SEASONAL EFFECTS ON THE ANATOMY AND HISTOLOGY OF THE REPRODUCTIVE TRACT OF THE MALE RODENT MOLE *BATHYERGUS SUILLUS SUILLUS* (SCHREBER)

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INTRODUCTION

Bathyergus suillus suillus (Schreber), the Cape mole-rat, inhabits the southern and western Cape Province of South Africa. This species belongs to the family Bathyergidae and the subfamily Bathyerginae (Roberts 1951). *Bathyergus* is not only the largest bathyergid but possesses a peculiar characteristic not found in the other genera, namely deeply grooved upper incisors with roots above the molars. As a result of these characteristics and others, some authors think that this genus should be classified in a family by itself (Walker 1964).

Much research has been done on reproduction in the Old World insectivore moles, the Talpidae (Eckstein and Zuckerman 1956). In contrast with this and apart from the paper by Jarvis (1969) on the breeding season and litter size of African mole-rats of the family Bathyergidae, no detailed study has been carried out on reproduction of these rodent moles. Moreover, although *Bathyergus* appears to be a strict seasonal breeder no research on the gross anatomy or histology of its reproductive system has been carried out. In view of this an attempt has been made in the present investigation to examine the breeding season and to describe the effects of season on the histology and gross anatomy of the male rodent mole *B. suillus suillus*, hereafter referred to as *Bathyergus*. The economic importance of this species as an agricultural pest provided additional motivation for the study.

PROCEDURE

Material: Sixty-two male and thirty-six female *Bathyergus* were obtained from Faure, ten miles west of Cape Town and from the farm "Klein Welmoed" seven miles south of Stellenbosch during 1969 and 1970, and provided the material for the investigation. The animals were caught by spring traps, specially designed for this purpose. In a few cases they were caught by hand above ground. Approximately five males were caught each month except during December and January, a period of sexual inactivity.

Histological technique: The animals were killed with ether within a few hours of trapping and the reproductive tracts immediately dissected out. The epididymis was separated from the testis and preserved in formal saline. Shortly afterwards sperm smears were made using a 10% aqueous nigrosin solution. Only one testis from each animal without the epididymis, was weighed to the nearest mg. This procedure was adopted as it had been previously established that the two testes from each animal were very similar in weight and the procedure also

allowed immediate fixation of the other testis. Seminal vesicles and prostate glands were also weighed to the nearest mg. Testis sections of each individual were fixed in 10% formalin to which a few drops of calcium chloride had been added to make the phospholipids insoluble. After fixation the material was kept overnight in a 2,8 mixture of compounds 1540 and 4000 of polyethylene glycol (carbowax) (Wade 1952). The material was sectioned at 15μ and stained with Sudan Black B according to the method of Chifelle and Putt (1951) or with Osmic acid according to Mallory (1944). Testis sections were also fixed in Bouins fluid and routinely imbedded in paraffin wax, sectioned at 5μ and stained with Gurrs Hematoxylin and counterstained with Eosin Y. The accessory reproductive organs were treated similarly. The penis material was fixed in Bouins fluid and afterwards kept in a solution of 7,5% nitric acid and 70% alcohol for four weeks to decalcify the os penis.

Tubular diameter of the testes was obtained by measuring thirty tubules in each testis by means of a projection apparatus and callipers.

RESULTS

Gross anatomy of the reproductive system

Bathyergus does not belong to the true Testiconda. Neither does it have a true scrotum, but only two small peritoneal evaginations of the tunica vaginalis propria as in the Talpidae, Soricidae, Solenodontidae, Erinaceidae, Orycteropidae and in many other rodents (Weber 1927). Here the so-called "scrotal sacs" lie antero-lateral to the penis and are partly formed by the transverse abdominal and internal oblique muscles. A mass of fat not only covers but also forms part of the ventral wall of the scrotal sacs.

The testes are slightly oval to round bodies which sometimes lie in the scrotal sacs, although their position is mostly inguinal. In the latter case the testes lie on either side of the bladder with the epididymides facing the bladder. The epididymis is attached to the medial and posterior sides of each testis and consists of a large head connected by a slender body to a very coiled tail. From the tail of each epididymis follows a short ductus deferens which forms a loop with the ureter, and runs for a short distance along the seminal vesicles before it enters the urethra. Externally it was difficult to identify distinct ampullae, but histological sections confirmed their presence (Figs. 1 and 2).

Two multi-lobed seminal vesicles lie dorsal to the bladder, the lobes being supported by connective tissue above the prostate. Although the prostate forms a single mass around the seminal vesicles and the urethra, it can be divided into three or four pairs of lobes. There is, however, not always a distinct separation between all the lobes of the prostate, but this problem will be discussed in the histological section. A number of ducts from the different parts of the prostate drain into the urethral sinus.

Two small bulbo-urethral glands lie just antero-dorsally to the corpus cavernosum on each side and are, like the seminal vesicles, ductus deferens and penis, covered by a large amount of fatty tissue. The penis is curved in a L-like fashion with the result that the animal urinates towards the tail. Furthermore, the penis is wholly covered by the prepuce and as in the guinea-pig, it is difficult to distinguish between male and female externally. It moreover appears that the penis of *Bathyergus* resembles in most respects that of not only the guinea-

pig but also the subfamily Caviinae as a whole. Both have a long and conical glans which measures about one-third of the penis length as well as an os penis which is present along the whole length of the glans. It is also this bone that gives the glans its form, being flattened medially, slightly inspissated distally and widened and much inspissated at the proximal end. In detail of glans structure the penis of *Bathyergus* differs from that of the Caviinae. This will be discussed in a later section.

The effect of season on the gross anatomy of the reproductive system

The macro-anatomical differences between the reproductive system of *Bathyergus* in the sexually active period and the inactive period were very obvious (Figs. 1 and 2). The differences in testis size could be clearly seen, being large in the active animal and very small in the inactive animal (Table 1). The active epididymides are highly vascularised and exhibit a very swollen appearance. Active seminal vesicles were greatly hypertrophied and the large amount of seminal fluid formed, filled this organ to capacity giving it a transparent appearance. Active prostate glands as well as bulbo-urethral glands also showed a marked increase in volume (Fig. 1).

In contrast to the sexually active animal, the inactive animal's reproductive organs were very much reduced in size and degree of vascularisation. The seminal vesicles probably exhibited the greatest degree of atrophy (Fig. 2).

In order to examine the effect of season on the gross anatomy more closely, testes, prostate and seminal vesicle weights were recorded throughout the year. These data, including the weights expressed as a percentage of body weight, have been summarised in Table 1. The latter calculation was carried out to minimise the effect of variable body weight within the relatively small monthly sample of four animals.

The data contained in Table 1 show that in February the mean testis weight was only 0,07% of the body weight. This was the lowest mean recorded throughout the year. Although the March sample was too small to compare with the other months, it seemed that there was an increase in testis weight. Between February and April there was a sharp increase in testis weight, this increase, expressed as a percentage of body weight, amounted to 163%. It is of importance to note that this increase coincided with the period of reduction in the photoperiod. From April to May there was a slight increase of 9% in testis weight expressed as a percentage of the body weight. This increase cannot, in view of the small size, be considered significant. The increase of testis weight as percentage of body weight from May to June was 47%, and increased from June to July by 47,4% to reach a maximum mean weight of 3,82 g. Although the mean testis weight in August was lower than in July, the single heaviest individual testis was recorded in August. Thus the possibility is not excluded that August was also a peak month for sexual activity. The very slight drop in testis mean weight from August to September also indicated that September was a month of high activity. The decrease in testis weight from August to September, expressed as percentage of body weight was only 6,2%. The slightness of the change most probably showed that the degree of sexual activity in September was similar to that of August. The observation that animals exhibited rather similar testes weights and sexual activity in the months July to September was supported by the fact that pregnant females were caught from August until the beginning of October.

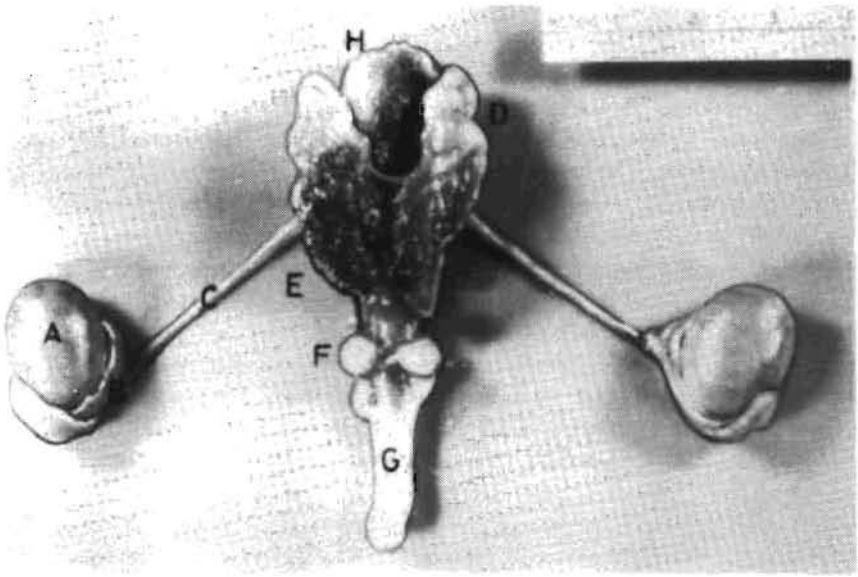

FIGURE 1
Active reproductive system. A: Testis, B: Epididymis, C: Ductus deferens, D: Seminal vesicles, E: Prostate gland, F: Bulbo-urethral glands, G: Penis, H: Bladder.

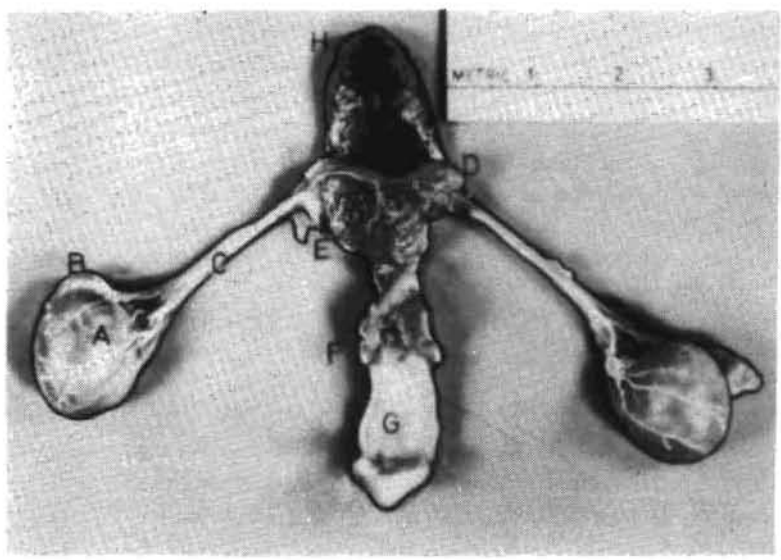

FIGURE 2
Inactive reproductive system. A: Testis, B: Epididymis, C: Ductus deferens, D: Seminal vesicles, E: Prostate gland, F: Bulbo-urethral glands, G: Penis, H: Bladder

Also the seminal vesicles and prostate glands showed maximum weights from July until September with a peak in August (Table I). Even without the knowledge of the "pregnant period" of the female, it could be surmised that copulation took place during the months July to September, and probably mostly in August.

