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Reproduction of the Bank Vole (Evotomys glareolus, Schreber). II. Seasonal Changes in the Reproductive Organs of the Male

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Reproduction of the Bank Vole (*Evotomys glareolus*, SCHREBER)*

II—Seasonal Changes in the Reproductive Organs of the Male

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[PLATES 12–15]

CONTENTS

	PAGE
I—INTRODUCTION	99
II—MATERIAL AND TECHNIQUE	100
III—STRUCTURE OF THE REPRODUCTIVE ORGANS	101
IV—GROWTH AND BREEDING SEASON	103
V—TESTES	106
VI—ACCESSORY SEXUAL ORGANS	111
a. Epididymides	112
b. Penis	114
c. Cowper's glands	114
d. Seminal vesicles and prostate	116
e. Prepucial glands	116
VII—SUMMARY	119
VIII—REFERENCES	120
IX—DESCRIPTION OF PLATES	

I—INTRODUCTION

The present paper deals with the male *Evotomys* and is concerned with two main problems ; the duration of the breeding and the non-breeding seasons, and the structure and growth of the reproductive organs. It is, in consequence, complementary to the preceding paper on the female. The only previous work we are aware of on the male of the British species is that of BAKER (1930) on a series of 359 males trapped near Oxford over a period of three consecutive years. BAKER,

* Since this paper went to press the British Museum have published a "List of British Vertebrates," in which the generic name "*Clethrionomys*" is used instead of "*Evotomys*."

taking the arbitrary criterion of 14 gm body-weight or over, found that 260 of these were adult. If spermatozoa were abundant in the tail of the epididymis, as determined from teased preparations, and also if the seminal vesicles were found to weigh 100 mg or over, the animal was said to be fecund. BAKER found that none of the 13 adult males obtained during the winter, October to February inclusive, of 1925-26 was fecund, while 16% of the 45 obtained in the following winter and 52% of the 27 obtained in the winter of 1927-28 were fecund. Thus he concluded that in one of the three winters concerned there was complete sterility.

II—MATERIAL AND TECHNIQUE

The total material consists of the 593 males obtained over the same period and in the same way as the females described in Part I. The body-weight was not known in four and the weights of the reproductive organs in six others. Thus 583 males were available for all purposes involving weights of body and reproductive organs.

The body-weights ($\pm$ 0·25 gm) were determined, and the reproductive organs were dissected out and removed in one piece. The organs were fixed whole in the alcoholic modification of Bouin's fluid. This fixative was chosen because of its rapid penetration and uniformity of action. The organs were transferred to 70% alcohol and stored for subsequent weighing. The testes, epididymides, seminal vesicles and prostate together, Cowper's glands, prepucial glands, and the penis were weighed on a torsion balance, accurate to 0·5 mg, after the superficial moisture had been removed on a pad of muslin.

The testes of all animals obtained from July to March inclusive, of all with testes under 500 mg, and a sample of 17 of the 199 adults with testes over 500 mg from April to June inclusive were sectioned. The sections were stained with Mayer's haemalum and aqueous eosin. The presence of mature spermatozoa in the testis, determined histologically, was considered a criterion of fecundity, whether they were few in number or numerous. Spermatozoa which retained the cytoplasm of the spermatid were not considered to be mature for this purpose.

During June, 9 animals had testes weighing under 100 mg and all these were devoid of spermatozoa. Otherwise all obtained during April, May, and June had testes over 100 mg. Testes weighing between 100 and 500 mg, numbering 41, were sectioned and found to contain spermatozoa. The presence of spermatozoa was determined histologically in 17 of the animals with testes over 500 mg, and as all gave positive results the remaining 182 were assumed to contain spermatozoa.

The mean diameter of the spermatic tubules in a testis was obtained as follows :—outline drawings were made, by means of a vertical projection apparatus, at a known magnification, of a group of 20 tubules situated at the periphery of a major transverse section of the testis. The greatest width at right angles to the long axis of the section of each tubule was taken as the diameter and the mean of the group of 20 was calculated.

The mean area of the interstitial cells was derived from camera lucida drawings of six to eight cells made at a magnification of 1000 diameters.

The data included in the present paper are given either in the form of scatter diagrams or as correlation tables. The latter were employed where the scatter of points was too close to permit of scatter diagrams being made, except on a large scale. No attempt was made to treat the data statistically in most cases, as it was felt that the relevant information was obvious from the diagrams and tables. Mathematical treatment was employed, however, for the spermatic tubules and interstitial cells. The diameters of the former were plotted against the cube root, and the areas of the latter against the square root of the weight of the testes. This method was adopted in order to express the size of the testes in comparable terms ; linear and plane respectively. In both cases a straight regression line was fitted and its significance tested, by using FISHER's (1930) table of t.

III—STRUCTURE OF THE REPRODUCTIVE ORGANS

The general arrangement of the reproductive organs of the male *Evotomys* resembles that of the mouse, but differs in details of the anatomy of the accessory glands.

The vasa deferentia are not provided with any visible ampullae, but each is surrounded at its base close to its junction with the urethra by a collar composed of several little lobed glands, fig. 9, Plate 13. These are normally hidden by the prostate, seminal vesicles and bladder.

The seminal vesicles in the adult during the breeding season are large sacculated organs, fig. 7, Plate 12, similar to those of the mouse, but shorter, thicker, and more regular in outline.

