STUDIES ON THE EMBRYOLOGY OF MICROCHIROPTERA

Part II. Reproduction in the Male Vespertilionid Bat *Scotophilus wroughtoni* (Thomas)

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INTRODUCTION

A STUDY of the reproductive phenomena in bats offers a number of interesting features. In this paper an attempt is made to record the cyclical changes in the male reproductive organs in the breeding and the non-breeding seasons. As mentioned in the first part of this series (1947)[3] the study is based entirely on the examination of the wild specimens for the obvious reason that any experimental study is impossible in the caged bats. The specimens were all collected round about Bangalore, which is a tropical zone of more or less unvarying climatic conditions throughout the year. A general account of the breeding seasons of this species of bats has formed the subject-matter of the first part of this paper. It was based upon a gross study of the females only. The results of the study of the male reproductive organs are incorporated in this paper; and these confirm the conclusions already arrived at regarding the breeding seasons.

HISTORICAL

Though a large volume of literature is available on the general breeding habits of the insectivorous bats, and also on the female sexual cycle of many species, it is a matter of considerable surprise that very little work has been done on the sex-cycle of the male bats. The litle information we have on the subject of the reproductive processes of the male bats is the result of a study of the female genitalia for the presence of spermatozoa in the vaginal tract or the oviduct and the casual observations on the exaggerated secondary sexual characters in the male during the breeding season.

A study of the literature on bat reproduction reveals that in a majority of the species inhabiting the temperate and cold climates, the males experience a height of sexual activity during late autumn when they copulate, followed by hibernation during winter. The spermatozoa also undergo hibernation in the genital tract of the female and fertilize the ovum in the next spring. A large volume of circumstantial evidence has also accumulated to substantiate this view. Courrier (1927)[2] has shown in *Pipistrellus pipistrellus* that the examination of the male genitalia revealed the fact that after copulation in late autumn the testes degenerated and throughout winter contained no spermatozoa, but only spermatogonia and sertoli cells. Nakano (1928)[8] working on *Vespertilio abramus* has come to similar conclusion that after copulation in October the testes degenerate. A very positive proof of autumn copulation was given by Harrison Matthews (1937)[5] working on the British Horse-shoe Bats. Because of the occurrence of a hard vaginal plug in the female throughout the winter after copulation he concludes "The ovum must have therefore been fertilized by one of the spermatozoa stored in the upper part of the genital tract and the spermatozoa must have been deposited in the previous autumn."

On the other hand, there are a few species of insectivorous bats in which copulation occurs in spring followed immediately by ovulation and fertilization resulting in pregnancy.

Baker and Bird (1936)[1] recorded in *Miniopterus australis* which is a tropical species that there is an annual sexual rhythm in the males which show sexual activity in July, August, September, and October (*i.e.*, the southern spring), and the testes would be nonfunctional during the rest of the year. They recorded as follows: "Looking at the material as a whole one sees clearly that copulation takes place about the end of August, and that the development of the embryo starts at once. Copulation occurs at a time of the year when the days begin to get longer and the temperature is rising." Recently, Harrison Matthews (1942)[6] recorded his observations on some of the South African bats in which copulation occurs in spring and is immediately followed by fertilization and pregnancy.

There is still a third kind of observation. Rolland, E. Miller (1939)[7] working on *Myotis lucifugus lucifugus* and *M. greisesens* observed that "Copulation is known to occur in the fall. The conditions of the accessory glands and the presence of sperms make recurrent copulations possible until spring." On examining the accessory reproductive glands he recognised that the glands were functional and the epididymis full of sperms throughout winter and spring. He was convinced that there was a period of spring copulation too. He is, however, not certain whether the ovum is fertilized by the sperm of spring copulation or fall copulation. Mary, J. Guthrie (1933)[4] recorded that spring copulation is a normal occurrence in some American cave bats. She believed that the spermatozoa stored in autumn copulation are destroyed by the numerous phagocytes of the genital tract and copulation occurs again in early spring.

It is evident from the foregoing summary that most of the work relates to bats of the temperate regions in which two very different types of observations are recorded. There is practically no work on tropical bats except that of Baker and Bird (1936)[1] and recently of Harrison Matthews (1942).[6] Both these authors observe that copulation takes place in spring and is immediately followed by fertilization and pregnancy.

Material and Methods

Bats were collected from the hollows of the trees in forests round about Bangalore. They were killed by chloroform and immediately dissected. Unfortunately their body weights were not taken. The genital organs, kidneys and suprarenals were fixed. Bouin's picro-formal-acetic was the usual fixative used. But other fixatives like Sanfelice's formula and corrossive acetic were also used. The weight of the testis and the epididymis was taken together after preservation in 70% alcohol. They were sectioned and stained in hæmetoxylin. The measurements of the diameters of the testis tubules and the tubules of the epididymis were taken by the use of a micrometer scale.

Table I gives the data of collections of the males and females. I began collections in May 1945 and it is still in progress.

Table I

Monthly record of collections: Scotophilus wroughtoni (Thomas)

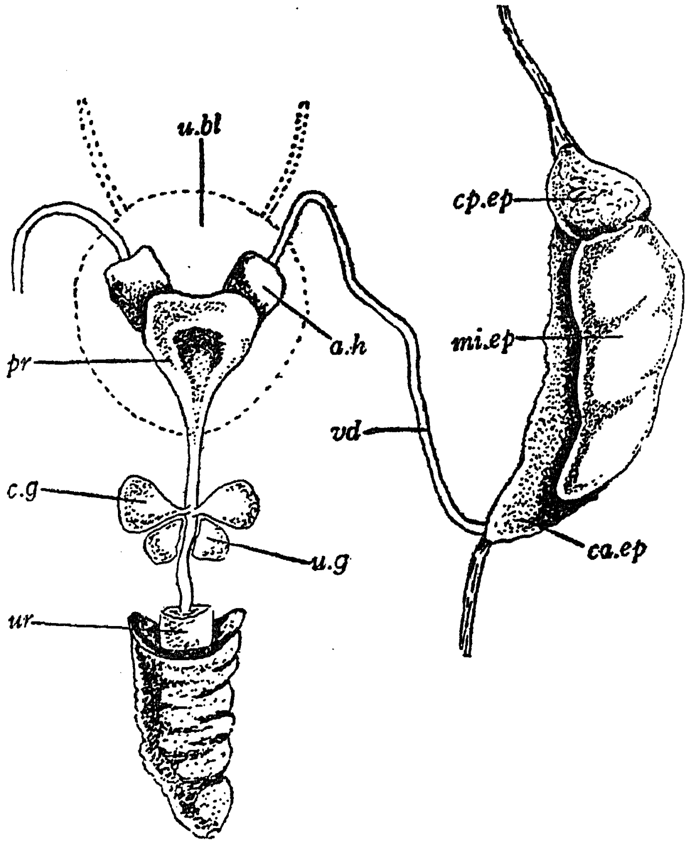
Month	Date	Males	Females
May ..	17—5—1945	2	28
,, ..	7—5—1946	2	2
June ..	7—6—1946	2	2
July ..	..	No collections	
August ..	..	do	
September ..	18—9—1946	1	1
October ..	20-10-1945	1	1
November ..	8-11—1945	2	2
December ..	7-12—1946	2	17
January ..	8—1—1947	3	5
February ..	10—2—1946	5	3
March ..	22—3—1946	2	4
April ..	1—4—1946	1	6
,, ..	22—4—1946	4	26
,, ..	28—4—1947	1	9
,, ..	29—4—1946	1	20
Total ..		29	126

The numbers do not give any idea of the sex-ratio or the population of these animals, primarily because of the small number of specimens collected and secondly because of the probability that the males and the females must have lived separately after the active breeding period. It is worth noticing, however, that during January and February the proportion of males to females is markedly higher than during the other months. This may probably roughly indicate that during this period the males and the females live together.

