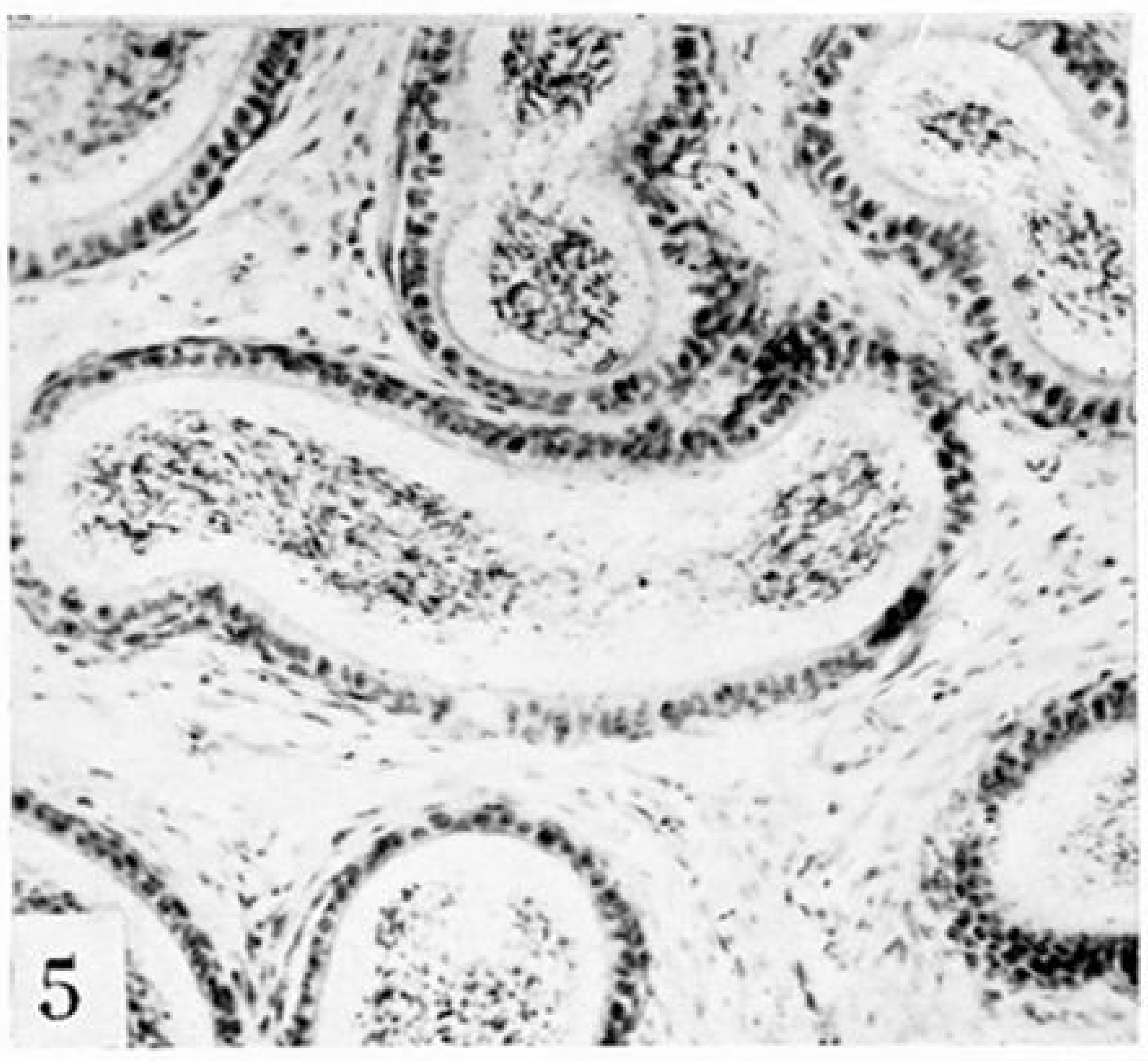

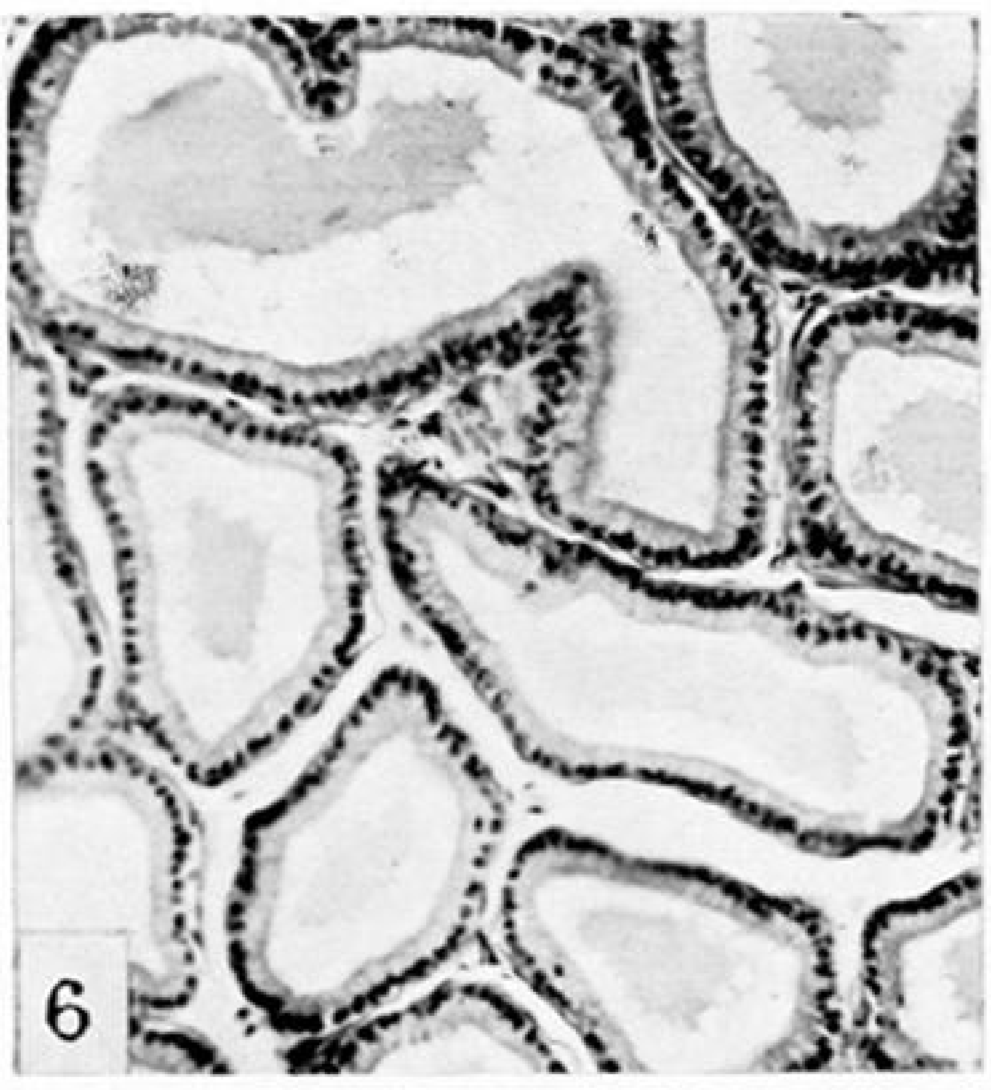

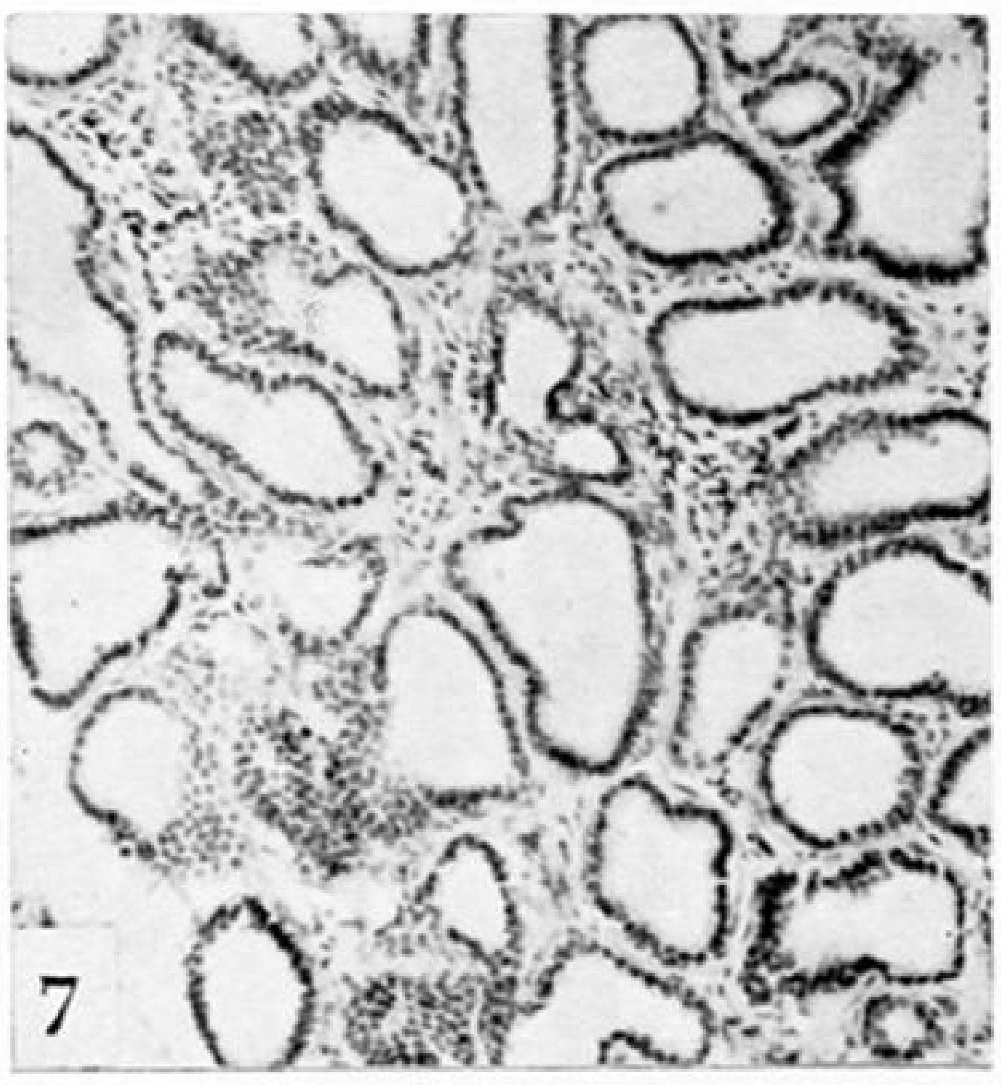

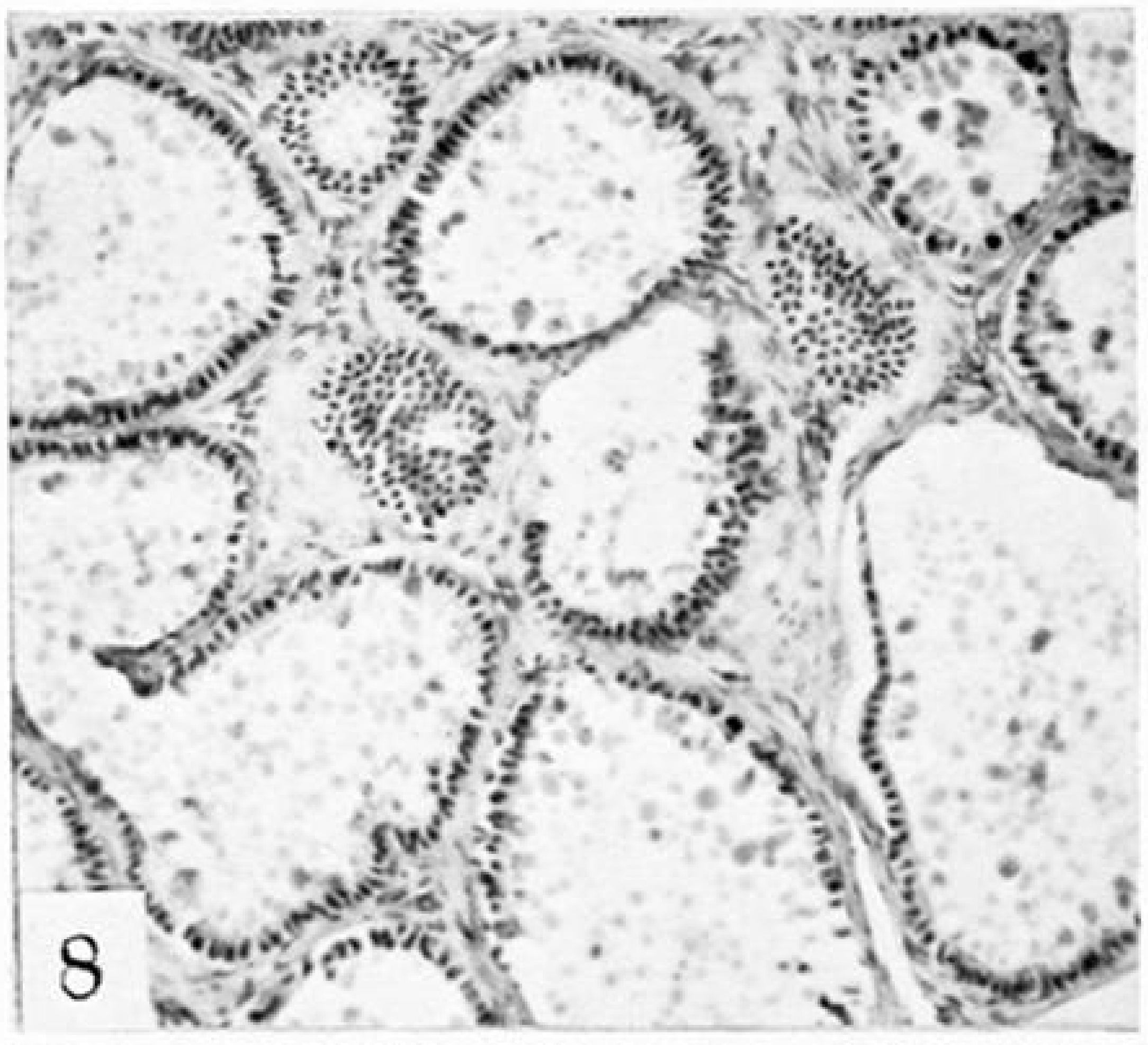