The prostate is composed of four pairs of lobes, figs. 7 and 8, Plate 12, surrounding the base of the bladder. Each lobe is composed of a number of unbranched tubules often bent upon themselves and joined together by connective tissue. One pair is situated ventrally, lying on the neck of the bladder immediately anterior to the pubic symphysis, fig. 8, Plate 12. These join the ventral surface of the prostatic portion of the urethra on either side close to the middle line where it joins the bladder. A second and larger pair overlaps these and the ventro-lateral surfaces of the urethra where the vasa deferentia join it. Two pairs of lobes, fig. 7, Plate 12, are situated on the dorsal surface of the urethra covering the bases of the seminal vesicles. The outer of these are long and narrow and lie along the inner sides of the curves of the seminal vesicles on each side, to which they are loosely attached. The inner pair is shorter and wider and meets in the mid-dorsal line. Both pairs join the urethra immediately behind the bases of the seminal vesicles.

The bulbus urethrae, fig. 9, Plate 13, is prominent and is situated at the base of the penis between the crus penis and the anus. The bulbo-cavernosus muscles, which are striped, surround the bulbus on all sides, except dorsally where the muscles do not extend between it and the rectum. A band of bulbo-urethral muscle, however, extends dorsally above the rectum. The glands of Cowper (bulbo-urethral glands) are pyriform in shape and are situated dorso-laterally to the bulbus and close to its anterior margin, figs. 7 and 9, Plates 12 and 13. They are thus situated on each side of the rectum close to the posterior margins of the ischia. The glands themselves are outside the bulbo-urethral muscles but their ducts run through these to open into the beginning of the cavernous part of the urethra. A large urethral sinus, fig. 7, Plate 12, occupies the centre of the bulbus. It is bilobed with glandular walls and a large central cavity which is continuous and which opens below directly into the urethra, fig. 1, close to the openings of the ducts of Cowper's glands. The

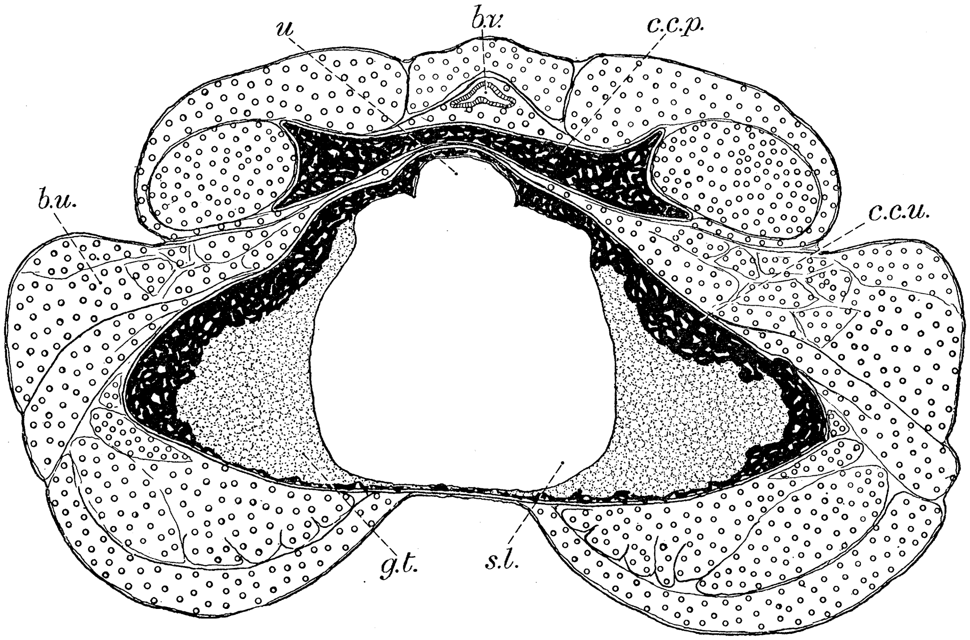

FIG. 1—Diagrammatic transverse section of the bulbus. The bulbo-urethral muscle, *b.u.*, on each side of the urethra, surrounds the urethral sinus, which consists of glandular tissue, *g.t.*, and erectile tissue of the corpora cavernosa urethrae, *c.c.u.* The lumen of the sinus, *s.l.*, is large and is seen to open into the urethra, *u.* *c.c.p.* = corpus cavernosum penis. *b.v.* = blood vessel.

erectile tissue of the corpus cavernosum urethrae extends around this sinus, being especially well developed laterally. The urethral sinus was recognized first by TULLBERG (1899, his Plates XLVIII–LI) in certain rodents and was found in the mouse by GROSZ (1905), and in other species by RAUTHER (1909). Since its structure and development are being investigated at present in this laboratory it is unnecessary to describe the sinus further here. Possibly it corresponds to the "bulbar glands" of MOSSMAN, LAWLAH, and BRADLEY (1932) who recently described them in a number of species of Sciuridae. There is no duct comparable to the long "penile duct" of many Sciurids, described by these authors, since the urethral sinus in *Evotomys* opens directly into the urethra.

The prepucial glands, fig. 9, Plate 13, are very flattened leaf-like glands lying on each side of the prepuce and closely attached to the superficial fascia of the ventral abdominal wall. They open by means of short ducts into the prepucial sac. During the non-breeding season these glands are very minute.