Observations

(A) *The Male Reproductive Organs* (Text-Fig. 1)

The male reproductive system consists of a pair of testes whose position and size varies during the different seasons of the year. The testes are abdominal in position during the non-breeding periods and becomes inguinal



TEXT-FIG. 1. Reproductive system of *Scotophilus wroughtoni* (Thomas) × circa 6. *a.h.* ampulla of Henle; *ca. ep.*, cauda epididymis; *c. g.*, Cowper's gland; *cp. ep.*, caput epididymis; *mi. ep.*, mid-epididymis; *pr.*, prostate; *u. bl.*, urinary bladder; *u. g.*, urethral gland; *ur.*, urethra; *vd.*, vas deferens.

and sometimes even post-anal at the height of sexual activity, consequent not only upon their migration but also upon their enlargement. Each testis is slightly tapering towards the caudal end.

The epididymis is not very clearly demarked into a caput (*cp. ep.*), a mid (*mi. ep.*), and a cauda (*ca. ep.*) epididymis. The names are given to the portions of the epididymis in the figure by reason of the position. But on the onset of the breeding season the cauda epididymis (*ca. ep.*) is much elongated. The vas deferens (*vd.*) arises from the cauda epididymis (*ca. ep.*) and passes upwards on the median side of the testes between it and the bladder (*u. bl.*). Each vas deferens at its distal end is swollen up into a bean-shaped structure—the ampulla of Henle (*a.h.*). A true seminal vesicle distinct from the ampulla of Henle is absent. Thus the structures bear resemblance to some of the South African bats described by Harrison Matthews (1942).[6] The ampullæ of Henle are embedded in the wall of the prostate glands (*pr.*) for nearly two-thirds of their length as in *Miniopterus minor* and *M. dasythrix* (Harrison Matthews, 1942).[6] The prostate is a fairly large structure lying below the bladder. The urethra (*ur.*) a little down below the prostate is joined by a pair of small pear-shaped glands—the Cowper's glands (*c. g.*). These lie just above the rectum. Posterior to the Cowper's glands are a pair of urethral glands (*u. g.*). The penis is directed caudally.

(B) *Seasonal Variations in Testis*

(i) *Macroscopic Examination*

Each testis was weighed along with its epididymis. Table II gives these weights for the several months of the year. It is a well-known fact that in

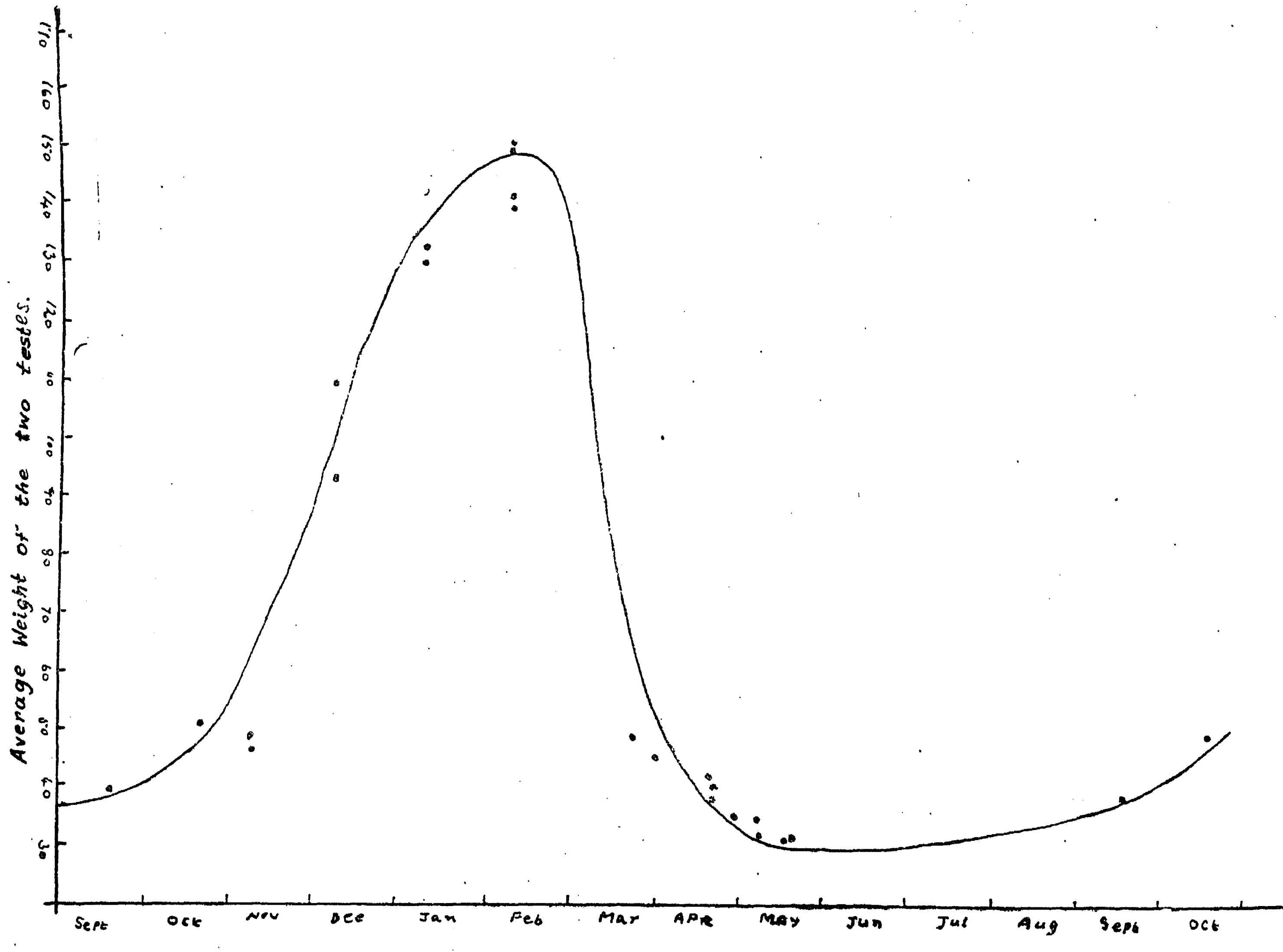
TABLE II

Scotophilus wroughtoni (Thomas)—*Macroscopic and Microscopic Measurements of the Testes and the Epididymides*