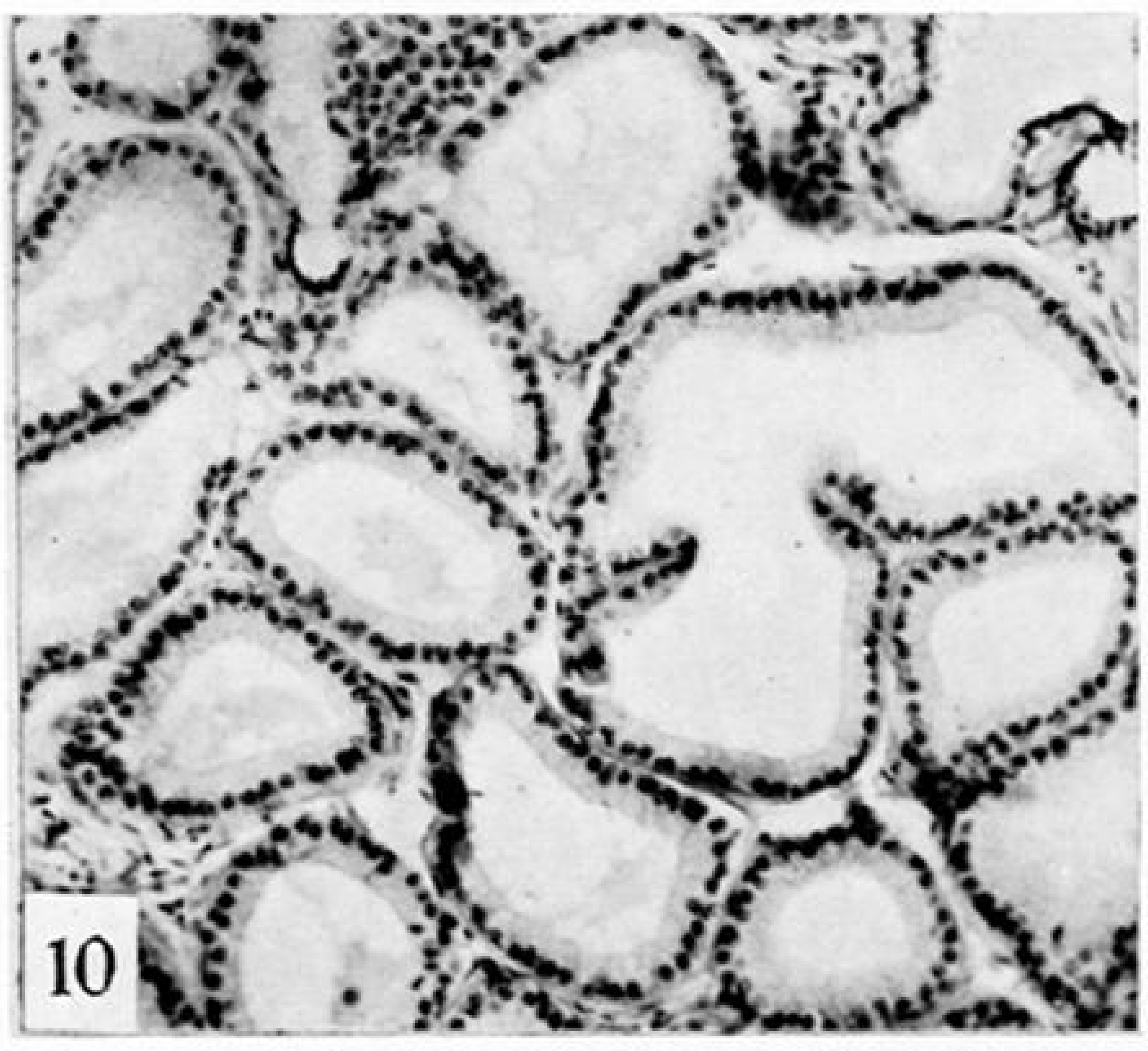

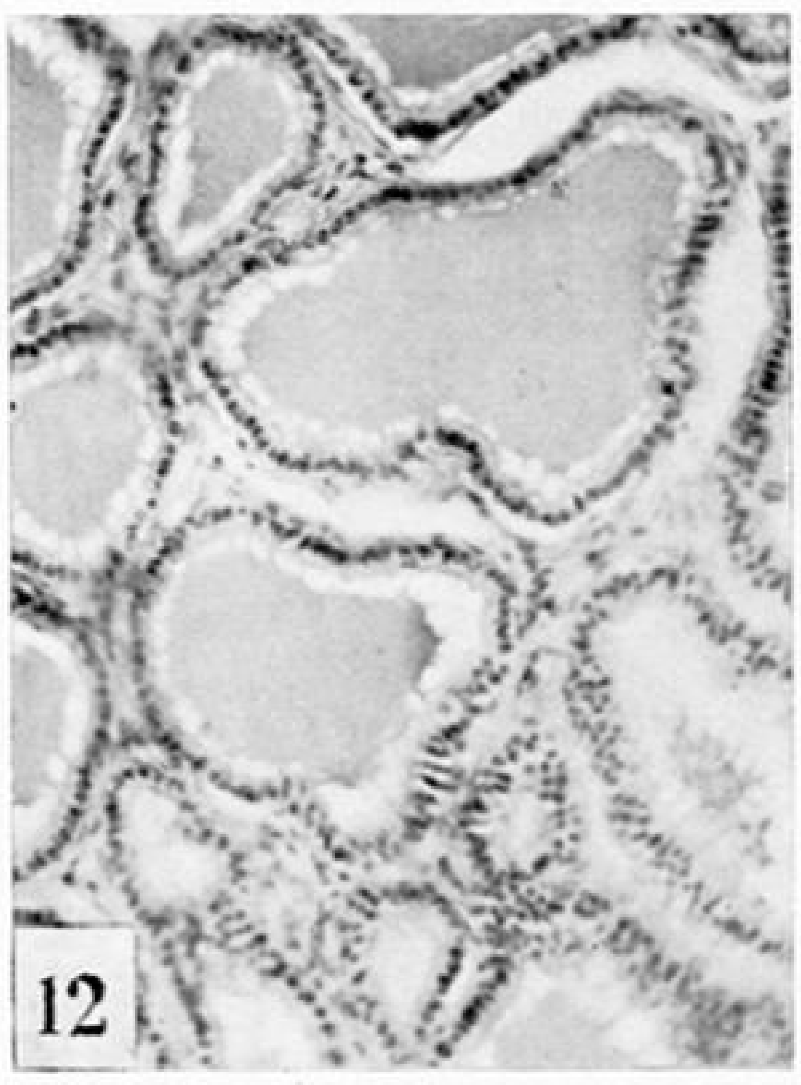

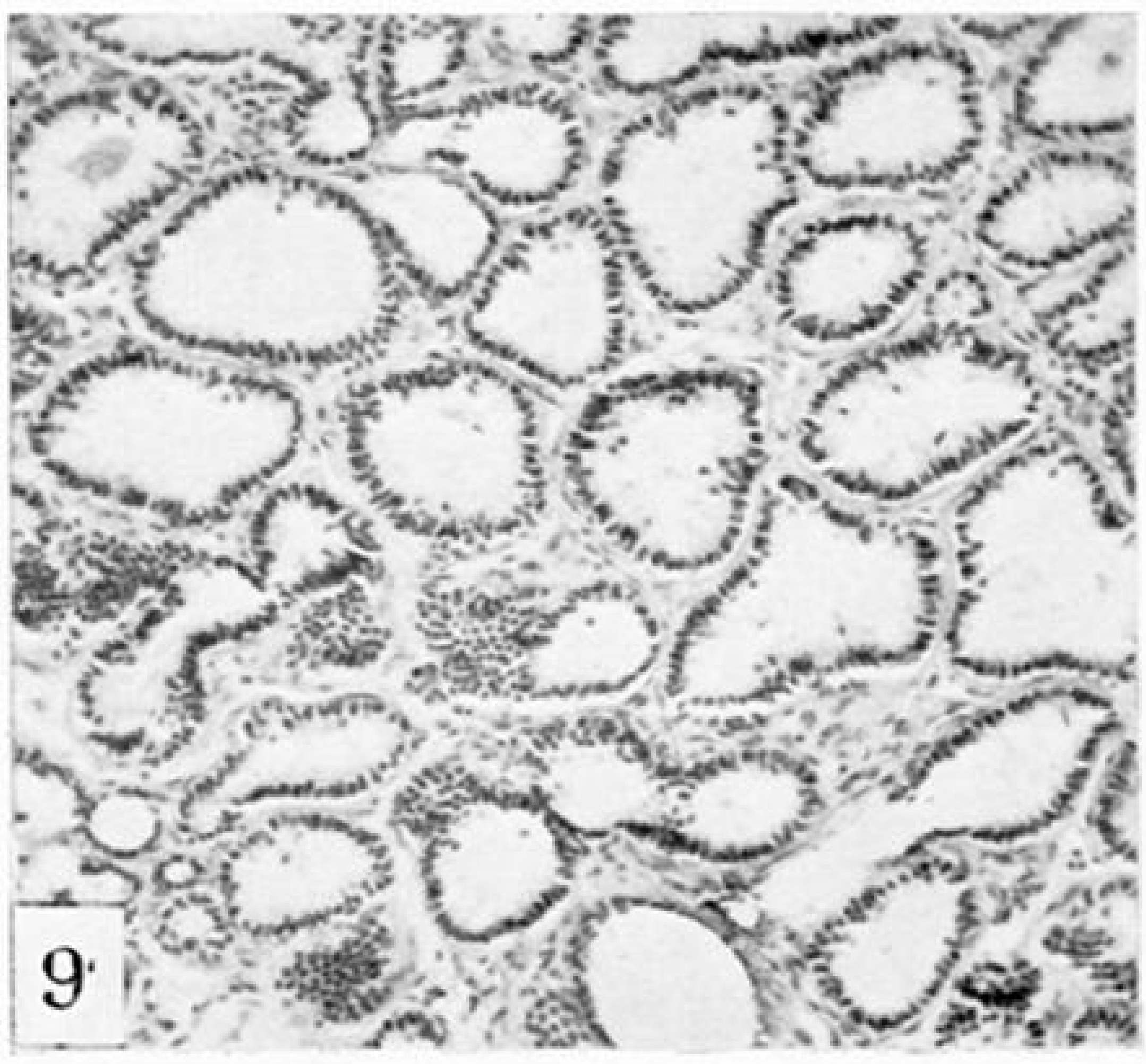

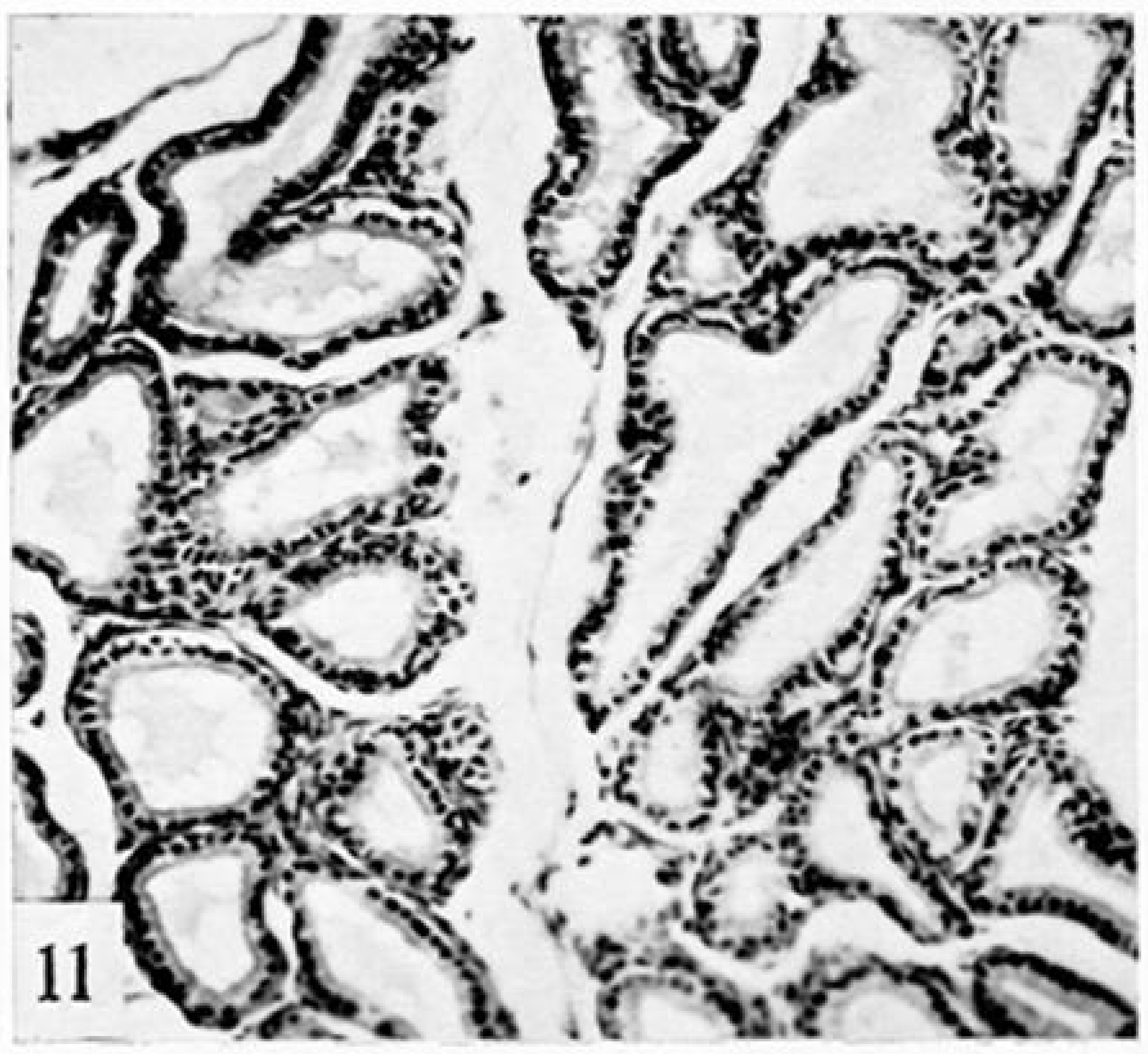

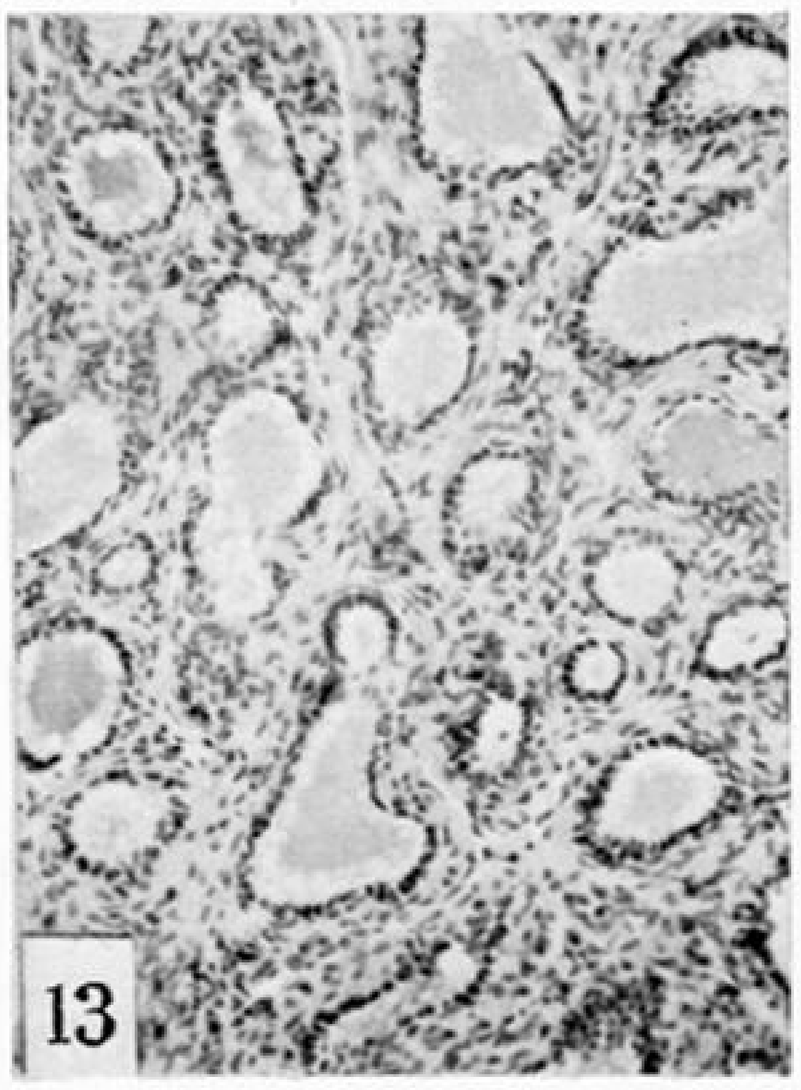