IV—Growth and Breeding Season

The body-weights of 589 males were available and are given in the form of a scatter diagram against month in fig. 2. During January and February the body-weights, with one exception at 19 gm, are between 12·5 and 17·5 gm. In March and April they rise rapidly, attaining a mean weight of 23·8 gm during May, when the breeding season is at its height. The heaviest animal was 29·9 gm and was obtained in May. During June, July, August, September, and the beginning of October the downward spread of body-weights is much greater, owing to the presence of young animals from 8 gm upwards. Only one animal under 8 gm was trapped. The maximum observed in each of the five months respectively being 29·7, 26·8, 25·5, 24·2, and 22·2 gm. By the months of November and December the body-weights have attained the winter range of 12·4 to 18·4 gm, with two exceptionally heavy animals in December at 20 and 22 gm respectively.

Fecundity, as judged by the presence of mature spermatozoa in the testes, is attained in March, as will be shown subsequently. The body-weight at which fecundity is attained is not, however, sharply defined. The lightest animal with spermatozoa in the testis was 13·5 gm and the heaviest without spermatozoa was 18·5 gm. A line drawn from 18 gm on March 1 to 15·5 gm on March 31 would, however, separate the fecund above from the infertile animals below, with few exceptions. During June, July, and August the correlation of fecundity with body-weight is even less clearly defined, the lightest animal with spermatozoa being 11 gm and the heaviest without spermatozoa being 17 gm. The numbers for each gram of body-weight are given in Table I.

Table I—(June, July, and August)

Body-weight gm	With spermatozoa	Without spermatozoa
18<	45	—
17 — 17·9	10	1
16 — 16·9	15	5
15 — 15·9	12	4
14 — 14·9	4	7
13 — 13·9	7	5
12 — 12·9	2	4
11 — 11·9	3	8
> 10·9	—	5

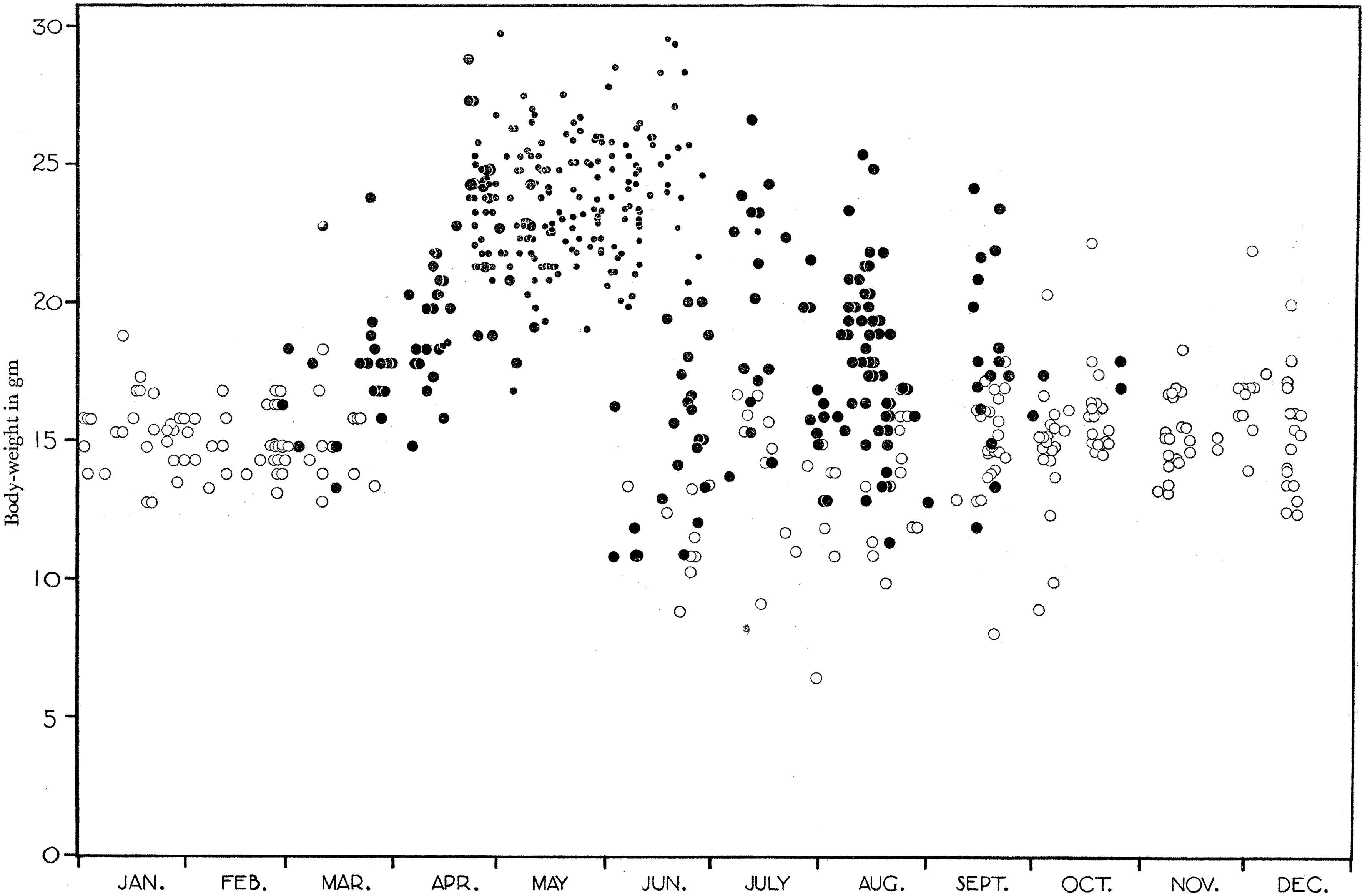

FIG. 2—Distribution of body-weights throughout the year. The large hollow circles represent animals in which spermatozoa are absent from the testis. The large solid circles denote the presence of spermatozoa in the testis while the presence of spermatozoa is assumed in animals represented by the small solid circles.