There was a sudden drop in activity from September to October. The highest single value recorded in October, however, exceeded the maximum testis weight recorded in September. From September to October the drop in mean testis weight, as percentage of body weight, was over 40%. Furthermore, the lowest value recorded in October was only 0,115% of the body weight in comparison to the highest value of the same month which was 0,417% of the body weight. This most probably indicated that the activity of the testis began to decrease during October. This also coincided with an increase in the photo-period. The mean testis weight, measured in November fell to almost the same low value for February and indicated a period of inactivity. Although no animals were captured in December and January it seems safe to assume that these months were also within the inactive sexual phase, particularly when the minimum values for November and February and the pregnant period of the female are considered.

From the data in Table I it would appear therefore that *Bathyergus* was in sexual activity from April to the beginning of October and inactive from October to March.

Histology of the testis

The testis of *Bathyergus* has the following basic structure. The testis is surrounded by two

TABLE I

THE EFFECT OF SEASON ON MEAN TESTIS, PROSTATE AND SEMINAL VESICLE WEIGHTS EXPRESSED AS A PERCENTAGE OF BODY WEIGHT

Month	*N*	*Testes weight (per pair) as % of body weight*		*Prostate weight as % of body weight*		*Seminal vesicle weight as % of body weight*	
		Range	*S.D.*	*Range*	*S.D.*	*Range*	*S.D.*
Febr.	4	0,066 – 0,081	± 0,0065	0,015 – 0,022	± 0,0031	0,006 – 0,018	± 0,0051
Apr.	4	0,166 – 0,238	± 0,0347	0,027 – 0,035	± 0,004	0,021 – 0,062	± 0,0189
May	4	0,164 – 0,255	± 0,0429	0,033 – 0,053	± 0,0095	0,023 – 0,118	± 0,0779
June	4	0,231 – 0,257	± 0,055	0,040 – 0,063	± 0,0105	0,047 – 0,114	± 0,031
July	4	0,328 – 0,450	± 0,051	0,057 – 0,076	± 0,0079	0,066 – 0,104	± 0,0156
Aug.	4	0,297 – 0,481	± 0,099	0,043 – 0,090	± 0,0179	0,086 – 0,162	± 0,0327
Sept.	4	0,252 – 0,410	± 0,074	0,047 – 0,056	± 0,0036	0,094 – 0,141	± 0,020
Oct.	4	0,115 – 0,417	± 0,133	0,014 – 0,097	± 0,040	0,022 – 0,179	± 0,074
Nov.	4	0.075 – 0,092	± 0,041	0,017 – 0,022	± 0,0021	0,023 – 0,028	± 0,0021

thick connective tissue layers, the tough tunica albuginea, and, partly on the outside thereof, the tunica vaginalis. Typical seminiferous tubules are found which give rise to the tubuli recti. These tubules form a connection between the seminiferous tubules and the rete testes.

The rete testes can be divided into three parts, the intratesticular, the intertunical and extratesticular rete. The intratesticular rete consists basically of one large tube which partly lies on the medial portion of the testis. Sometimes small tubes run from the intratesticular rete and anastomose with each other. The intratunical rete follows the intratesticular rete and gives rise to several tubules which anastomose with each other. The extratesticular rete can in turn be divided into two parts, namely, a system of many tubules which anastomose with each other to form a network of tubules and secondly a very large tube or sinus, the so-called "rete blastema". Finally the whole rete is lined with a cuboidal epithelium.

The effect of season on the histology of the testis

From the end of October until the beginning of March the testes showed a marked reduction in activity. In these months there were no signs of spermiogenesis in the tubuli seminiferi contorti. The seminiferous tubules appeared lumenless in the inactive animal, only Sertoli cells, spermatogonia and primary spermatocytes being present in the lining of the tubules. Therefore the seminiferous tubules of some of the testes were not unlike the tubuli recti. This was not always the case as secondary spermatocytes were sometimes present. The maximum activity observed, however, were signs of spermatocytogenesis and never of spermiogenesis.

The diameter of the seminiferous tubules was also very much reduced in the inactive period from November to middle March. Four individuals in this period were randomly chosen and the seminiferous tubule diameter measured. These animals were adults and their weights ranged from 665 g to 1 200 g. In spite of these differences in body weight, the diameter of the tubules was remarkably constant and varied between 82μ and 99μ with a mean diameter of 92μ, the standard deviation being only 7,1 (Table 2). These small tubules showed a close resemblance to those found in foetal testes having large areas of interstitial cells and tissue between them. Although the activity of the cells of the seminiferous tubules was reduced to a minimum, sperm were found in zone 6 of the epididymis of one individual. The interstitial cells of Leydig were abundant in the inactive period and filled the large spaces between the dispersed tubules.

Conversely, in sexually active animals, from the end of March to September, the testes showed all phases of spermatogenesis and spermiogenesis (Fig. 3). The seminiferous tubules were closely packed and the mean tubular diameter of four active individuals, randomly chosen, was 172μ. The standard deviation was also small, being 18,4 – the diameter varying between 161μ and 181μ.

In the sexually active animal the interstitial cells of Leydig were closely packed between the tubules and their activity appeared to be high. In most animals, both sexually active and inactive, fat droplets occurred between the interstitial cells. The nature of the droplets was confirmed by suitable staining methods such as Sudan Black, Osmic Acid and Nile Blue. In sections prepared by routine alcohol dehydration the fat droplets were apparently dissolved and resulted in clear areas being formed within and immediately around the Leydig cells

(Fig. 3). Although fat droplets occurred throughout the year it seemed that more fat was present in sexually active animals the droplets being considerably smaller in inactive animals. However, one inactive animal in February exhibited more and larger fat droplets than another active animal in May.

TABLE 2
TUBULAR DIAMETER OF SEXUALLY ACTIVE AND INACTIVE TESTES

Reproductive status	*N*	*Tubular diameter μ*	
		Range	*S.D.*
Active	4	161–181	± 17,9
Inactive	4	82– 99	± 7,1

Histology of the efferent ducts

The efferent ducts in *Bathyergus* form a connection between the rete testes and the epididymis and can histologically be divided into two zones, namely, an initial and a terminal zone. The epithelium of the highly convoluted tubes of the initial zone is simple low columnar and is made up of two kinds of cells, principal and ciliated cells. A distinct characteristic of this zone is the very light staining cytoplasm of the cells. The nuclei are spherical and granular. This zone ends abruptly and goes over into the terminal zone. In structure and form the cells of the terminal zone resemble those of the initial zone. There are, however, three obvious differences between the two zones; firstly, the tubular diameter is much smaller,

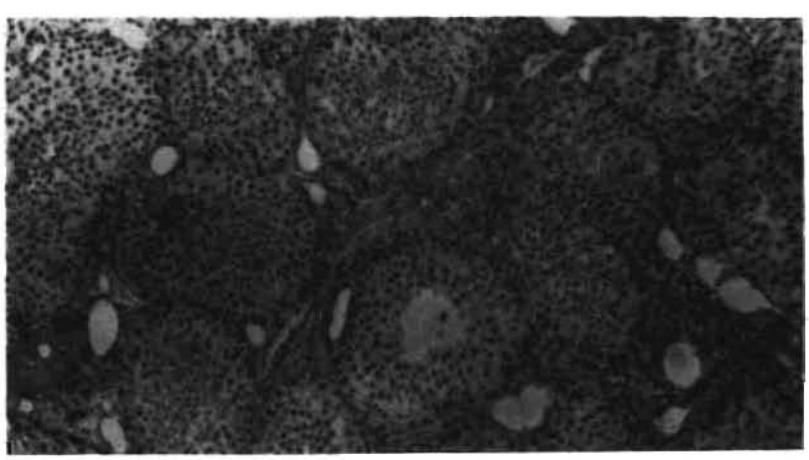

FIGURE 3
Cross section of active testis.

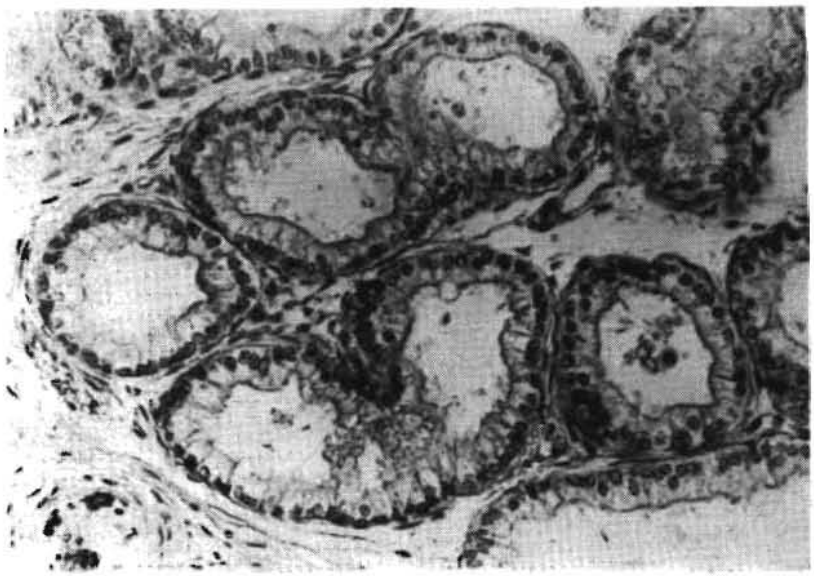

FIGURE 4
Cross section of initial zone of efferent ducts.