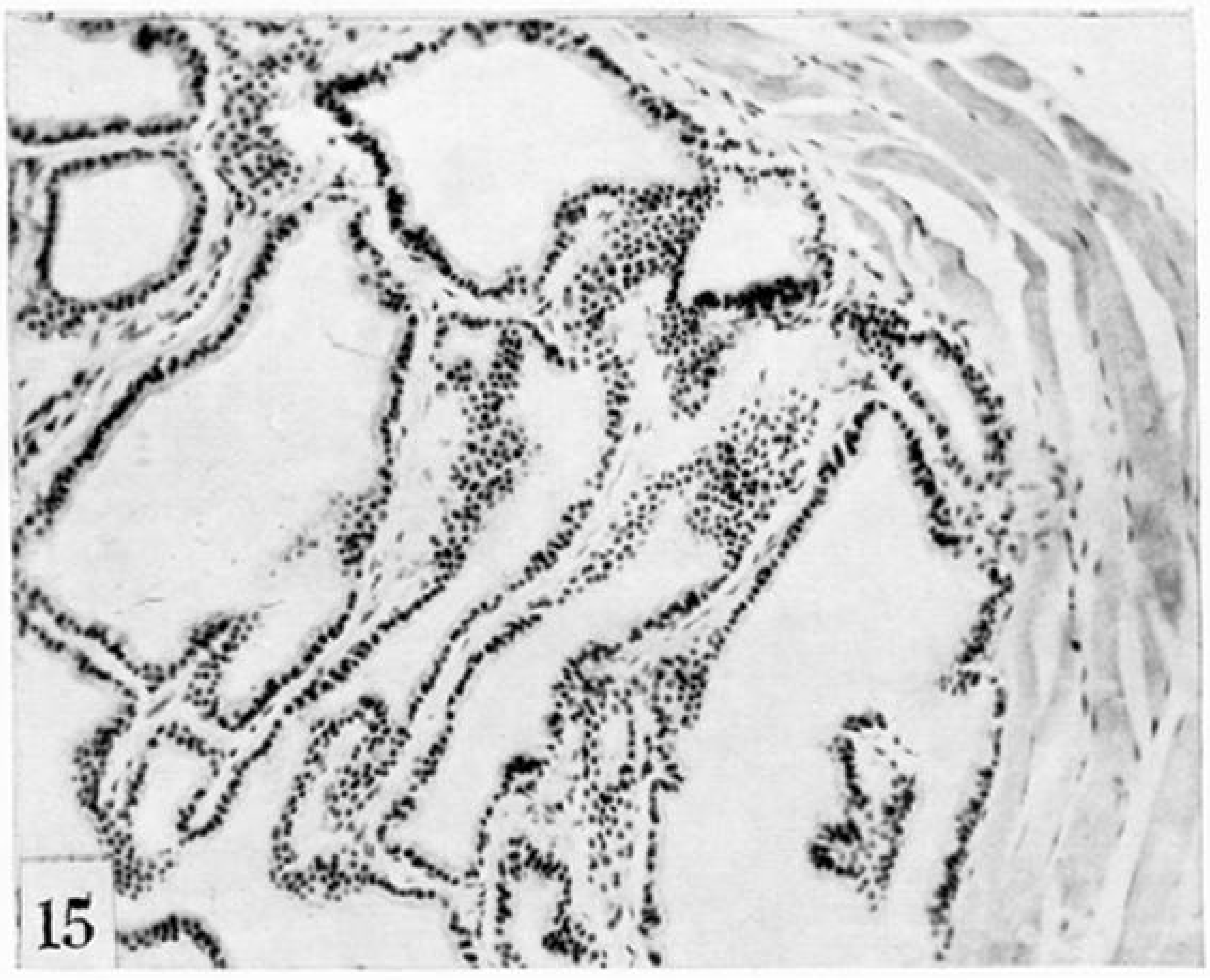

DESCRIPTION OF PLATE 2

Photomicrographs of transverse sections of the genital tubules and accessory glands, stained with Heidenhain's iron-haematoxylin and eosin, and photographed through a Wratten no. 11 green filter. (Magn. × 100.)

FIGURE 5. Near the union of the corpus and the cauda epididymides, the former with higher columnar cells.

FIGURE 6. The ventral prostate gland during the breeding season.

FIGURE 7. The ventral prostate gland during the non-breeding season.

FIGURE 8. The inner anterior dorsal prostate gland during the breeding season.

FIGURE 9. The inner anterior dorsal prostate gland during the non-breeding season.

FIGURE 10. The posterior dorsal prostate gland during the breeding season.

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FIGURE 12. The middle dorsal prostate gland during the breeding season.

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FIGURE 14. The uterus masculinus during the breeding season.

FIGURE 15. Cowper's gland with its striated muscle capsule, during the breeding season.