It is apparent that the line above which 50% or over are fecund occurs at approximately 14 gm body-weight, and this may be taken as the weight at the time of puberty. It is clear in consequence that those young animals which become sexually mature in the summer of their first season may do so at a lighter body-weight than that which animals reaching puberty in the following spring have attained.

It will be shown subsequently, from histological examination of the testes, that the winter animals include some which have previously been mature, and are consequently in a state of quiescence, as well as young animals, presumably born late in the season, which have not attained puberty. It is clear, therefore, from the distribution of body-weights in late summer and autumn that the heavier adult animals, presumably born during the previous season, either die or undergo a loss of body-weight during the autumn. The ranges of body-weight of the pre- and of the post-pubertal animals overlap during the winter months.

The extent of the breeding season in the male *Evotomys* may be judged by the occurrence of mature spermatozoa in the testes, fig. 16, Plate 15. Using this criterion it is apparent that the breeding season extends from March to September inclusive. Outside this period only five animals with spermatozoa were caught, one on February 28 and four in October. The data are given in Table II and the percentage of animals with spermatozoa in the testes is represented graphically in fig. 3.

It can be seen that none occurs in November, December, and January. The peak of the breeding season is reached in April and May when 100% have spermatozoa,

Table II—Number of Animals With and Without Spermatozoa Obtained Each Month

Month	Total number	Without spermatozoa	With spermatozoa	Spermatozoa presumed	% with spermatozoa
January	28	28	—	—	0·0
February	29	28	1	—	3·4
March	33	13	20	—	61·0
April	60	—	30	30	100·0
May	103	—	7	96	100·0
June	86	9	21	56	89·5
July	35	12	22	1	65·7
August	77	19	58	—	75·3
September	41	24	17	—	41·5
October	45	41	4	—	8·9
November	26	26	—	—	0·0
December	24	24	—	—	0·0
	587				

but a second smaller peak occurs in August. This must mean that animals born in the earlier part of the year reaeh maturity in the same season, but the condition of the winter testes shows that other animals, probably born at the end of the season, do not reach maturity until the following spring. The testes, fig. 12, Plate 14, of one or two animals obtained at the beginning of the period of rapid hypertrophy, which precedes the onset of the breeding season, show clearly that they have been mature in the preceding season. This demonstrates that mature animals can pass through the non-breeding season in a state of quiescence and become sexually active again the following year.

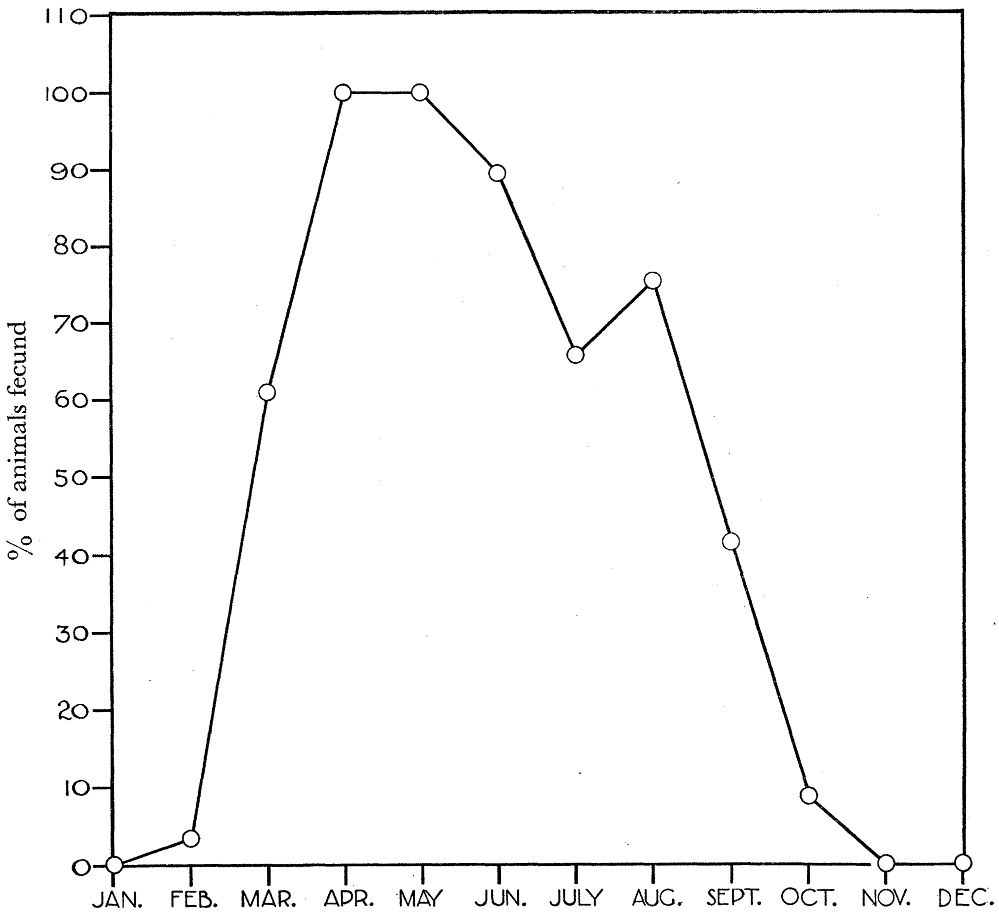

FIG. 3—Graph giving monthly percentage of animals with spermatozoa in the testis. During the months of April, May, and June the presence of spermatozoa is assumed in some of the animals with large testes.