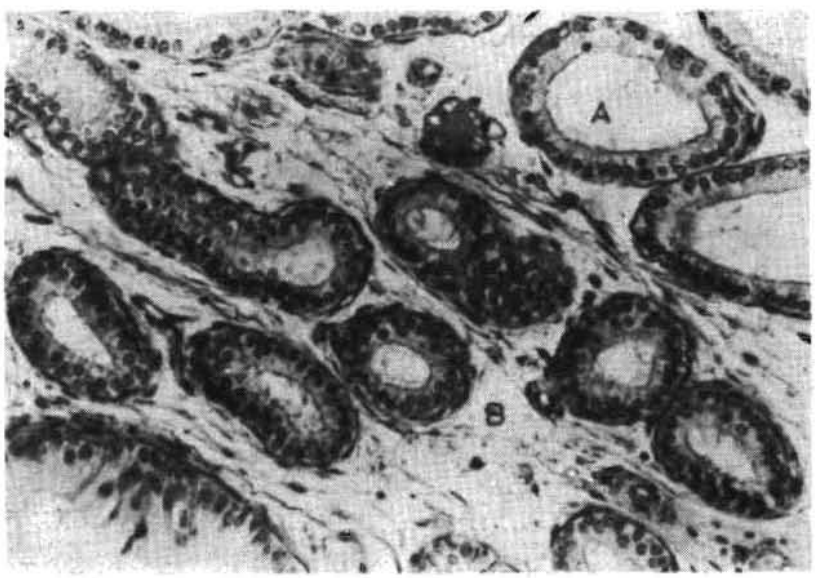

FIGURE 5
Cross section of efferent ducts. A: Initial zone, B: Terminal zone.

secondly, the epithelium appears to be pseudostratified columnar and thirdly the cells of the terminal zone stain darker than those of the initial zone. The terminal zone gives rise to the epididymis.

The effect of season on the histology of the efferent ducts

The initial zone was highly secretory in sexually active animals and a mass of secretory products was found on the brushborder. Sometimes the activity of the cells increased to such an extent that they became distended and bulged into the lumen, or their apical borders were obscured by the secretory products (Figs. 4 and 6). Only a few sperm were observed in this zone in active animals. The ciliated cells also assumed a typical goblet appearance which was not the case in inactive animals.

In the inactive animal the secretory activity of the cells of the initial zone was very much reduced by comparison. Many spermatocytes and eosinophilic spheres were also present in the tubules of inactive animals.

No secretion was apparent in the terminal zones of either active or inactive animals (Figs. 5 and 6). The only clear differences found throughout the year were that the active terminal zones possessed sperm and eosinophilic granules. The inactive terminal zone on the other hand was clear of sperm and the tubular diameter decreased.

Histology of the epididymis

The epididymis of *Bathyergus* can be divided into six zones. These zones correspond basically to zones found in the rat epididymis. Judging by the description of these zones by

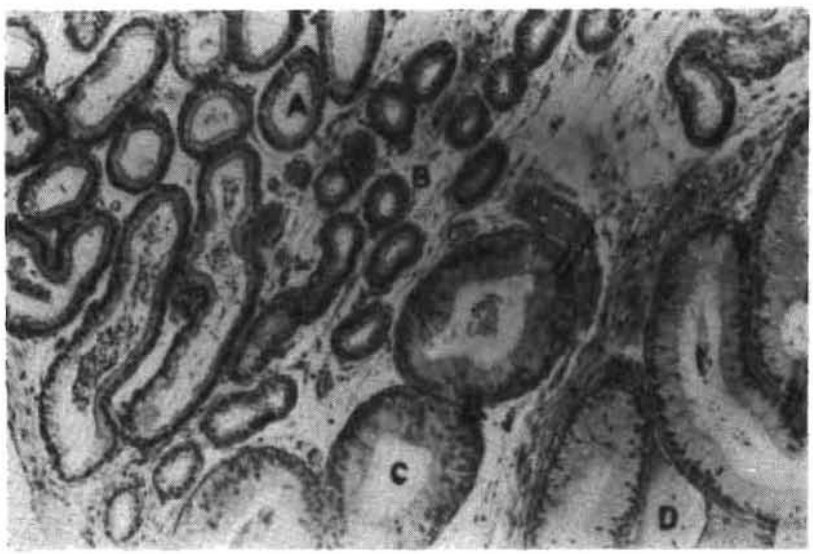

FIGURE 6
Cross section of efferent ducts and epididymis. A: Initial zone, B: Terminal zone, C: Zone 1C of epididymis, D: Zone 2 of epididymis.

Cleland and Reid (1957) they appear to be better demarcated in the rat than in *Bathyergus*.

Some of these zones could be divided into subzones; zones 1, 2, 3 and 4A are found in the head of the epididymis, zones 4B and 5A in the isthmus and zones 5B and 6 in the tail of the epididymis. Zone 1 in the epididymis of *Bathyergus* can be divided into two subzones. These subzones agree basically with subzones 1A and 1C found in the rat (Fig. 6). A subzone 1B might be present, but the present investigation did not yield sufficient evidence to support this. Towards the end of subzone 1C the principal cells show small vacuoles at their apical ends (Fig. 6). The epididymis of this subzone differs from that of the rat in that the nuclei are not as well aligned and the epithelial height does not differ significantly from that of subzone 1A.

Zones 2 and 3 of *Bathyergus* typically resemble that of the rat (Figs. 6 and 7). Zone 2 is typically recognised by the large vacuoles in the apical portions of the principal cells and by the fact that the nuclei are very well aligned basally. Although the cells of zone 3 of *Bathyergus* have the same histological structure as that of the rat, particularly in relation to the uneven alignment of the cells, the clear supranuclear area and the darkly staining upper apical ends of the cells, there is one important difference. This concerns the height of the epithelium and thus the lumen diameter. In *Bathyergus* the epithelium is high columnar and does not differ much from that of adjacent zones whereas in the rat the epithelium of zone 3 is the lowest among the epididymal ducts in the head. As in the rat zone 3 is highly secretory. Zone 4 also resembles that of the rat, but subzones 4A and 4B are not as clearly demarcated. Small vacuoles at the apical ends of the cells of both these subzones are numerous in *Bathyergus* in contrast with the rat where, although present they do not form such a distinct feature of zone 4. A further very distinct characteristic of zone 4 in *Bathyergus* is that the nuclei stain considerably

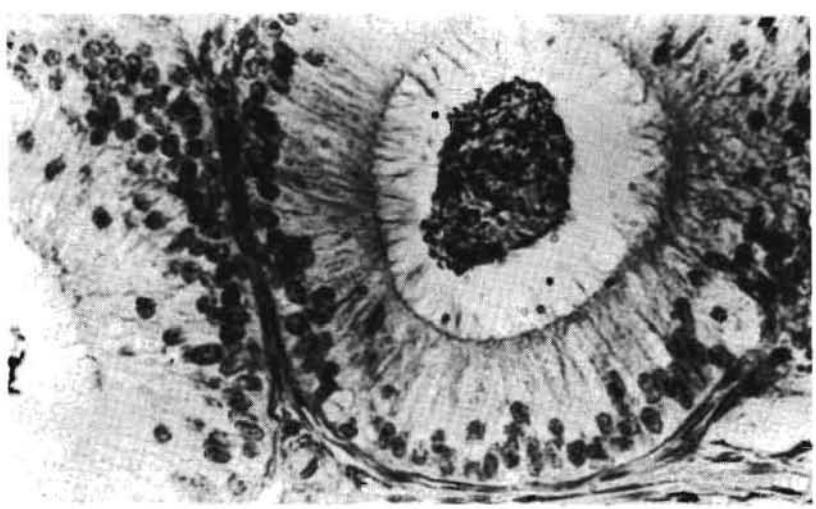

FIGURE 7
Cross section of zone 3 of the epididymis.

lighter than any other nuclei of the epididymis. Sometimes these lighter areas surrounding the nucleoli resemble minute vacuoles within the nuclei. Active clear cells are very common in zone 4B. These cells are easily recognised by the contrast between them and the more deeply staining principal cells among which they lie. The juxtanuclear vacuoles that identify this part as zone 4 and the indentation of the nuclei could be clearly distinguished in *Bathyergus*. Although the indentation is not so regular and clear as in the rat, zones 4A and 4B could be distinguished in *Bathyergus*. Zone 4A show suprajuxtanuclear vacuoles in contrast with zone 4B where the vacuoles appear more peri- to infrajuxtanuclear. Zones 5 and 6 also resemble that of the rat. It was however, difficult to distinguish the subzones from each other.

The effect of season on the histology of the epididymis

The epithelium of zone 1 is extremely folded in the sexually active animal and eosinophilic granules are quite common in the lumen. The epithelium was sometimes folded to such an extent that the sides of the duct came close to touching each other. Towards the end of zone 1 the folding was less marked. Very few sperm occurred in the lumina and when sperm were present in zone 1, they were usually attached to the eosinophilic granules. In the sexually active animals the sperm density slowly increases from the end of zone 1 to zone 3, being quite high in zone 3. This is in contrast with the rat where the sperm density increases towards the end of zone 2 and suddenly decreases in zone 3. From zone 4 the sperm density rapidly increases to reach a maximum in zone 6.

In the inactive epididymis the epithelium of zone 1 was never folded. Eosinophilic granules appeared in almost all the zones of the epididymis and it was difficult to find any sperm throughout the epididymal ducts. Sperm, however, occurred in zone 6 of one animal in the inactive period. Other cellular debris, most probably from the testes, was also found in the epididymal ducts. Because this debris was usually mixed with the eosinophilic granules, it was difficult to decide on its nature. In some cases the debris appeared to resemble primary spermatocytes. Whatever the nature of these products, they, with the eosinophilic granules, are most abundant in zones 4 to 6.

Another feature of the inactive epididymis was the large amount of eosinophilic lumen fluid found, particularly in zones 5 and 6 but also in zone 3. The fluid found in zones 5 and 6 filled the lumen completely and stained uniformly.

Histology of the ductus deferens

The histological structure of the ductus deferens has the same general plan as that of most mammals. The epithelium varies over the length of the ductus deferens from columnar to pseudostratified columnar. *Bathyergus* does not have a scrotum and thus has a very short ductus deferens which widens slightly towards the ampullae. The ductus deferentia enter the wall of the urethral sinus more or less parallel with the two ducts from the seminal vesicles and various ducts from the prostate. All these tubes run in a longitudinal ventral fold, the urethral crest, within the wall of the urethral sinus. The urethral crest bulges into the lumen of the urethra which is here lined with a highly secretory epithelium. The epithelium is of the transitional type.

Effect of season on the histology of the ductus deferens

Sperm were found in the ductus deferens from middle April to the end of October and in one animal also in March.

As the tubular diameter varies greatly along the length of the ductus deferens, it was not possible to compare tubular diameters of animals in sexual activity with inactive animals. It appears also that the muscular wall of the ductus deferens varies along its length, being very thick near the epididymis and thinner near the urethral sinus.

The only clear evidence of activity found in the ductus deferentia was the presence of sperm and the secretory activity of the cells of the ampullae. These are pseudostratified columnar with secretory products at their apical borders. The height of the columnar cells of sexually active animals was clearly greater than in the inactive state.