Month	Date	Index No.	Weight of the testes and epididymides in milligrammes				Diameters of the seminiferous tubules (in microns)			Diameters of the epididymal tubules (in microns)		
			Right	Left	Total	Average	Smallest	Largest	Average of 10	Smallest	Largest	Average of 10
January ..	8—1—47	123	145	142	287	143·5	156	170	160	93	114	101
do	do	128	130	136	266	133·0	..	..	..	..	..	..
do	do	129	132	128	260	130·0	140	170	151	107	114	108
February ..	10—2—46	32(i)	143	140	283	141·5	..	..	..	..	..	..
do	do	32(v)	..	..	..	..	..	..	..	..	..	..
do	do	32(vi)	150	152	302	151·0	171	189	178	107	128	120
do	do	32(vii)	135	144	279	139·5	167	186	174	110	128	118
do	do	32(viii)	148	153	301	150·5	..	..	..	..	..	..
March ..	22—3—46	33(*c*)	48	51	99	49·5	..	..	..	..	..	..
do	do	33(*d*)	52	53	105	52·5	78	111	101	70	104	78
April ..	1—4—46	45	46	46	92	46·0	..	..	..	..	..	..
do	22—4—46	57	42	40	82	41·0	68	93	87	54	68	62
do	do	63	40	42	82	41·0	..	..	..	..	..	..
do	do	64	38	47	85	42·5	..	..	..	..	..	..
do	do	66	40	36	76	38·0	..	..	..	..	..	..
do	28—4—47	138	36	38	74	37·0	..	..	..	..	..	..
do	29—4—46	88	38	33	71	35·5	..	..	..	..	..	..
May ..	7—5—46	100	32	33	65	32·5	57	86	69	29	50	38
do	do	101	36	..	..	36·0	..	..	..	..	..	..
do	17—5—45	9	34	30	64	32·0	..	..	..	..	..	..
do	do	27	33	29	62	31·0	53	78	64	29	48	38
June ..	7—6—46	108(*a*)	..	..	..	..	..	..	..	..	..	..
do	do	111(*f*)	..	..	..	..	61	86	68	24	41	35
July	No specimens were available and all the						..	..	..	..	..	..
August	expeditions for collections were fruitless						..	..	..	..	..	..
September	18—9—46	113(*a*)	38	41	79	39·5	71	93	80	43	60	56
October	20-10—45	30(*a*)	49	51	100	50·0	73	106	96	50	73	61
November	8-11—45	31(*c*)	47	50	97	48·5	..	..	..	..	..	..
do	do	31(*d*)	46	46	92	46·0	114	143	120	64	93	81
December	7-12—46	106(*a*)	90	96	186	93·0	134	161	150	93	114	100
do	do	118(*b*)	107	112	219	109·5	121	157	144	71	100	92

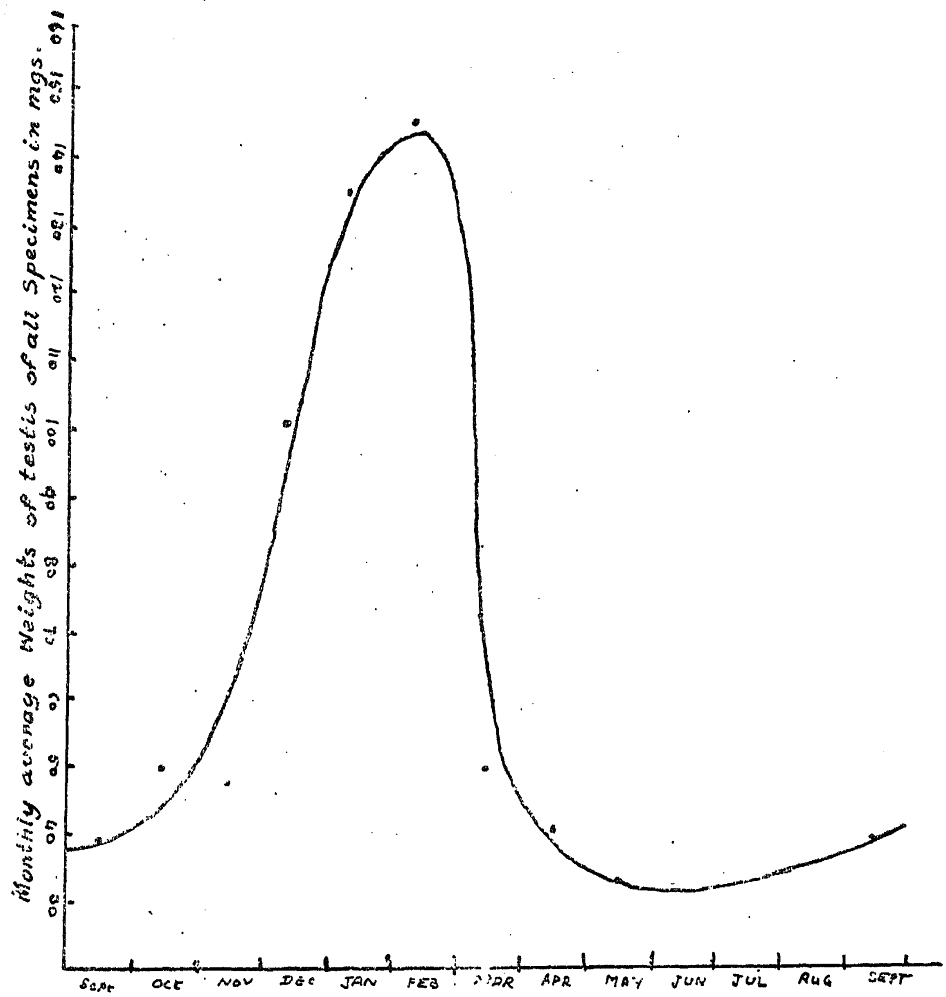
the case of the insectivorous bats the growth of the young is very rapid and furthermore, unlike the bats of the temperate and cold climates all the males were fecund during the breeding seasons.

Text-Fig. 2 is a graph of the average weights of the testis and epididymides of the two sides plotted against the months. Text Fig. 3 gives the graph of the weights of the testes average of all specimens of the month plotted against the months.



TEXT-FIG. 2. Graph to indicate the increase in the weight of the testis during the breeding season. The average weight in milligrammes of the two testes of each specimen is plotted against the different months of the year. There is an enormous increase in the weight of the testes during the months of January and February.

The graphs clearly indicate that the weight of the testis increases rapidly during the months of December, January and February, and suddenly decreases during the month of March, after copulation, and the following months till September. The weight begins to increase from October onwards which marks the onset of sexual activity. The February testis is nearly four times as heavy as the testis of September.