V—TESTES

The combined weights of the two testes of 587 animals are given in the form of a scatter diagram in fig. 4. In a few animals only one testis was available ; when this occurred twice its weight was taken. During the winter months of November, December, January, and the first three weeks of February the testes weigh from 3·5 to 40 mg, the average during the first three months being 10·8 mg for all animals, and 23·7 mg for the infertile adults alone. The testes of the immature

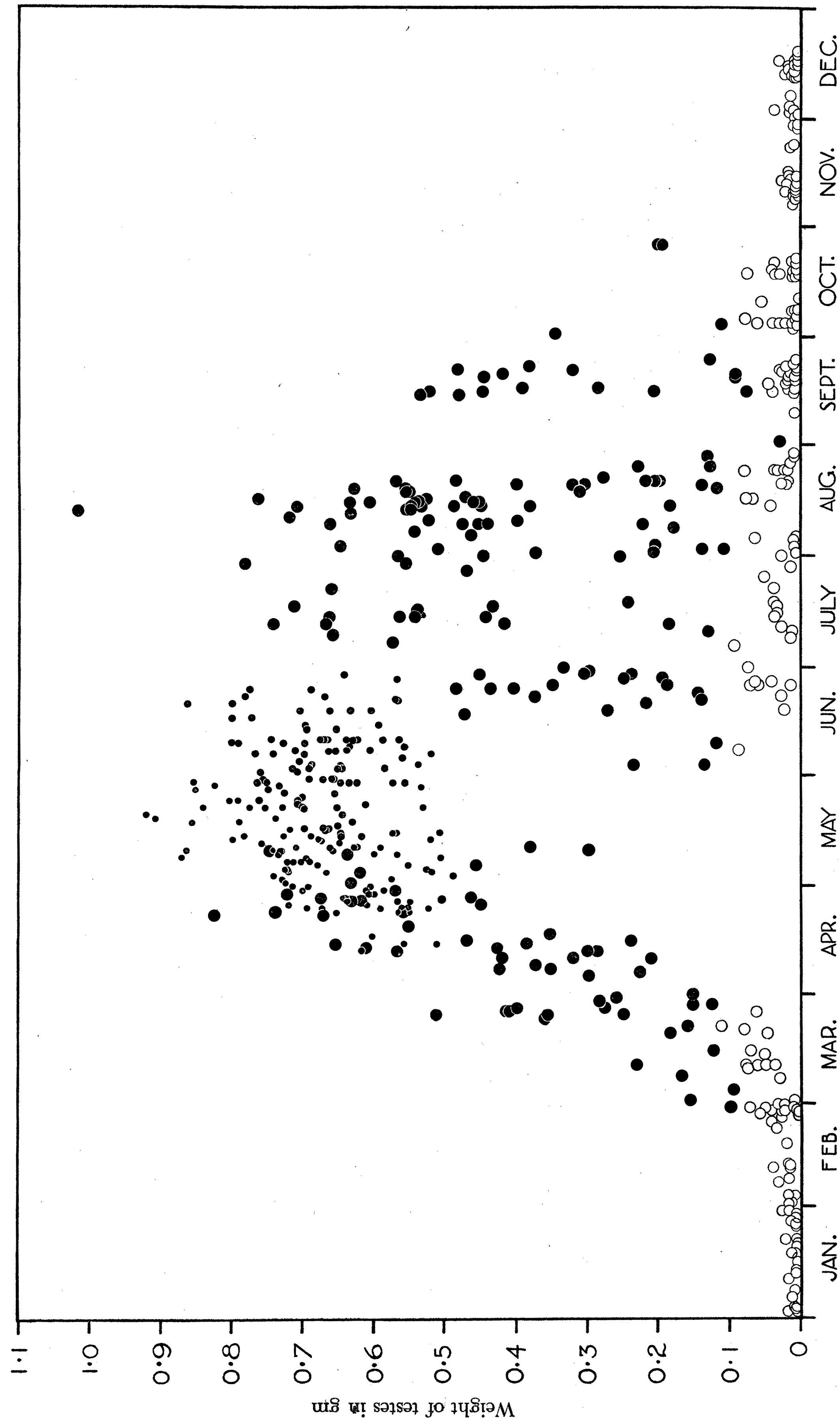

FIG. 4—Distribution of the weights of the testes throughout the year. The presence (actual and assumed) and absence of spermatozoa in the testes is denoted similarly to fig. 2.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

animals during these months are generally somewhat lighter than those of the adults. They begin to increase in weight during February and do so rapidly during March and April, attaining a mean of 682 mg in May. The variation in the weights of the testes during the height of the breeding season is, however, considerable, the highest weight recorded in May being 922 mg and the lowest 298 mg. Subsequently the highest recorded weights fall off regularly, with the exception of a single animal in August in which the testes were 1·02 gm, the heaviest recorded. The maximum for each month, excepting this animal, is: June 865 mg, July 782 mg, August 765 mg, September 535 mg, and October 343 mg. The downward spread after May merges with the upward spread of the young animals. The most remarkable conclusion is that the testes of adult animals average 682 mg in May but only 24 mg during the winter months.