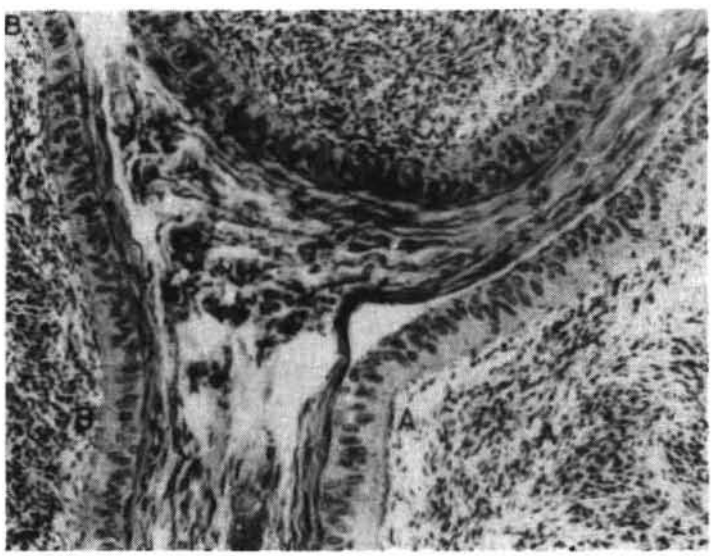

FIGURE 8
Cross section of epididymis (Active). A: Zone 5, B: Zone 6.

Histology of the prostate gland

The prostate in *Bathyergus* is not typical of that found in most rodents. For example in the rat and guinea-pig, the prostate is clearly divided into lobes, while in *Bathyergus* it is a more or less compact organ. According to Price and Williams-Ashman (1961) there is still much confusion in regard to the nomenclature of the prostate. This arises mainly from the general application of the word lobe. The prostate in *Bathyergus* forms a "body" around the dorsal and lateral sides of the seminal vesicles and the dorsal wall of the urethral sinus and from macro-examination, no clear-cut separation into lobes could be made. On histological grounds, however, it could be divided into four sections each of which forms a clear and separate unit, with thick connective tissue separating most of them. It appears, therefore,

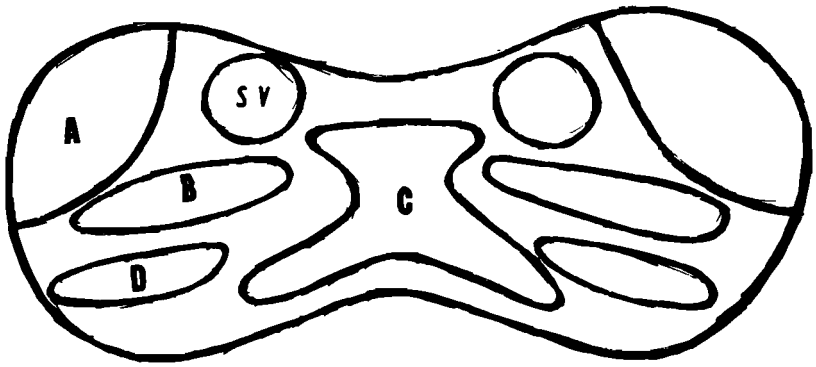

FIGURE 9
Diagramatic representation of the prostate gland where the lobes either lie next to each other or where they overlap. A: Section A; lateral prostate. B: Section B; dorsal prostate. C: Section C; coagulating gland. D: Section D; ventral prostate. SV: Seminal vesicles.

that the prostate of *Bathyergus* is imperfectly divided into three or four pairs of lobes. Fig. 9 is a diagramatic representation of the position of each lobe as revealed in a transverse section where the lobes lie either next to each other or where they overlap.

Section A: The epithelium of this section is extremely folded and the cells are of the high columnar type. The nuclei lie mostly at the basal ends of the cells which are closely packed. The apical ends of the cells are serous and the secretory products in the lumen form large granules or amyloid bodies (Fig. 10).

Section C: This section resembles section A, but there are certain obvious differences. The apical borders of the cells in C are larger than those in A and are of the zymogen type. This results in very light apical regions which resemble large vacuoles. The basal membrane at the apical part of the cells is also clearer in C than in A. Further differences are that the nuclei of C stain darker than those of A and the cells in C are not as closely packed as in A. The secretion of C has the same general appearance as A, being granular but C differs from A in that the secretion is eosinophilic, while in A the secretion stains very faintly (Fig. 11).

Section B: The epithelium of this section is never folded and the alveoli are large and form very large lumina. The epithelium is of a very low columnar to cuboidal type and stains very darkly. The secretory products are very interesting, being rod-shaped, oval bodies surrounded by a very fine granular secretion which is eosinophilic (Fig. 12).

Section D: This section resembles B in that the epithelium is seldom folded and that the lumina are very large. It differs in that the epithelium although of the low columnar type is higher than in B. The epithelium and nuclei of D stain lighter than in B and the secretions differ greatly, being finely granular to large granular in D and lacking the rod-shaped and oval bodies present in B (Fig. 12).

To compare these sections with prostate lobes commonly found in other rodents purely on a histological basis is difficult but the following homologies could be made. Although the connective tissue strands are not as clear and well developed between sections B and D as between the other sections, B and D clearly differ from each other. Section B resembles the

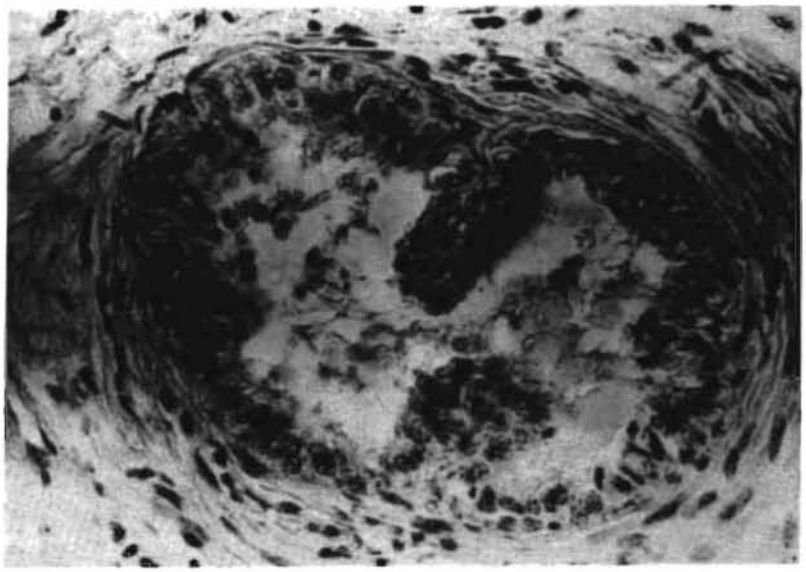

FIGURE 10
Cross section lateral prostate: section A.

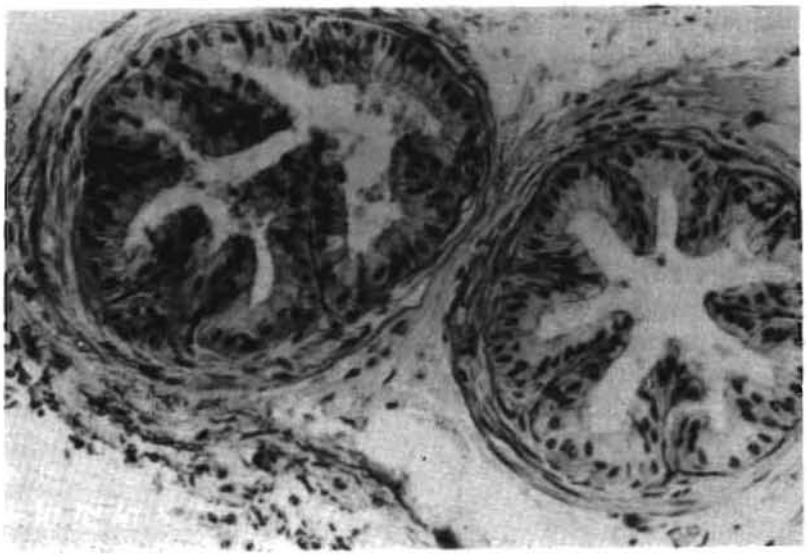

FIGURE 11
Cross section of coagulating gland; section C.

typical dorsal prostate of other rodents such as the rat. The epithelium of section D resembles the ventral prostate of the rat in that both have a columnar epithelium with secretory basal nuclei and the same granular secretion. The only clear difference between section D of *Bathyergus* and the ventral prostate of the rat is that the alveoli of the latter are more folded than those of *Bathyergus*. In similarity of position and in close resemblance of epithelia and secretory products section A of *Bathyergus* is homologous with the lateral prostate of the rat. The coagulating gland of the rat shows a marked resemblance to that of section C in *Bathyergus*. These homologies are summarised in Figure 9.

The effect of season on the histology of the prostate gland

The prostate varied in weight through the year and the following histological differences between active and inactive glands were observed. The active prostate is highly secretory and the lumina of the alveoli are usually filled with secretory products. Sometimes, and particularly in the case of the lateral prostate, secretory activity was so great at the apical borders of the cells that the epithelium of the alveoli was partly obscured by granules. Although the secretory activity of the cells did not cease in the inactive prostate it was clearly reduced and secretory products were only just visible in the lumina.

Folding of the epithelia of the alveoli occurred to a great extent in the inactive prostate. This was particularly clear in the coagulating gland where the epithelium of the alveoli partly invaded the lumen. Other cells also seemed to invade the lumen and they appeared to be reticular in character (Fig. 13). The epithelia of some of the alveoli of the lateral and ventral prostate and coagulating gland disappeared, apart from occasional patches. The degenerated

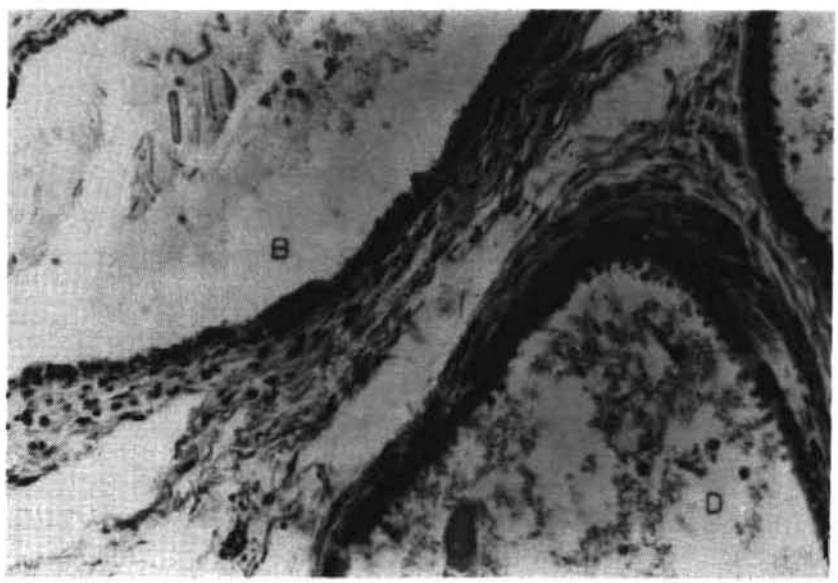

FIGURE 12
Cross section of active prostate. B: Dorsal prostate; section B. D: Ventral prostate; section D.