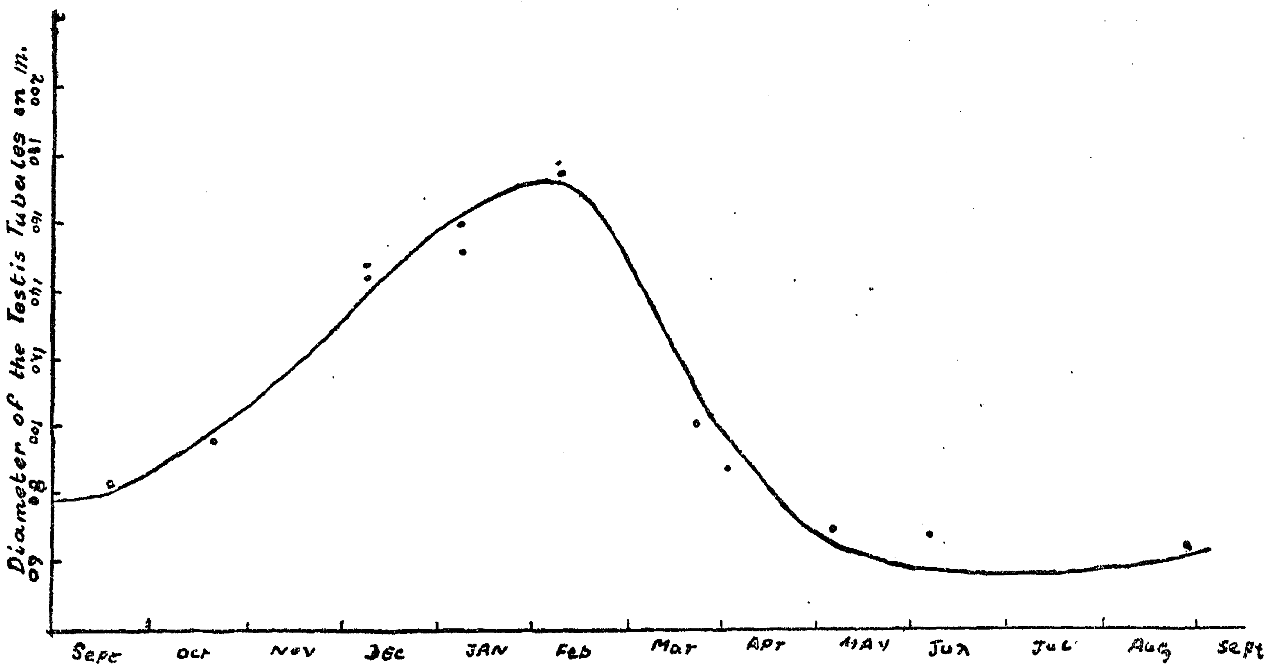


TEXT-FIG. 3. Graph of the average weight of the testes of all specimens of each collection plotted against the months.

(ii) *Microscopic Examination*

(*a*) *Diameter of the seminiferous tubules.*—The size of the seminiferous tubules varies during the several months of the year according to the activity of the testis. Table II gives the diameters of the seminiferous tubules during the different months of the year. For the sake of convenience the measurements of the seminiferous tubules of only one specimen from the collection of each month is taken. There is no marked difference among the testis tubules of the several specimens of any one collection. Diameters of ten tubules are taken, five situated near the periphery and five near the centre and a mean value is arrived at. Text-Fig. 4 is a graph representing the variation in the diameter of the seminiferous tubules from the specimens collected during the different months of the year.

The mean diameter which was only 80 μ in September suddenly increases on the onset of the activity of the germinal epithelium and increases to 150 μ during December and January, and reaches a maximum diameter of 180 μ



TEXT-FIG. 4. Graph to indicate the increase in the diameter of the tubules of the testes during the breeding season. There is a considerable increase in the diameter of the tubules during the months of January and February. The diameters are taken in microns.

in February (10–2–46). As already remarked the testes of the several specimens of any one collection show similar seminiferous tubules. It is an important fact to note as it gives us a possible age of the specimens at which the male bats become sexually mature.

During March there is a sudden decrease in the diameter of the seminiferous tubules, and the tubules of May specimens show a small diameter of $60\,\mu$ to $70\,\mu$, and very much the same as the September testis.

The diameter of the testis tubules seems steadily to increase with the weight of the testis. Text-Fig. 6 is a graph to show the relationship of the diameter of the testis tubules and the weight of the testis.

(*b*) *Histological changes in the testis.*—The microscopic examination of the sections of the testis indicates that in the specimens collected between the months of April to November, the tubules are inactive showing the germinal epithelium cells with resting nuclei. The tubules have no lumina, and the intercellular spaces are large. But in specimens collected in December the tubules have sprung up to activity showing plenty of mitotic figures. The spermatogenetic activity reaches its maximum vigour during January and February.

In May the testis tubules are small and have no lumina (Plate IV, Fig. 1). The tubules are composed of resting spermatogonia and sertoli cells. The nuclei of the spermatogonia are large, spherical and lightly stained and the individual cells are clearly marked out. The sertoli cells are not so distinctly marked out. Their nuclei are small, are more densely stained, and they appear to be floating in the sertoli syncytium.

The sections do not show the presence of many capillaries.

The condition of the testis remains more or less the same till September. The testis tubules are still without lumina, and the sertoli cells are small and darkly stained. There are two or three layers of spermatogonia at the periphery with large spherical nuclei. Some spermatogonia are undergoing division. The intertubular spaces are still large. The vascularisation of the testis is still low.

The testes of November collection show lumina in a few of the peripheral tubules, but the tubules in the centre are still without lumina. The intertubular area is reduced. The tubules contain mainly the darkly staining spermatocytes and the sertoli cells, which are few in number.

In December the testis tubules have greatly enlarged and most of the tubules have clear lumina. The germinal epithelium is active showing all stages of spermatogenesis (Plate V, Fig. 3). The peripheral part of the tubule contains a few spermatogonia with large faint nuclei abutted against the wall of the tubule and very few in number. But the majority of the cells are spermatocytes in various stages of spermatogenesis. Towards the central part of the tubule there are a large number of spermatid nuclei, which are characterised not only by their small size but also by their darkly staining nuclei. A few of the spermatids have undergone spermateleosis and consequently the lumen presents even ripe spermatozoa. The sertoli cells are reduced in number.

In January and February the testis is in full swing of activity with large numbers of meiotic nuclei (Plate V, Fig. 4 and Plate VI, Fig. 6). The lumen of the tubule is enlarged and is packed with spermatozoa. All the sper matids are undergoing the final change and large swarms of sperms are found radiating towards the centre.

As the tubules have greatly hypertrophied the intertubular space is reduced to a minimum.

The vascularisation of the testis is markedly high and a number of capillaries are seen in the sections, both in the mass of the testis and also in the walls.

(C) *Seasonal Variations in the Epididymis*

The epididymis also shows a seasonal variation corresponding to the variation in the testis. Table II gives the data regarding the variation in the diameter of the epididymal tubules during the different months of the year.