The presence of mature spermatozoa is correlated remarkably closely with the weight of the testes. All those at 100 mg and over, which were examined, were found to contain spermatozoa except one pair in March of 113 mg. No testes less than 100 mg in weight contained spermatozoa, with the exception of five animals. Of these, one was in March with testes weighing 96 mg, while the remaining four were in September, with testes at 30, 77, 91, and 92 mg respectively, and were probably animals which had bred and were in a state of regression, figs. 17 and 18, Plate 15, the spermatozoa having remained in the tubules after the testes had dropped below the critical size. The close correlation between the presence of spermatozoa and testes weighing 100 mg and over is in marked contrast with the absence of any such relation between body-weight and fertility.

The relation of the weight of the testes to the body-weight is clearly brought out in Table III in which the data for 583 animals are given in the form of a correlation table. Whereas the correlation is obviously significant and approximates to a straight line relationship the spread of the data is wide, especially for the lower testis weights, as would be expected from the foregoing results.

It is not the purpose of this paper to discuss the detailed histology of the testis except as regards the bearing of this on the problems of the duration of the breeding and non-breeding seasons. No attempt is made therefore to describe the development of the testis or its condition during the breeding season.

The histology of the testis during the winter months has, however, a very direct bearing on the problems with which this paper is concerned. During November, December, and January all the testes exhibit an entire cessation of spermatogenesis and the tubules are completely inactive. They are small in size and generally devoid of a lumen. Within the tubules Sertoli nuclei are numerous but the only germ-cells present are spermatogonia. The spermatogonia are situated next the wall of the tubule and between it and the zone of Sertoli nuclei surrounding the centre of the tubule, which is filled with the cytoplasm of the cells and is free from nuclei. The nuclei of the spermatogonia are large, spherical, and stain less densely than the small oval Sertoli nuclei, from which they are easily distinguished. The chromatin in the resting spermatogonial nucleus is very finely granular and uniformly

TABLE III

Weight of testes in gm	5·0				9·9	10·0				14·9	15·0				19·9	20·0				24·9	25·0				29·9
1·000																					1				
0·999																									
																					1	1	1		
																				1	1		3		
																		1	1	1	1	1		2	1
0·750																	1	2	3		5	5		2	
0·749															1	2	3	7	3	7	7	9	2		1
																1	7	6	13	9	9	3	2		
														1	2	4	10	7	5	9	4	2			
													2		5	5	5	7	6	6	3				
0·500										1		1	2	4	2	2	3	7	1	3	2				
0·499									1		2	2	1	3	2	4	3		1						
											2	2	4	4		2		2							
												3	2	5	2	1	1								
											2	3		2	1	1									
0·250									2	1	1	1	3	1	2	1			1						
0·249							1		1	1	4	2	4		1	1			1						
								1	1		2	4		5											
							2	1	1	3	1	4	4	1											
						1	6	1	7	3	6	3	2	1		1		1							
0		1		1	3	2	3	10	19	44	48	40	18	4	1	1		1							

30·0

Body-weight in gm

dispersed, giving the nucleus its characteristic appearance. One, two or more conspicuous plasmosomes are present close beneath the nuclear membrane.

The testes of all animals obtained during the months of November, December, and January in the winters of both 1931 and 1932, resembled each other in these respects but otherwise they fell into two clearly defined groups.

The testes of the first group, figs. 13 and 15, Plates 14 and 15, are characterized by their flabby appearance on dissection and in sections by irregularity in outline arising from crumpling of the tunica albuginea. The tunica albuginea itself is very thick, has a strong affinity for eosin and its surface is traversed by fine folds as though it had undergone considerable contraction. Within the tunica the tubules are loosely arranged with relatively enormous inter-tubular spaces between them. The tubules themselves exhibit a characteristic wide zone of faintly eosinophil and rather fibrillar cytoplasm next the wall of the tubule which is free from nuclei. This zone separates the Sertoli nuclei, which form a ring around the centre of the tubule, from the wall. The spermatogonia are not plentiful and are situated in this cytoplasmic zone close to the Sertoli nuclei rather than close to the wall. Some of the tubules have a distinct lumen but in others it is occluded.

The second group, figs. 10 and 11, Plates 13 and 14, differs strikingly from the first, in that the testes appear firm on dissection and are plump and regular in contour. The tunica albuginea in sections is thin and evenly extended over the surface of the testis. Within, the spermatic tubules are closely packed together, the interstices being occupied by interstitial tissue and lymphatic spaces. The tubules themselves differ from those of the other group of animals in that the zone of Sertoli nuclei is situated close to the wall of the tubule, without a wide intermediate zone of cytoplasm. Spermatogonia are much more numerous and there is no trace of a lumen in the tubules. These testes closely resemble those of young animals in summer prior to the onset of puberty and it would appear reasonable to assume that they are in fact prepubertal. The testes of the first type, on the other hand, obviously belong to animals which have bred previously and which are therefore in true non-breeding condition. The characteristics of these testes are such as would be expected when the enormous size difference between those of breeding and non-breeding animals is considered.

The relation of the diameter of the spermatic tubules to the weight of the testes is clearly brought out in fig. 5, in which the mean diameters of the spermatic tubules are plotted against the cube roots of the weights of testes of 91 animals.

It can be seen that there is a linear relationship between the diameter of the tubules and the dimensions of the testes. A straight regression line was fitted of the form

$$y = 217 \cdot 4\, x - 6 \cdot 25$$

where y = mean diameter of the spermatic tubules in μ and

$$x = \sqrt[3]{\text{weight of the testes in gm.}}$$

This regression was found to be highly significant.