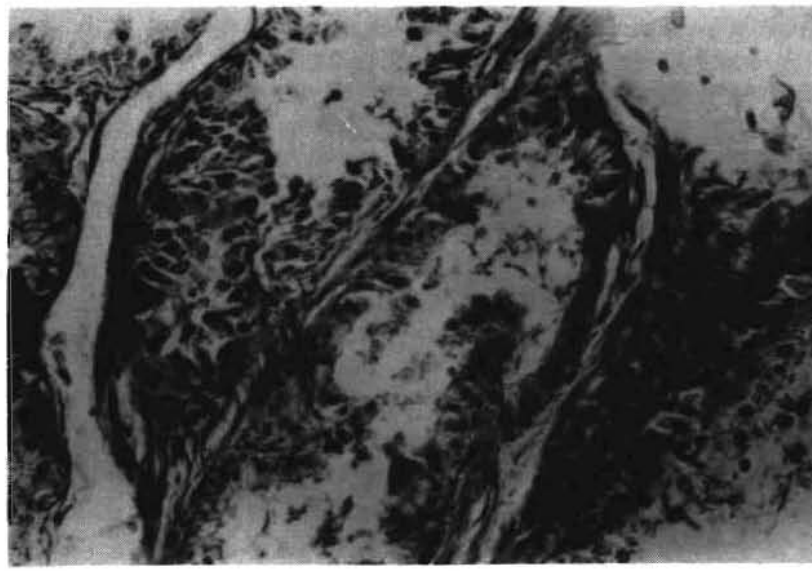

FIGURE 13
Cross section of inactive prostate.

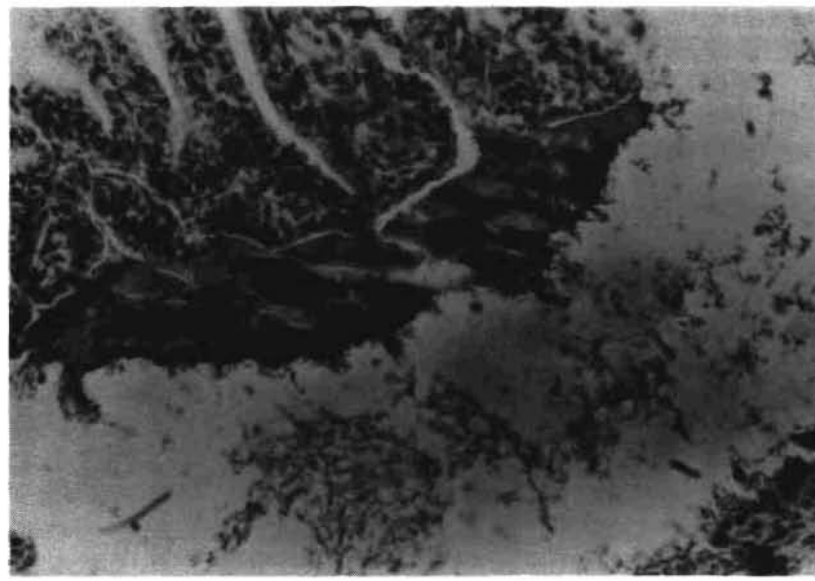

FIGURE 14
Cross section of active seminal vesicles.

epithelium filled the lumina of the alveoli and stained faintly. The epithelium of the dorsal prostate did not show marked folding and the cells had more or less the same histological appearance as in the active prostate. The alveoli, however, were much reduced in size, forming a narrow lumen in comparison to the active prostate where the lumina of the alveoli were large. The columnar epithelium in all the lobes was reduced in the apical region. In the case of the coagulating gland the apical portion stained faintly.

The active prostate on the other hand showed the following characteristics. Lateral prostate: the high columnar epithelium was very much folded but less so than in the inactive prostate. The secretory products consisted mainly of amyloid bodies which formed a bulky mass in the lumina of these alveoli and stained faintly (Fig. 10). Ventral prostate: The columnar epithelium secreted very fine granular material. The alveoli were very large in comparison to those in the inactive prostate (Fig. 12). Coagulating gland: The epithelium was of a very high columnar type. Clear zones were common around the dark-staining nuclei. The secretory products were granular as in the lateral prostate but slightly larger and darker staining, forming eosinophilic bodies (Fig. 11). Dorsal prostrate: The secretory products are mainly eosinophilic, rod-shaped and oval structures suspended in a homogenous eosinophilic fluid (Fig. 12). Smooth muscle fibres and connective tissue strands around the alveoli were better developed in active prostate glands than in the inactive glands

Histology of the seminal vesicles

The wall of the seminal vesicles of *Bathyergus* consists of three layers; an outer thick layer of elastic fibres, a narrow longitudinal muscular coat, a very narrow circular muscular coat and a glandular epithelium. Each seminal vesicle is drained by a duct which runs along the urethral crest and eventually opens in the urethral sinus. The epithelium of the seminal vesicles is strongly folded and the degree of folding and convolution of the tubules increases towards the anterior margin of the gland.

The effect of season on the histology of the seminal vesicles

The weights of seminal vesicles throughout the year differ markedly between sexually active and inactive animals (Table 1). The seminal vesicles of animals in sexual activity showed the following characteristic histology. The lumina were always filled with seminal fluid clearly eosinophilic in character. The very large surface area of the folded epithelium was highly secretory. The secretory products at the apical borders of the cells were finely granular and the nuclei were large and round to oval in appearance. In areas where the lumina of the vesicles were filled to capacity with fluid the folded epithelium was stretched to form an almost smooth layer (Fig. 14) and as a result the epithelial cells became low columnar to cuboidal but nevertheless highly secretory.

The epithelia of the inactive seminal vesicles were extensively folded. Secretory products could not be discerned and secretory activity was greatly reduced. The epithelium of the seminal vesicles also declined, but to a lesser extent than in the prostate. In certain areas a mass of cells was observed in the lumen. These were probably mostly epithelial debris but it also appeared as if cells other than epithelial, invaded the lumen. As in the prostate these cells appeared to be reticular in character.

The penis

The histology of the penis of *Bathyergus* basically resembles that of other rodents and particularly that of the guinea-pig e.g. the very thick tunica albuginea around the corpus cavernosum penis and the wide urethra which distally is dorso-ventrally flattened and proximally, laterally flattened. In certain features, mainly the structure of the glans, the penis of *Bathyergus* differs from the basic rodent pattern.

In the *Bathyergus* glans a dorsal groove, possibly the homologue of the sacculus urethralis in other rodents, splits distally to form a T-slit, dorsal to the tip of the os penis (Figs. 15 and 16). This dorsal groove is lined with a keratinised epithelium with horny papillae. Towards the middle of the glans the groove, here connected to the urethra by a narrow tube, widens considerably and possesses sharp horny spikes. These backwardly pointing spikes are also common on the surface of the glans (Fig. 16). Behind the connection between the dorsal groove and the urethra the groove, although still possessing small spikes, now runs as a shallow depression dorsally to the os penis. The horny spikes on the glans itself become more numerous and bigger towards the proximal end. A prepuce, lined on the inside with a keratinised epithelium, is very much folded and fimbriated and covers the glans in the normal way.

In the guinea-pig the spikes are not only larger but there are two large horny spikes measuring 4 mm each near the distal end of the glans. The guinea-pig does not possess a dorsal groove but has a definite sacculus urethralis, a blind-ending sac found in many rodents, particularly in the family Caviidae (Dathe 1937).

These differences are of functional importance and will be discussed later.

DISCUSSION

Gross anatomy of the reproductive system

The reproductive system of *Bathyergus* is typical of that found in most rodents. Weber (1927) observed that many rodents, particularly the smaller ones, did not have a scrotum but only two slight peritoneal evaginations. This is the case also in *Bathyergus* and it is found also in the insectivore moles of the family Talpidae. In moles the lack of a scrotum would be of obvious advantage in giving protection to the testis.

All the reproductive organs except the prostate resemble that of the rat and the guinea-pig as discussed by Eckstein and Zuckerman (1956) and the hamster, as described by Price and Williams-Ashman (1961). Macroscopically the prostate differs from that of most rodents in being a more or less compact organ rather resembling that of the rabbit (Krause 1921). Among rodents the guinea-pig prostate lobes are also intimately connected to each other, although they can be separated by careful dissection. Histological studies, however, confirmed the presence of four pairs of lobes in *Bathyergus*. These lobes were histologically similar to those of the rat (Price and Williams-Ashman 1961).

The large differences between active and inactive reproductive organs of *Bathyergus* agree with the findings of Allanson (1934) on the hedgehog and also on the ferret (1932). The genital tracts of these animals also show marked atrophy during the sexually inactive period. Furthermore, there is a close similarity between the length of the sexually active period of the hedgehog and ferret and that of *Bathyergus*. The active period of the male hedgehog

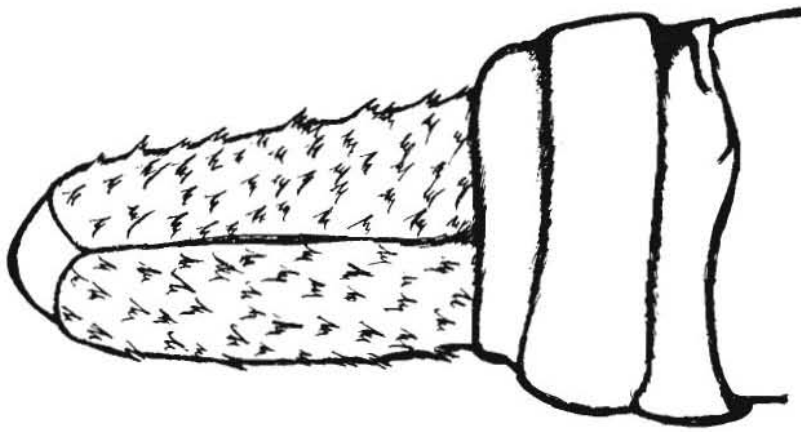

FIGURE 15
Diagramatic representation of glans penis (dorsal view) with prepuce folded backwards to show dorsal groove and T-slit.