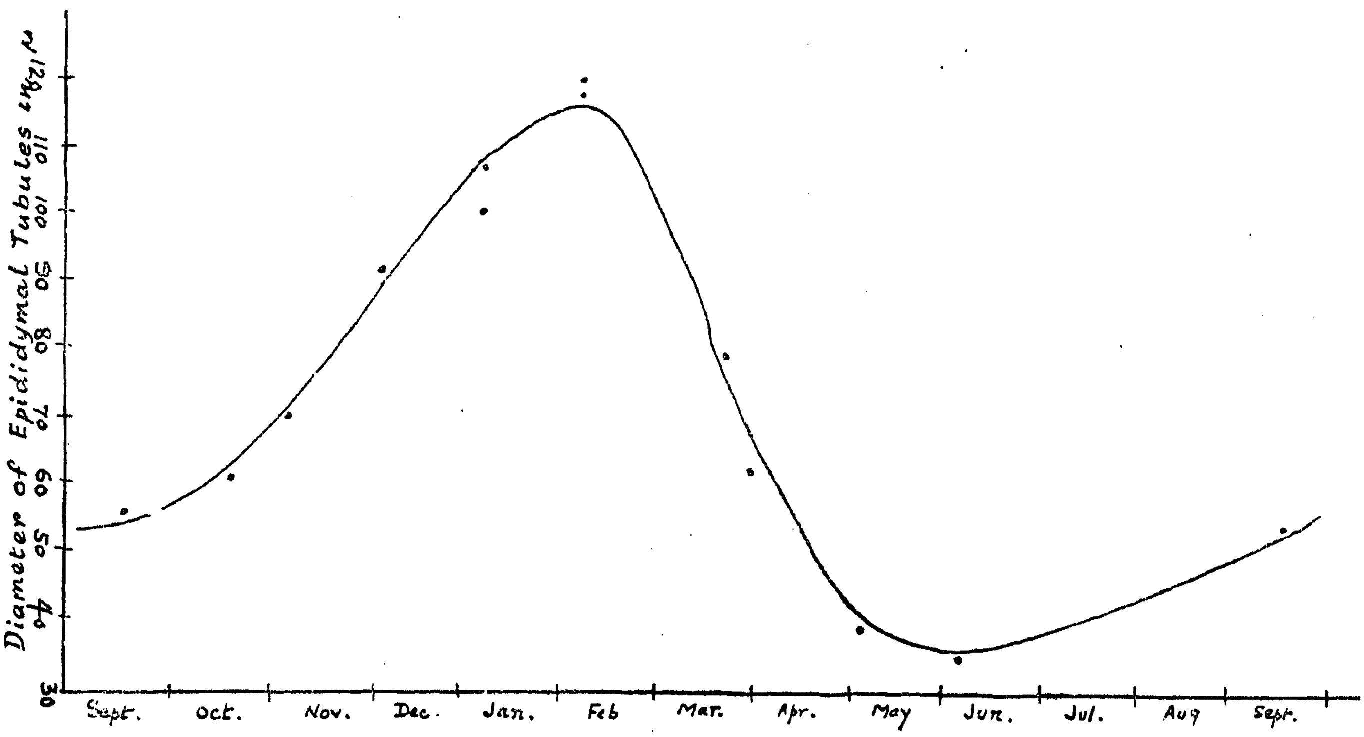
The tubules which were very narrow during the months between May and September, widen out from November onwards. The epithelium which appears to be two or three layered (due probably to shrinkage) flattens out into a single layered cubical epithelium.

From May to September there does not seem to be any change in the diameter of the tubules. It is narrow and varies from 29 μ to 43 μ in May to 43 μ to 60 μ in September. The intertubular area is large and is traversed by connective tissue and circular muscles (Plate IV, Fig. 2).

During November the diameter of the tubules is already large (57 to 64 μ). And in December the diameter increases to 100 μ to 114 μ and the inter-tubular spaces are much reduced. Furthermore the lumina contain spermatozoa.

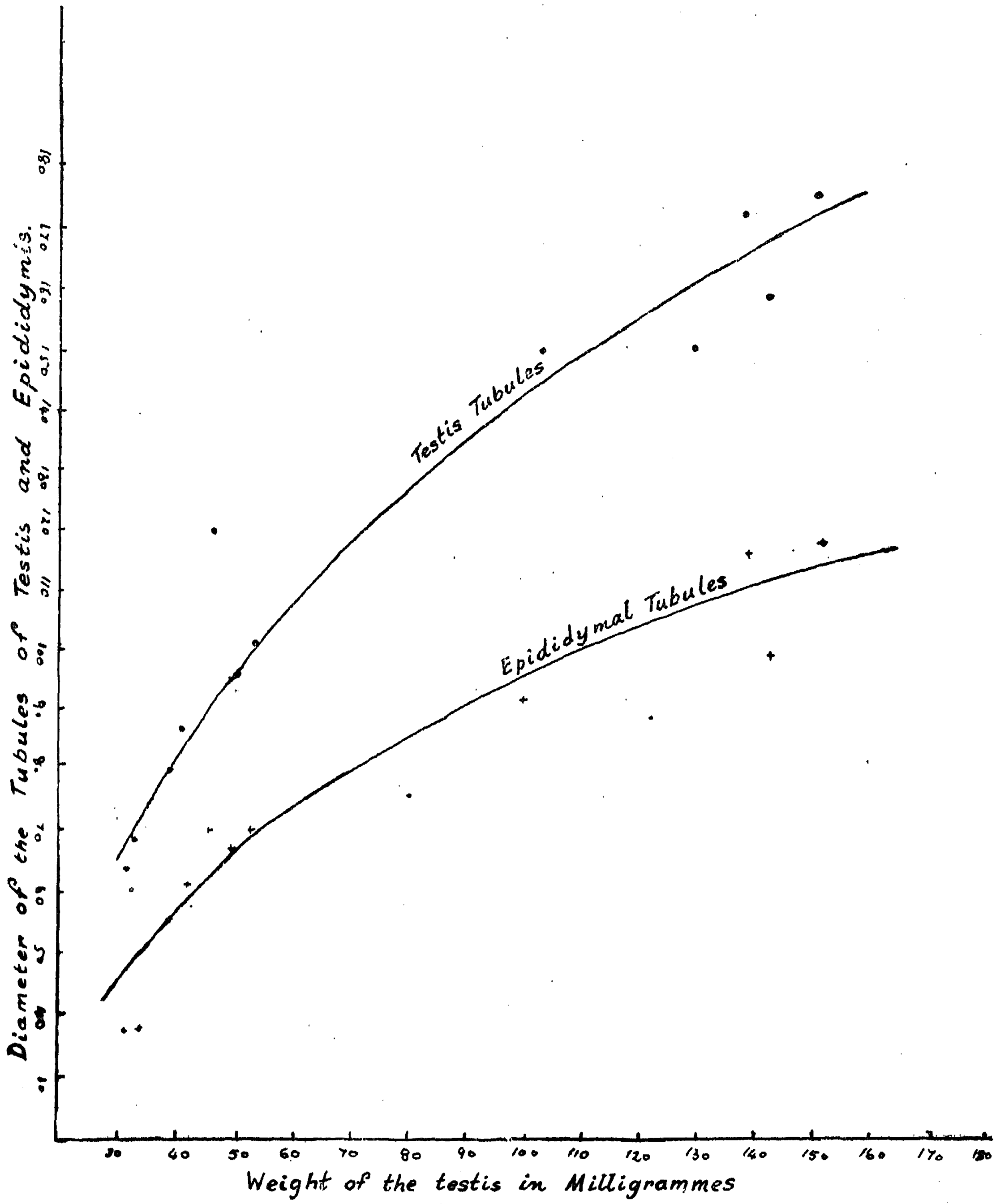
During January and February the diameter of the epididymal tubules reaches a maximum of 114 μ to 128 μ and all the lumina are packed with spermatozoa. The intertubular space is negligible (Plate VI, Fig. 5 and Plate VII, Fig 7).