The size of the interstitial cells was examined in 19 animals. It was found that the mean area of the cells bore a direct relation to the weight of the testes, as can be seen from fig. 6 in which the mean area of the cells is plotted against the square root of the weight of the testes.

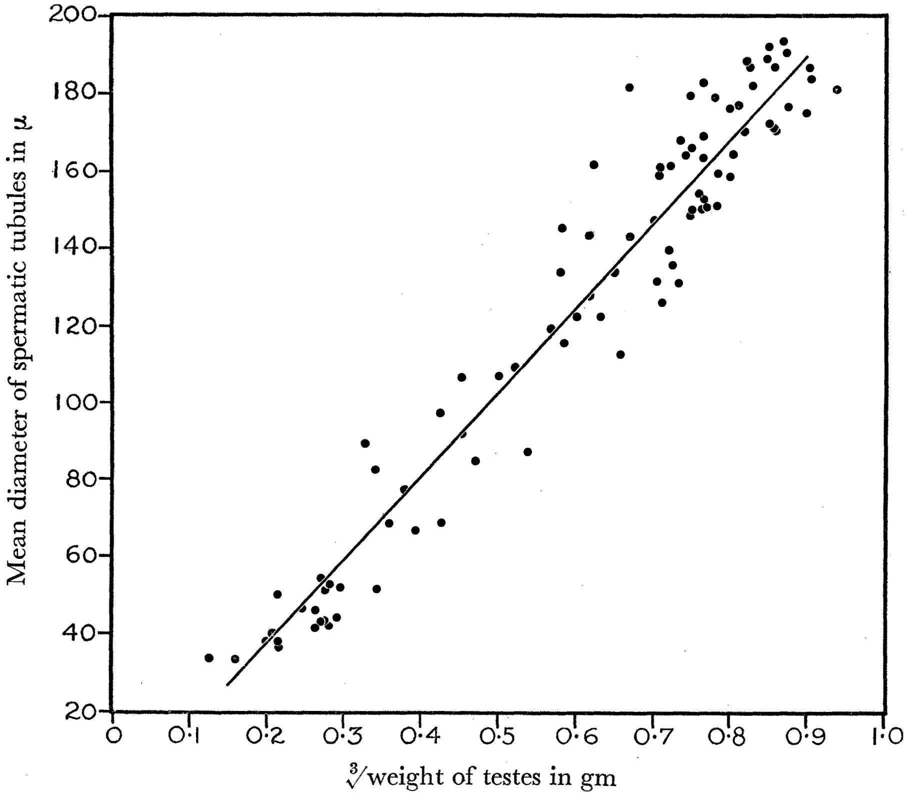

FIG. 5—Scatter-diagram showing the relation of the diameter of spermatic tubules to the weight of the testes. The mean diameter of the spermatic tubules in μ is plotted against the cube root of the weight of the testes. The straight regression line which was fitted to these points is given.

A straight regression line was fitted to these data and was found to be significant. The regression line is of the form

$$y = 100{\cdot}68 + 12{\cdot}06\,x$$

where $y =$ the mean area of the interstitial cells in sq μ and

$$x = \sqrt[2]{\text{weight of the testes in mg.}}$$

VI—Accessory Sexual Organs

The size changes in the epididymides, penis, Cowper's (bulbo-urethral) glands, seminal vesicles and prostate combined, and the prepucial glands were examined. It was found that in all these organs the closest correlation exhibited was with the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

weight of the testes. The data are given in consequence in the form of correlation tables of the weights of the organ and the weights of the testes.

a. Epididymides

These organs exhibit a close correlation with the weight of the testes. It can be seen from Table IV that this relation approximates to a straight line regression and that the spread is small.

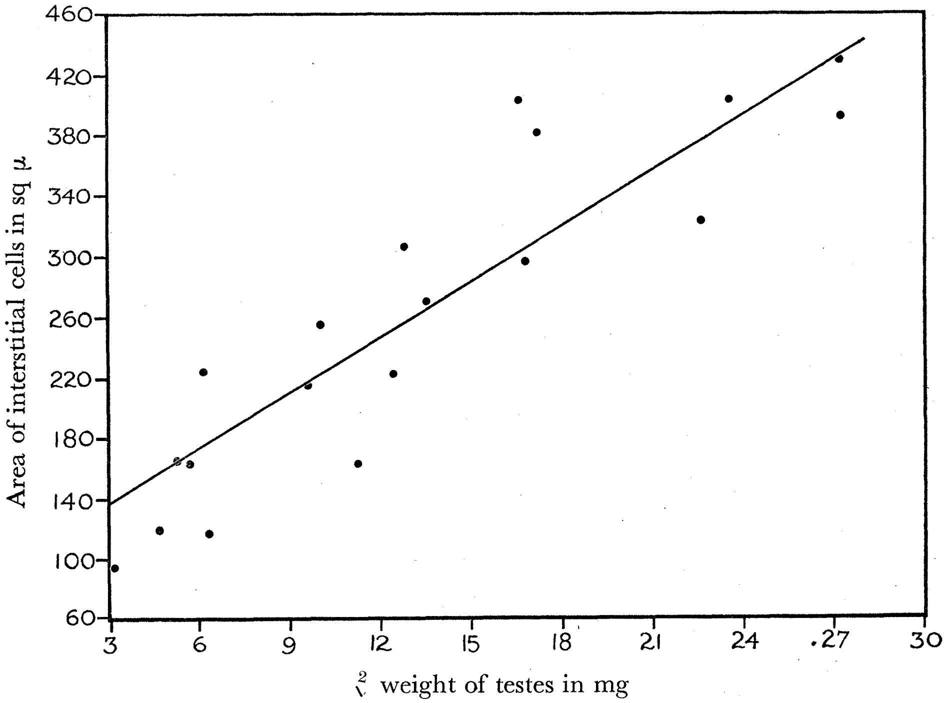

Fig. 6—Scatter-diagram illustrating the relation between the size of the interstitial cells of the testis and the weight of the testis. The area of the interstitial cells in sq μ is plotted against the square root of the weight of the testis. The straight regression line for these points is given.