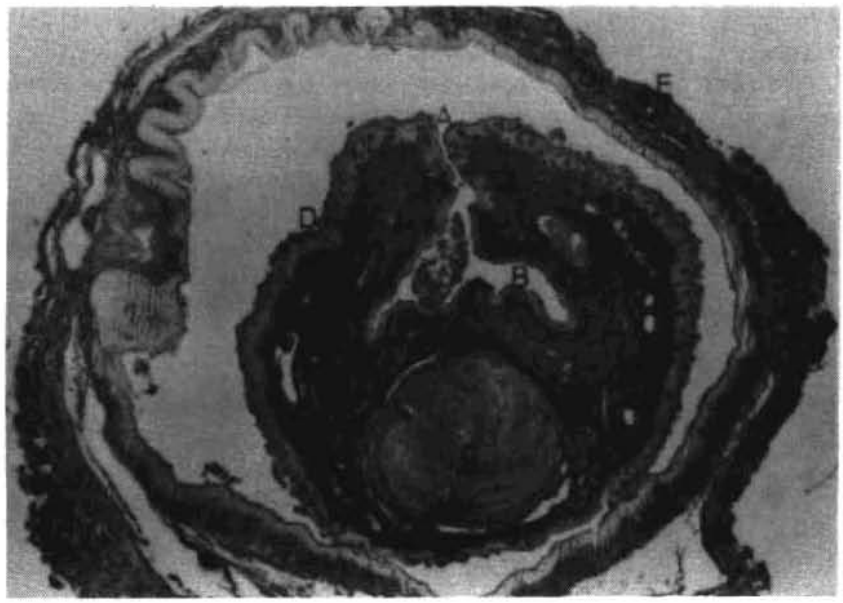

FIGURE 16
Cross section of glans penis.
A: Dorsal groove, B: Urethra, C: Os penis, D: Horny papillae with spikes, E: Prepuce.

starts in January and activity ceases in September. In *Bathyergus*, in the southern hemisphere, activity starts in late March and ceases towards the end of October. The testes during the sexually active period reached a weight five times greater than in the inactive period. Such large differences are common in rodents. In other mammals, too, large differences are found: for example, in the insectivore mole *Parascalops breweri* (Eadie 1939) the maximum testes weight is also five times that of the testes in the inactive period and in the ferret the testes can weigh as much as ten times their inactive weight (Allanson 1932). Allanson, however, concluded that the weights of the testes could not always be taken as an index of their activity. My data on *Bathyergus* agree basically with this, for instance, an animal trapped in October with a much lower relative testis weight than an animal trapped in July showed the same spermiogenic activity. However, the period of maximum testis weight lasted from July to September with reasonably high values in June and somewhat lesser values in October and the heaviest testes in the active period could always be correlated histologically with a high activity. Also low testis weights in February and November could be correlated with inactivity. Moreover, there was a close correlation between maximum testis, prostate and seminal vesicle weights and the number of pregnant females caught. Jarvis (1969) found that female *Bathyergus* became pregnant from July through September to the beginning of October. She also found that in very dry seasons when food was limited, the females would not breed, and that late rainy seasons could delay the breeding period. My results agree with those of Jarvis, for in the past two years, when the present investigation was conducted, the winter rains came exceptionally late in the Cape. As a result the first pregnant females were not caught before August. Embryos of 85–90 mm appeared to be full-term. Jarvis (1969) stated that full-term embryos measured 75 mm and that the first full-term embryos were obtained at the end of September. I obtained full-term embryos from August to October and also very small embryos in October. One female was pregnant in December. Most lactating females, were, however, caught in October. If one correlates this pregnant period with male sexual activity, measured histologically, it seems that copulation took place mostly during July, August and September. The fact that very small embryos were also found in October and a pregant female in December, raises the possibility that a female could produce two litters in one breeding season. This is common among rodents. For example, gophers can raise two litters within a single breeding season.

The effect of season on the histology of the testes

Mossman, Hofman and Kirkpatrick (1955) found that the testes of the infantile fox squirrel contain small lumenless seminiferous tubules with a single row of spermatogonia, Sertoli cells and a few spermatocytes. Koller (1936) found that the testes of the adult mole, *Talpa*, resemble the embryonic or infantile appearance in the inactive period. In *Bathyergus* this also appeared to be the case. Very small lumenless seminiferous tubules dispersed between the interstitial cells were a feature of the inactive period. In the inactive period, moreover, the tubular diameter decreased by approximately 100‰, from 172μ to 92μ. This decrease in diameter may have caused occlusion of the lumen. The lining of these tubules consisted almost exclusively of Sertoli cells, spermatogonia and primary spermatocytes and in this way resembled the infantile or embryonic state. This situation is typical for seasonal breeders, such

as the American ground squirrel (Johnson, Foster and Coco 1933) and the hedgehog (Marshall 1911, Courrier 1927, Allanson 1934).

In the active period there is a sudden and dramatic increase in testes activity in *Bathyergus*. All phases of spermatogenesis and spermiogenesis suddenly appear and the tubular diameter increases from 92μ to 172μ. In the hedgehog, Allanson (1934) found that the tubular diameter increased from 130μ to 190μ. In other mammals such as the ferret the increase in tubule diameter can be considerably greater. It is of interest to note that in the beginning and at the end of the breeding season primary spermatocytes appeared in the lumen of the seminiferous tubules of *Bathyergus*. Rasmussen (1917) made the same observation and also found spermatocytes in the seminiferous tubules of the woodchuck *Marmota* during dormancy.

There was a close correlation between the increase in size of Leydig cells and the increase in testes activity in *Marmota* (Rasmussen 1917) and the hedgehog (Allanson 1934) in the active period. In the insectivore mole *Talpa*, also a seasonal breeder, the Leydig cells do not vary conspicuously in size and number throughout the year (Courrier 1927). In *Bathyergus* the impression was that more Leydig cells were present in the inactive period, although it seems that the size of the Leydig cells did not vary much throughout the year. This impression might, however, be false as a result of the large difference in seminiferous tubule diameter recorded between the two seasons. In the active period the tubules almost doubled in size and the secretory Leydig cells were compressed between these tubules. In the inactive period large areas of Leydig cells were found between the compressed seminiferous tubules. In *Marmota*, however, the seminiferous tubules enlarge but become separated as a result of the development of the interstitial tissue (Rasmussen 1917). It seems, therefore, that *Bathyergus* is similar to *Talpa* where the number and size of the Leydig cells do not differ markedly throughout the year. The secretory activity of the interstitial cells, however, is reflected in changes in their lipid content (Eckstein and Zuckerman 1956). In *Bathyergus* in the sexually active state significantly more lipid material was deposited by the Leydig cells. This is in agreement with results obtained in *Marmota* and many other seasonal breeders.

In conclusion it was found that the testes increased in size and weight as a result of the deposition of lipid by the Leydig cells and mainly as a result of the great increase in tubular diameter of the seminiferous tubules.

The effect of season on the histology of the epididymis

Mietkiewski (1935) was the first to differentiate between six zones in the epididymis of the guinea-pig. Cleland and Reid (1957) remarked that Mietkiewski was fortunate to study the epididymis of the guinea-pig first, for the zonation is here very clear and marked. In 1957, Cleland and Reid published an impressive paper on zonation of the rat epididymis. They remarked that in the rat six fairly distinct zones with subzones occur. Although I only used three complete series for an investigation of zonation in the epididymis of *Bathyergus* it was possible to distinguish six zones. It was quite easy to differentiate and to homologise zones 1, 2 and 3 with those of the rat. Zone 3 does not fully resemble that of the rat in that the epithelial lining has more or less the same height as adjacent zones whereas in the rat it is lower than in any other zone. In other respects zone 3 of *Bathyergus* resembles that of the rat. Zone 3 is of great importance in *Bathyergus* as this was clearly the only zone where secretion occurred.

Cleland and Reid (1957) also speculate on the secretory activity of this zone in the rat. This will however be fully discussed in the effect of season.

It was far more difficult to homologise zones 4 to 6 with those of the rat, particularly their subzones. Although I am fairly certain of the existence of these zones in the epididymis of *Bathyergus*, I feel that further research may reveal some interesting differences between *Bathyergus* and the rat. For example, zone 4 should receive special attention in view of the nuclei which differ greatly in their extremely light staining capacity.

Benoit (1926) and Cleland and Reid (1957) found in the guinea-pig a low density of spermatozoa in the lumen of the efferent ducts and initial zone of the epididymal duct, the density usually rising rapidly in the duct immediately distal to this zone. In the rat on the other hand, Cleland and Reid (1957) found that the sperm density increases from the efferent ducts to reach a maximum in zone 2. In zone 3 the sperm density decreases and increases again from zone 4 to reach a maximum in zone 6. *Bathyergus* resembles the guinea-pig where there was a steady increase in sperm density from the head towards the tail of the epididymis.

In zone 1 of the active epididymis of *Bathyergus* excessive folding of the epithelium occurred and very few sperm were found. In the rat folding also occurs particularly in zones 1A and 1B in the active animal (Cleland and Reid 1957). There was no folding of the epithelium nor sperm present in zone 1 of the inactive epididymis of *Bathyergus*. The folded epithelium, particularly where the folds of opposite sides nearly met, may be a reflection of peristaltic activity for conveying the still immotile sperm but is more probably a reflection of secretory or absorptive activity. Peristaltic activity of the duct was first shown in the guinea-pig by Simeone (1933) and in the rat by Muratori (1953) and has been confirmed by Bishop (1961) and recorded cinematographically by Risley (1958).

Cleland and Reid (1957), Van der Stricht (1893) and Myers-Ward (1897) observed that certain zones of the epididymis have a secretory function. Cleland and Reid further state that luminal sperm density could give information on this aspect of epididymal function and conclude that on this basis zone 3 is one where fluid secretion occurs. It was found that zone 3 of the epididymis in *Bathyergus* was highly secretory in the active period. Those regions of the tubules that were secretory contained almost no sperm and sperm density increased in zone 3 where almost no secretion was present. These findings correlate well with those of Cleland and Reid. It was also interesting to note that secretion occurred in cells with clear areas in their cytoplasm, namely zone 3 and in the initial zone of the efferent tubules. Zone 3 of an almost inactive epididymis of *Bathyergus* was also secretory towards the end of the breeding season. Unfortunately not enough inactive animals were examined to establish whether the secretion of this zone ceases in the inactive period. In the active epididymis the sperm density increased greatly from zones 4 to 6. In the almost inactive epididymis only fluid, eosinophilic granules and spermatocytes were found in the epididymis. Rasmussen (1917) also mentions that spermatocytes filled the lumen of the seminiferous tubules during dormancy in the woodchuck. The duct contents, visible in the inactive epididymis of *Bathyergus*, may be due to fluid and spermatocytes from the testes which are conveyed through the rete and efferent ducts to the epididymis. It has also been found that the tail of the epididymis is a storage area for mature sperm (Tesh and Glover 1961). In sexually active *Bathyergus* sperm are most probably stored in zones 5 and 6 of the epididymis for sperm concentration here reached a maximum.