Text-Fig. 5 is a graph to indicate the increase in the diameter of the epididymal tubules during December, January and February, and its comparatively narrow condition during the rest of the year.



TEXT-FIG. 5. Graph to indicate the increase in the dameter of the tubules of epididymis during the breeding season. The diameters are the largest between the months of January to March. The diameters are measured in microns.

Text-Fig. 6 shows the relationship that exists between the increase in the diameter of the tubules of the epididymis and the increase of the weight of the testis.



TEXT-FIG. 6. The diameters of the tubules of the testes and of epididymis plotted against the weights of the testes. The graph is a rising curve indicating that the diameters increase with the weight of the testes. The upper grapb indicates the relation between the weight of the testes and the diametcrs of the testes tubules and the lower graph shows the relation between the weight of the testes and the diameter of the tubules of the epididymis.

The figures clearly show that the increase in the diameter of the epididymal tubules runs parallel to the increase in the weight of the testis, which in its turn is directly related to the functional activity of the testis.

CONCLUSIONS

1. *The Breeding Season.*—The progressive increase in the weight of the testes during the months from December to January, and its weight being at its lowest during the other months of the year taken along with the fact

that the testis contains the spermatozoa only during these months, indicates that the height of sexual activity is reached in these animals during these three months and the animals are sexually quiescent during the rest of the year.

The examination of the males alone cannot give us any definite proof regarding the exact period of copulation. The occurrence of large swarms of spermatozoa in the epididymis during January and February indicates the probability of copulation during these months. But the examination of the female genitalia (Gopalakrishna, 1947)[3] has revealed that the females have not only not ovulated on the 10th February but their genetalia contained no spermatozoa. Thus copulation had not occurred till the 10th of February. The conclusion therefore seems to be that the males become sexually active and functional nearly 6 to 8 weeks before the females ovulate. Further during the months of July and August the females are all lactating, and there is no evidence to show that lactating females become pregnant. Hence the absence of collection during July and August does not seriously impede us from concluding, without any possibility of error, that the males like the females experience an annual breeding cycle, and this roughly corresponds to the same months as the females, the males becoming sexually active a little (6 to 8 weeks) earlier than the females.

After copulation which I have shown to occur between the 10th February and the 22nd March (1947 *a*), the males probably live separately from the females, for during the rest of the summer though many expeditions were made and large number of specimens collected, the number pf males captured was very low (Table I).

2. *Age of Maturity.*—A second important conclusion we may arrive at from the available data is that, as all the males collected during December, January and February were sexually active, animals born at about the end of June must have a rapid growth and must become sexually mature during the next January, *i.e.*, before they are one-year old. This seems to be a very unique phenomenon in the case of the insectivorous bats for no other author has recorded a similar feature in any of the microchiroptera. All authors are, however, agreed upon the fact that the bats have a very rapid period of growth even though they may remain sexually immature. But they believe that the bats come to sexual maturity during their second season.

Roland E. Miller (1939)[7] stated that "Young males of *Myotis lucifugus lucifugus and Myotis greisesens* do not enter into reproductive activity until their second spring". Harrison Matthews (1937)[5] working on the British Horse-shoe bats found that "The males do not reach their functional sexual activity until their second autumn".

And this view is confirmed by most of the authors working on the bats living in cold and temperate climates. This is probably because in these bats which inhabit the colder climates copulation takes place during autumn and the spermatozoa hibernate in the genital tract of the female during winter and fertilize the ova in the next spring. In the tropical bats on the other hand the problem of winter hibernation is bypassed and the males are nearly seven months old at the breeding season.

But Baker and Bird (1936)[1] working on the tropical bats in New-Hebrides stated that " None was definitely too small to be adult, but it is a well-known fact that bats become fully grown before they are sexually mature. The young could be detected by the size of their testes, which usually fell, fairly sharply into two groups as regards size. Those of the young naturally weighed about two milligrammes (both testes together), and sperms were never found in their epididymides ".

Van der Stricht (1910) was the only other author who recorded that in *Nyctalus noctula,* in Europe, the young females copulate in the same year as that in which they are born (from Baker and Bird).

The observations recorded in this paper give ample evidence to show that *Scotophilus wroughtoni* becomes sexually mature before it is one year of age. All the specimens collected in January and February were fecund, as indicated not only by the testis-weight but also by their microscopic structure. It would indeed be highly improbable that all collections during these months should not include a single immature specimen—the greater probability is that all males and females do become sexually active in their first year. Probably the variation in the period of copulation makes all the difference between the bats of the temperate and the tropical zones regarding the age at which they attain their sexual maturity.

As regards the determination of the age in these male bats it is impossible to decide from their sexual activity only. I have only to reiterate the statement of Harrison Matthews (1937) " The changes taking place in their genitalia do not throw any light on the duration of life of these animals, though presumably it is approximately the same in both sexes ".

A detailed study of the interstitial cells of the testis and the changes in the accessory reproductive organs in the male of this species will be dealt with in a separate paper.

SUMMARY

1. Twenty-nine male specimens of the bat *Scotophilus wroughtoni* were collected during the different months of the year. Collection were made during two successive years from May 1945 to April 1947.

2. The weight of the testis of these bats increases from the month of December and reaches a maximum weight during February. There is an increase nearly four times in the testis-weight from September to February.

3. The diameter of the seminiferous tubules also increases corresponding to the increase in the testis-weight and progressively vigorous spermatogenetic activity is seen in the germ cells. The diameter of the tubules of the epididymis also increases during these months.

The occurrence of sperms in the tubules of the testis and the epididymis indicates that the breeding season is confined to these months.

4. The males, like the females, probably attain their sexual maturity in their first season, *i.e.*, before they are one year old.