Moreover, the tubular diameter of these zones is very large and distended to form a large area for storage.

Bishop (1961) mentions that although extensive work has been done on zonation of the epididymis of several species, this knowledge has contributed very little towards elucidation of the function of the epididymis. For example no work has been carried out on the cytology of the epididymis of seasonal breeders in activity and in inactivity. Such a study should reveal at least some functions of this complex organ.

Effect of season on the histology of the ductus deferens

A short ductus deferens is commonly found in mammals with inguinal testes as in *Cavia* (Eckstein and Zuckerman 1956), the short tail shrews *Sorex* and *Blarina* (Arnbäck-Christie-Linde 1917, Brambell 1935 and Pearson 1914) and many other mammals. *Bathyergus* is no exception. The presence of a urethral sinus is very common among rodents. Examples are field mice, voles, rats and the golden hamster (Eckstein and Zuckerman 1956), but not the guinea-pig (Hall 1936). *Bathyergus* falls within the first group.

No sperm are usually found in the ductus deferentia of seasonal breeders during the inactive period. A few weeks after the start of sexual activity sperm were present in the ductus deferentia of the mouse (Edwards 1939). This was also the case in *Bathyergus*. It was furthermore observed that the epithelium of the ductus deferens in *Bathyergus* was folded in the active period and not in the inactive state. Martins and do Valle (1938) showed that sperm transport through the ductus deferens was due to peristaltic activity. The folding in the active ductus deferens may also be a reflection of secretory activity.

Allanson (1932) observed that there were cyclical histological changes in the ductus deferens of the ferret during the year and that it could be correlated with changes in the testes. She found that the cells of the ductus deferens of the active ferret were highly secretory and regressed in the inactive period. This was also observed in *Bathyergus*. Benoit (1926) and Allanson (1934) were able to prove that after castration the cells of the ductus deferens undergo regression and that androgen affects the activity of the ductus deferens.

Position of cytoplasmic droplet

In a recent review Hafez (1962) concludes that the sperm mature or ripen during their passage through the epididymis. He also states that the cytoplasmic droplet, which is attached to the proximal end of the sperm midpiece at the head of the epididymis, moves distally so that in the tail of the epididymis the droplet is attached to the distal end of the midpiece. This was also observed in *Bathyergus*.

The effect of season on the histology of the prostate

The epithelial lining of the alveoli of the different lobes of the prostate and their secretions in *Bathyergus* agree basically with those of the rat. The prostate of *Bathyergus* can therefore be regarded as imperfectly divided into four lobes, the dorsal and ventral lobes are quite similar to each other and the lateral lobe and coagulating gland resemble each other quite closely.

Eckstein and Zuckerman (1956) found that in the mouse folding of the epithelium of

the coagulating gland occurred, but no such folds were found in the dorsal and ventral prostates. This is true also of *Bathyergus*.

Eadie (1948) stated that in the insectivore mole *Condylura* breeding ceased during midwinter. He also observed that, although there were no obvious external changes in the size or appearance of the prostate lobes, internally a definite change had occurred. The simple columnar epithelium disappeared except for occasional patches and was replaced by a mass of cells with faintly staining cytoplasm which appeared to be reticular in character. My observations on *Bathyergus* basically agree with those of Eadie. Although the epithelia of many prostate lobes in *Bathyergus* degenerated, they did not disappear but filled the lumina of the alveoli in the form of cellular debris. Moreover, reticular cells appeared in the lumen.

Price and Williams-Ashman (1961) observed that the cytologic structure of the prostate and seminal vesicles of the rat and mouse is one of the most sensitive indicators of the level of circulating androgen. Moore, Price and Gallagher (1930) and Moore, Hughes and Gallagher (1930) examined the effect of castration and testosterone administration on the histology of the rat prostate. They found that after castration the cells of all the lobes were reduced in size. After administration of testes extracts the cells again reached peak activity. In *Bathyergus* the cells of the prostate in the inactive period resemble those of a castrated animal. Androgen hormones are in all likelihood responsible for the high degree of activity of the cells of the prostate in the active period and vice versa in the inactive period. The fact that secretion of the prostate cells does not completely cease in the inactive period could be explained on the basis that the Leydig cells do not degenerate entirely and are slightly secretory during the inactive period. There appear, however, to be factors, other than androgens, involved in the decline of the cells of the inactive prostate and the invasion of the lumina of the alveoli by other cells. The nature of these factors is not known.

The effect of season on the histology of the seminal vesicles

The histology of the seminal vesicles of *Bathyergus* is typical of that of rodents such as the rat, guinea-pig and hamster (Price and Williams-Ashman 1961). There are clear-cut differences in the histology of this gland during the sexually active and inactive periods.

Moore, Hughes and Gallagher (1930) found that the cells of the rat decreased in size after castration and increased in size after administration of testosterone. In the latter situation the cells became highly secretory. In *Bathyergus* the secretory activity of these cells was at a maximum in the active period. Although the secretory activity of the cells of the inactive animal ceases or nearly ceases there seem to be no significant increase in cell height of seminal vesicles in the active period. In fact, the large amount of seminal fluid formed, caused a stretching and flattening in some areas of the epithelium. The result was that some cells appeared cuboidal and not columnar as in the inactive animal. The epithelium of the inactive seminal vesicle seems to decline but not to the same extent as was noticed in the prostate. The factors that influence the histological changes through the year are probably the same as that of the prostate, namely the level of circulating androgen.

The penis

In mammals the structure of the glans penis shows much variation. In the ram the glans

penis has a 3–4 cm twisted filiform appendage, the processus urethrae, containing the terminal part of the urethra. This filiform body rotates rapidly during ejaculation and sprays the semen around the external uterine opening (Hafez 1962). In the shrew *Blarina* the glans forms a folded tip. When erect, the glans in this species expands laterally at its base and becomes much curved in a vertical plane. Its tip is long, slender and very flexible (Eckstein and Zuckerman 1956). This flexible tip in *Blarina* may serve the same purpose as in the ram by assisting the dispersion of semen in the vagina. In *Bathyergus* no such process exists but there is a structural adaptation which may assist the dispersion of the semen towards the two horns of the uteri. The fact that a T-slit is found at the tip of the penis and that this slit allows the urethral groove to circumvent the distal end of the thickened os penis, may influence the semen to leave the penis through the lateral grooves of the slit, with the effect that the semen will be spread towards the two horns of the uteri duplex.

Many rodents and insectivores have a glans with horny spikes and papillae. Pearson (1944) observed these spikes on the glans of *Blarina*. Dathe (1937) also noted horny spikes and papillae on the glans of several rodents belonging to the family Caviidae. Dathe thinks that these spikes may serve a dual purpose: they may serve both the purpose of *Wollustorgane*, stimulating the cervix during copulation and as "anchoring structures" in the vagina. In *Bathyergus* the spikes face posteriorly and it could be presumed that during full erection they might become anchored in the folded vaginal epithelium. Similar spikes are found in many other mammals such as the cat (Buschke 1909), *Ornithorhynchus*, *Talpa* and even in some primates, for example, *Macacus rhesus* (Dathe 1937).

Environmental factors controlling sexual activity in Bathyergus

Rowan (1926, 1929) in the Canadian bunting, *Junco hyemalis*, was the first to prove that an increase in the photoperiod was the trigger mechanism for onset of sexual activity. Soon after many workers began to realise how important the effect of light was on reproduction. For example, it was found that an increasing photoperiod stimulated sexual activity in several species such as the ferret (Bissonette 1932), the mink (Aulerich, Holcomb, Ringer and Schaible 1963) and the raccoon (Bissonette and Csech 1937, 1939). It was also found that the mink became sexually active through the addition of no more than eight minutes of extra light to the normal photoperiod during winter. Conversely a steady decrease in daylength could cause onset of sexual activity in autumn breeders such as the goat (Bissonette 1941).

Before considering the possible trigger mechanism in *Bathyergus*, its behaviour and habitat should first be considered. *Bathyergus* most probably leaves its tunnel system during the night to feed above ground. In support of this, green plant material was always found in the stomach and intestines. Moreover, many *Bathyergus* are run over by cars during the night and animals are very seldom seen above ground during the day. However, moles are able to pull green plant material growing above the ground down into their tunnel systems.

In the present investigation *Bathyergus* were obtained from only one area where food was abundant throughout the year. The relative humidity of the tunnel systems was always high as *Bathyergus* does not appear to burrow in dry ground. It was also observed that the drier the ground becomes, the deeper the burrow. Limited temperature data indicated that burrow temperatures did not vary greatly throughout the year. Jarvis (1969) also observed

that temperature fluctuations in mole-rat burrows were not great. Moreover, Gates (1962) demonstrated that diurnal fluctuations in air temperature had no effect on the soil temperature at a depth below 30 cm. The burrows and nests of *Bathyergus* lay at a depth greater than 30 cm. This was also observed by Jarvis (1969). It would therefore appear that annual temperature cycles are not important in stimulating sexual activity in *Bathyergus*.

Although the eyes are reduced in *Bathyergus* it nevertheless seems that this species is at least able to differentiate between dark and light. Dissection showed that the optic nerves are present although reduced. It should be remembered that the sudden increase in weight of the reproductive organs coincided with the period just after the March equinox when daylight length was steadily decreasing. The sudden drop in sexual activity also coincided with the September equinox when daylight length was steadily increasing.

Baker and Ranson (1932) state that light has a direct controlling effect upon the breeding season of all wild mammals, but that the mole and nocturnal mammals are unlikely to be affected. This is open to question as moles frequently leave their burrows during the night and while burrowing during the day they occasionally break through to the surface. It would seem therefore that they would at least be aware of cyclical changes in the length of the dark period if not of the photo-period. Moreover, Crawford (1966) has suggested that various types of signals may be perceived by the mole in its underground habitat: not only seismic earth movement, vibration etc. but also light, infra-red radiation and other electromagnetic disturbances.

It would thus seem that nutrition, humidity and temperature can be excluded as trigger mechanisms for the onset of sexual activity. The most likely trigger mechanism for sexual activity in *Bathyergus* is the progressive decrease in the photo-period or the progressive increase in the dark period, the critical stage being reached just after the March equinox.

SUMMARY AND CONCLUSIONS

Male *Bathyergus* possesses a reproductive system that basically resembles that of many rodents such as the rat, guinea-pig and hamster.

The occurrence of a limited period of sexual activity was demonstrated which extended from the end of March to the end of October.

In the active period the reproductive organs particularly the testes, prostate and seminal vesicles increased markedly in size and weight. The heaviest testes, prostate and seminal vesicle weights were recorded during July, August and September.