Acknowledgement

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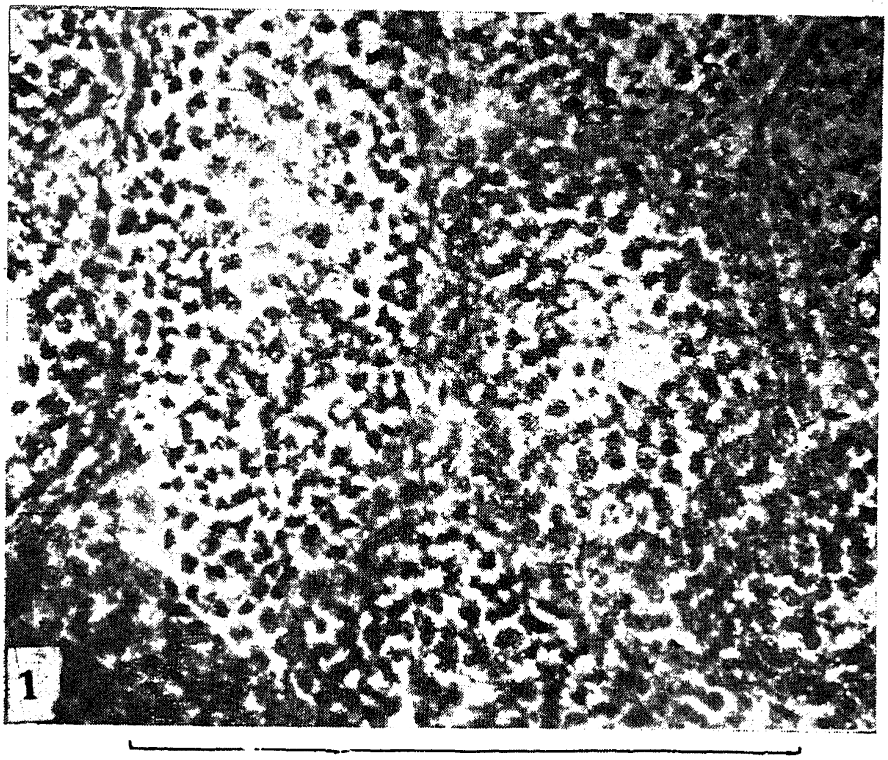
(*P. S.*—References marked in asterisk were not available in their original.)



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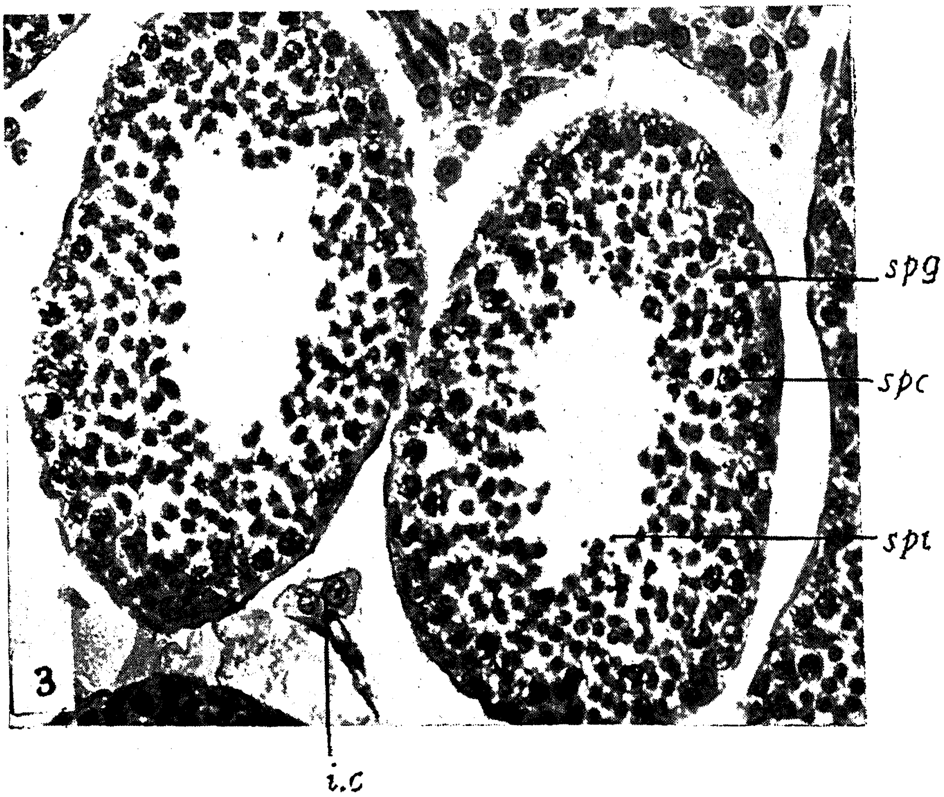
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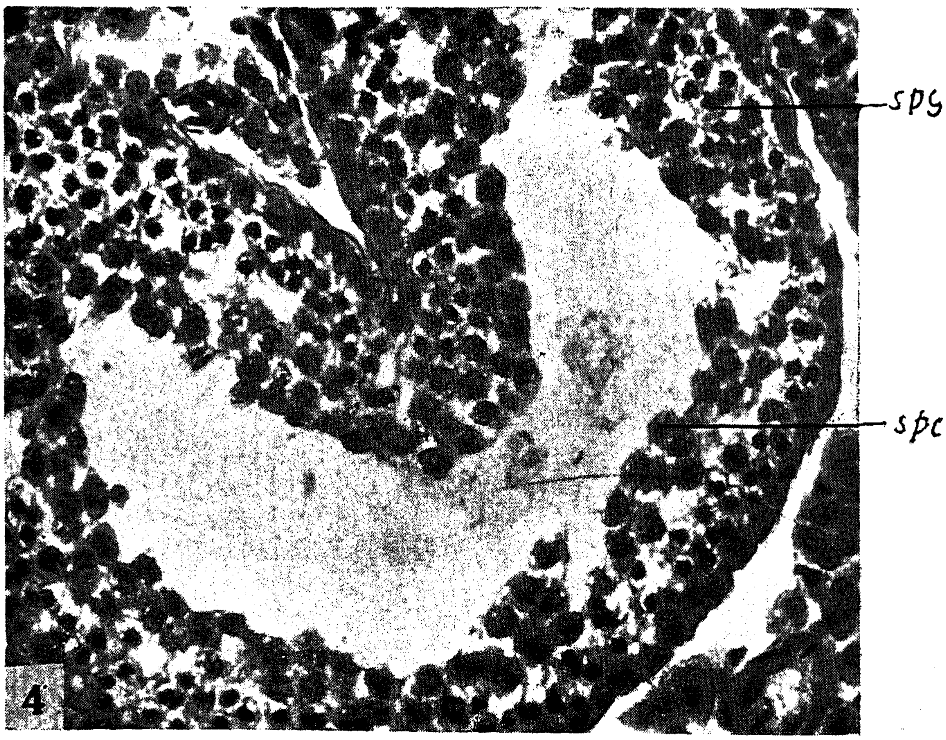
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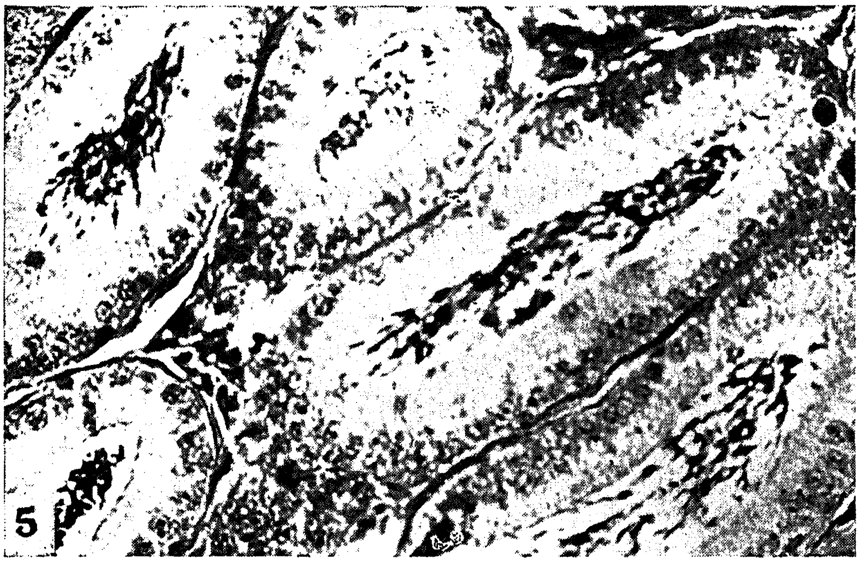
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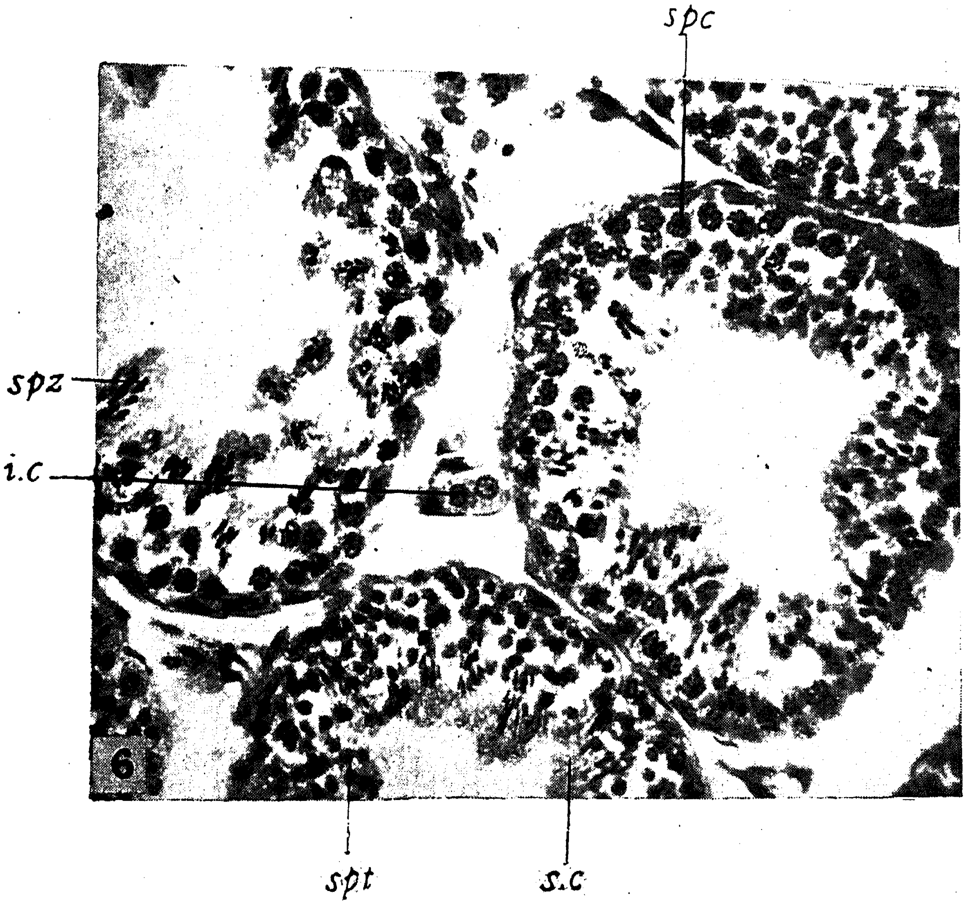
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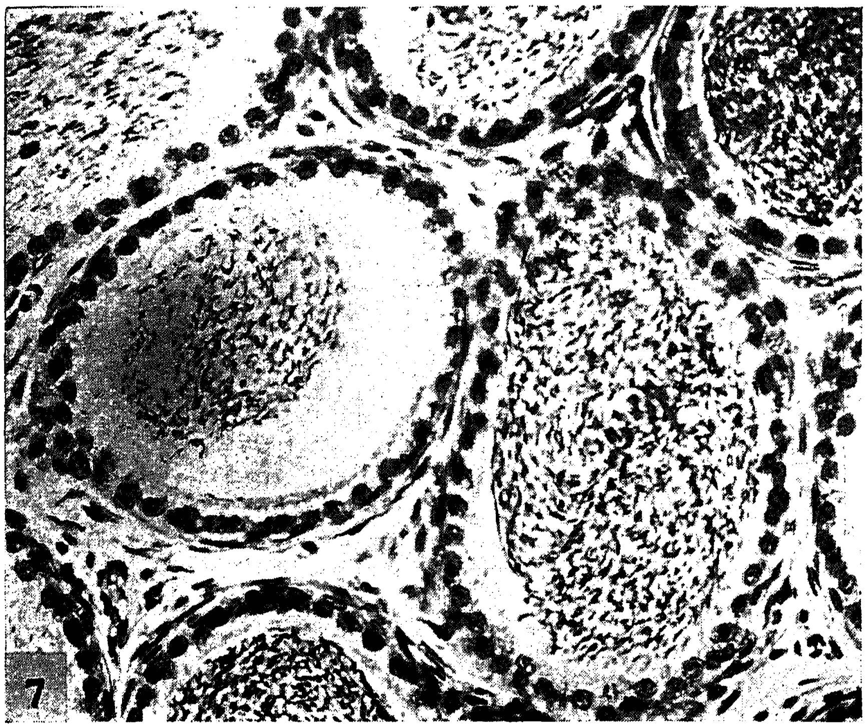
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Explanation of Plates

All figures are photomicrographs. *Magnification of all figures is the same as of Fig.* 1.

Figs. 1–7. Fig. 1. Two seminiferous tubules from a transverse section of the testis of a specimen collected in May (17–5–1945). The tubules have no lumen and consist of resting spermatogonial cells. Fig. 2. Epididymal tubules of the same specimen. The tubules are empty, *i.e.*, contain no spermatozoa. There is a large amount of intertubular tissue. Fig. 3. Two seminiferous tubules from a transverse section of the testis of a specimen collected in December (7–12–1946). The cells are in various stages of spermatogenesis. The tnbules have a distinct lumen. Fig. 4. One tubule from a transverse section of the testis of a specimen collected in January (8–1–47). Note the large lumen. Most of the germinal cells are in the final stage of spermatogenesis. The spermatocytes are abundant. Fig. 5. Epididymal tubules of the same specimen showing the sperms in the lumen of the tnbules. The epithelium of the tubules is still columnar. The lumen is not so large as it is in a later specimen. Fig. 6. Seminiferous tubules from a transverse section of the testis collected in February (10–2–1946). Spermatids and the spermatozoa are abundant. Fig. 7. Epididymal tubules of the same specimen. The lumen is large and full of spermatozoa. The epithelial cells of the tubules are cubical instead of columnar.