Maximum cell activity occurred during these months and it was found that maximum weights of reproductive organs were correlated with maximum activity and vice versa.

Although cell activity of the seminiferous tubules ceased in the inactive animal, the Leydig cells remained slightly secretory. In the active period Leydig cells were highly secretory and spermatogenesis was evident.

The efferent ducts consist of two distinct histological zones and the initial zone is highly secretory during activity. A low sperm density was observed in the efferent ducts during sexual activity.

The epididymis could be divided into six zones with ten subzones. Zone 3 of the epididymis

is highly secretory. In active animals the sperm concentration increases steadily from the efferent ducts to reach a maximum in zone 6. Very few if any sperm occur in the inactive epididymis, while spermatocytes and testes fluid were frequently observed during this period.

The ductus deferens also reveals cyclical histological changes. In the active animal the ampullae are secretory. The ductus deferens as well as zones 5 and 6 of the epididymis also serve as a storage organ for sperm during activity.

The seminal vesicles exhibited a marked increase in secretory capacity during the active period. Very little secretory activity was evident in the inactive animal. The fluid secreted was eosinophilic in character.

Although the prostate forms a compact organ it could be histologically divided into four pairs of lobes viz., the dorsal, ventral and lateral prostates plus the coagulating gland. Secretory activity was very high in the active animal but did not cease in the inactive animal. The epithelium of the alveoli of the prostate declined partially in the inactive animal. It was thought that the large number of corpora amylacea in the different lobes may contribute towards the formation of the vaginal plug.

It was concluded that the T-split on the dorsal glans penis may facilitate dispersion of spermatozoa during copulation.

Finally, in assessing the possible environment factors which may control sexual periodicity in male *Bathyergus*, it was concluded that either the progressive decrease in the photoperiod or the progressive increase in the dark period during March equinox was the most likely stimulus.

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REFERENCES

ALLANSON, M. 1932. The reproductive processes of certain mammals III. The reproductive cycle of the male ferret. *Proc. roy. Soc. Lond.* (B), 110: 295–311.

ALLANSON, M. 1934. The reproductive processes of certain mammals VII. Seasonal variation in the reproductive organs of the male hedgehog. *Phil. Trans.* (B), 223: 277–303.

ARNBÄCK-CHRISTIE-LINDE, A. 1907. Der Bau der Soriciden und ihre Beziehung zu Saugetieren, *Morph. Jb.* 36: 463.

*AULERICH, R. J., HOLCOMB, L. C., RINGER, R. K. and SCHAIBLE, P. J. 1963. Influence of photoperiod on reproduction in mink. *Q. Bull. Mich. St. Univ. agric. Exp. Stn.* 46: 132–138.

BAKER, J. R. and RANSON, R. M. 1932. Factors affecting the breeding of the field mouse (*Microtus agrestis*). Part. I. Light. *Proc. roy. Soc.* (B), 110: 313–322.

*BENOIT, J. 1926. Recherches anatomiques, cytologiques et histophysiologiques sur les voies excrétices du testicule chez les mammifères. *Arch. Anat., Strasbourg.* 5: 174–412.

BISHOP, D. W. 1961. Biology of spermatozoa, p. 707–796. In W. C. Young, *Sex and internal secretions*, Third Edition, Vol. 2. The Williams and Wilkins Co., Baltimore.

BISSONETTE, T. H. 1932. Modification of Mammalian sexual cycles; reactions of ferrets (*Putorius vulgaris*) of both sexes to electric light added after dark in November and December. *Proc. roy. Soc.* (B), 110: 322–336.

BISSONETTE, T. H. and CSECH, A. G. 1937. Modifications of mammalian sexual cycles VII: Fertile matings of raccoons in December instead of February induced by increasing daily periods of light. *Proc. roy. Soc.* (B), 122: 246–254.

BISSONETTE, T. H. 1941. Physiol. Zool. 14: 379. In W. S. Bullough, *Vertebrate Reproductive Cycles.*

BRAMBELL, F. W. R. 1935. Reproduction in the common shrew (*Sorex araneus Linnaeus*). The oestrus cycle of the female. *Phil. Trans. B*, 255: 1.

*BUSCHKE, A. 1909. Über die Bedeutung der "Papillen" der Corona glandis. *Med. Klinik*, 5, Bd. 2, S. 1621–1623.

CHIFELLE, T. L. and PUTT, F. A. 1951. Propylene and ethylene glycol as solvents for Sudan IV and Sudan Black B. *Stain Tech.* 26: 51–56.

CLELAND, K. W. and REID, B. L. 1957. The structure and function of the epididymis. i. The histology of the rat epididymis. *Austr. J. Zool.* 5: 223–246.

*COURRIER, R. 1927. Étude sur le déterminisme des caractères sexuels secondaires chez quelques mammifères a activité testiculaire périodique. *Arch. Biol., Paris*, 37: 173.

CRAWFORD, B. H. 1966. Perception underground. Review of physical aspects and measurements. *J. Zool. Lond.* (1966) 149: 102–106.

DATHE H. 1937. Über den Bau des männlichen Kopulationsorganes beim Meerschweinchen und anderen hystricomorphen Nagetieren. *Morph. Jb.* 80: 1–65.

EADIE W. R. 1939. A contribution to the biology of *Parascalops breweri. J. Mammal.* 20: 150.

EADIE, W. R. 1948. The male accessory reproductive glands of *Condylura* with notes on a unique prostatic secretion. *Anat. Rec.* 101: 59–79.

ECKSTEIN, P. and ZUCKERMAN, S. 1956. "The oestrus cycle in the Mammalia", p. 226–396 and "Morphology of the reproductive tract", p. 43–147. In A. S. Parkes, Marshall's *Physiology of Reproduction*, Third Edition. Vol. 1, Part 1. Longmans, Green and Co., London–New York–Toronto.

EDWARDS, J. 1939. The effect of unilateral castration on spermatogenesis. *Proc. roy. Soc.* (B) 128: 407–421.

GATES, D. M. 1962. *Energy exchange in the biosphere.* Harper and Row. New York.

HAFEZ, H. S. E. 1962. *Reproduction in farm animals*, p. 64. Bailliere, Tindall and Cox, London.

HALL, K. 1936. The structure and development of the urethral sinus in the male white mouse with notes on its occurrence in other rodents. *J. Anat. Lond.* 70: 413.

JARVIS, J. U. M. 1969. The breeding season and litter size of African mole-rats. *J. Reprod. Fert.* (Suppl. 6): 237–248. Scientific Publications, Oxford and Edinburgh.

*JOHNSON, G. E., FOSTER, M. A. and COCO, R. M. 1933. The sexual cycle of the thirteen lined ground squirrel in the laboratory. *Trans. Kans. Acad. Sci.* 36: 250.

KOLLER, P. C. 1936. Chromosome behaviour in the male ferret and mole during anoestrus. *Proc. roy. Soc. Lond.* (B), 121: 192.

KRAUSE, R. 1921. *Mikroskopische Anatomie der Wirbeltiere*, p. 148. Walter de Cruyter and Co., Berlin and Leipzig.

MALLORY, F. B. 1944. *Pathological Technique.* W. B. Saunders Co., Philadelphia.

MARSHALL, F. H. A. 1911. The male generative cycle of the male hedgehog; with experiments on the functional correlation between the essential and accessory sexual organs. *J Physiol.* 43: 247.

*MARTINS, T. and VALLE, DO J. R. 1938. Influence de la castration sur la motilité du canal déférent du rat. *C.R. Soc. Biol.*, Paris, 127: 464–466.

*MIETKIEWSKI, C. 1935. Reserches morphologiques cytologiques et histophysiologiques sur l'epididyme du cobaye. *C.R. Soc. Biol., Paris*, 120: 474–8.

MOORE, C. R., PRICE, D. and GALLACHER, T. F. 1930. Rat prostate cytology as a testis hormone indicator and the prevention of castration changes by testis extract injections. *Am. J. Anat.* 45: 71–107.

MOSMAN, H. W., HOFMAN, R. A. and KIRKPATRICK, C. M. 1955. The accessory genital glands of male grey and fox squirrels correlated with age and reproductive cycles. *Am. J. Anat.* 97: 257.

*MURATORI, G. 1953. Sulla motilità spontanea del canales dell'epididimo del ratto. *Ann. Univ. Ferrara, Anat. umana.* 1: 29–36.

MYERS-WARD, C. F. 1897. Preliminary note on the structure and function of the epididymis and ductus deferens in the higher mammalia. *J. Anat. Lond.* 32: 135–140.

PEARSON, O. P. 1944. Reproduction in the shrew (*Blarina brevicauda* Say). *Am. J. Anat.* 75: 39.

PRICE, D., MANN, T. and LUTWAK-MANN, C. 1955. The stimulating effect of female hormones on the metabolic activity and histological structure of male rat accessory reproductive glands. *Anat. Rec.* 122: 363–380.

PRICE, D. and WILLIAMS-ASHMAN, H. G. 1961. The accessory reproductive glands of mammals, p. 371. In W. C. Young, *Sex and internal secretions*, Third Edition. The Williams and Wilkens Co., Baltimore.

RASMUSSEN, A. T. 1917. Seasonal changes in the interstitial cells of the testis of the woodchuck (*Marmota monax*). *Am. J. Anat.* 22: 475.

RISLEY, P. L. 1958. The contractile behaviour in vivo of the ductus epididymides and vasa efferentia of the rat. *Anat. Rec.* 130: 471.

ROBERTS, A. 1951. *The mammals of South Africa.* Central News Agency, South Africa.

*ROWAN, W. 1926. On photoperiodism, reproductive periodicity, and the annual migrations of birds and certain fishes. *Proc. Boston Soc. nat. Hist.* 36: 147–189.

*ROWAN, W. 1929. Experiments in bird migration. 1. Manipulation of the reproductive cycle: seasonal histological changes in the gonads. *Proc. Boston nat. Hist.* 39: 151–208.

SIMEONE, F. A. 1933. A neuromuscular mechanism in the ductus epididymis and its impairment by sympathetic denervation. *Am. J. Physiol.* 103: 582–591.

*STRICHT, VAN DER O. 1893. La signification des cellules épithéliales de l'épididyme de *Lacerta vivipara. C.R. Soc. Biol., Paris.* 45: 799–801.

TESH, J. M. and GLOVER, T. D. 1969. Ageing of rabbit spermatozoa in the male tract and its effect on fertility. *J. Reprod. Fert.* 20: 287–297.

WADE, W. H. 1952. Notes on the carbowax method of making tissue sections. *Stain Tech.* 27: 71–79.

WALKER, E. P. 1964. *Mammals of the world*, Vol. 2. The John Hopkins Press, Baltimore.

WEBER, M. 1927. *Die Säugetiere*. Jena: Gustav Fischer Verlag.

* Original not seen.