Sections of the epididymides of a large number of animals were examined for the presence of spermatozoa, particular attention being paid to those of animals taken in spring, at the onset of the breeding season in which spermatozoa were present in the testes, and of mature animals which were regressing during September, October, and November, and in which spermatozoa were absent from the testes. All animals with testes under 200 mg in weight in which spermatozoa were present during March and the single animal at the end of February were examined and were found with one exception to have spermatozoa in the epididymis. This exception (E 400) was obtained on March 4, and was the only animal with spermatozoa in the tubules in which the testes weighed under 100 mg. All the other animals examined throughout the season in which spermatozoa were present in the testes also had spermatozoa in the epididymides. It is clear from these results that mature spermatozoa can be found in the epididymides almost immediately after their appearance in the testes. The presence of mature spermatozoa in the testes may, therefore, be taken for practical

TABLE IV

Weight of epididymides in mg																					
														1		1					
200															1			1	1		
199													1				1				
												1		1					1		1
																1		1			
										1	1	1	1	5	5	5					
150												2	3	4	5	2	2	2			
149											5	1	4	10	11	5					
											2	4	8	14	8	2	4	1			
											3	5	8	7	9	2					
									3	4	4	10	14	5	2	1					
100							1		2	3	6	5	5	3	2						
99								2	1	3	3	8	2								
							1	2	1	5	1	2									
							1	2	1	2	2										
					1	1	1	2	3		1										
50	1			1	1	3	1	3	4	1											
49		1	1	2	3	4	4	2													
		3	3	1	6	4	1	1	1												
	6	2	5	8	4	1		1													
	33	16	7	2	1																
0	198	8																			
					0·249	0·25				0·49	0·5				0·749	0·75				0·99	1·0

Weight of testes in gm

purposes, to indicate their presence in the epididymides. The epididymides of 22 animals obtained in September, October, and November that were definitely adult but in which spermatozoa were not found in the testes were examined. It was found that spermatozoa were present in the epididymides of 13 of these, 12 obtained during September and October and 1 in November, but were absent from the other 5 obtained during the former months and from 4 of those obtained in November. The data are given in Table V. It is apparent, therefore, that the spermatozoa persist in the epididymides for a considerable time after they have disappeared from the testes, as is known to occur normally after castration in a number of animals.

TABLE V—ADULT ANIMALS IN AUTUMN IN WHICH SPERMATOZOA WERE NOT FOUND IN THE TESTES

Ref. No.	Date	Weight of testes mg	Spermatozoa in epididymides
	September		
140	16	18	0
901	17	24	+
907	18	22	+
908	18	18	+
915	20	26	+
927	21	30	+
168	24	21	+
	October		
936	4	30	+
939	4	22	+
941	4	39	+
954	5	77	+
959	5	8	0
977	7	20	0
978	18	76	+
979	18	30	+
981	18	12	0
989	19	40	0
	November		
1014	10	22	0
1025	12	20	0
1027	13	28	0
1031	15	16	+
205	23	12	0

b. Penis

It is obvious from Table VI that the relation of the weight of the penis to the weight of the testes approximates to a straight regression line. The spread is wider than for the epididymides, as would be expected from the greater difficulty of accurately separating the penis from its attachments.

c. Cowper's Glands

Although the correlation of the weight of these glands with that of the testes is not so close as with the epididymides and penis, it is sufficiently obvious from Table VII that a similar relation exists.

TABLE VI

Weight of penis in mg																					
180 179												1									
															2						
													1		2	1		1			
120										1	1			1			1	2	1		1
119									1		4	1	1	6	7	2	2				
						1			1	1	3	4	7	11	10	10	2	2	1		
								1		2	5	8	15	11	10	5	3	1			
		1						2	1	5	5	14	8	17	8	1					
		1		1	1		3		2	2	6	6	6	2	3	1					
60		1	2	1	1	2	2	4	5	6	2	5	6		1						
59	4		1	2	2	3	2	1	4		1	1	1								
	8	2	1	1	4	2	1	4	1	2											
	14	3	3	4	4	5		2													
	38	8	7	4	4																
	129	14	2	1																	
0	5																				
	0				0·249	0·25				0·49	0·5				0·749	0·75				0·99	1·0

Weight of testes in gm

TABLE VII

Weight of Cowper's glands in mg											
24							1				
23											
							1				
					1			3	2		
16						1		5		1	
15					1	5	8	10	4		
		1		1	4	6	20	6	4		1
			1		4	14	25	18	3		
8			2		4	12	22	19	1	1	
7			1	9	8	13	6	4			
	1		3	6	6	8	1				
	2	5	7	2							
0	1	1	1	1							
	0				0·49	0·5				0·99	1·0

Weight of testes in gm

d. Seminal Vesicles and Prostate

The relation of the weight of these organs to the weight of the testes is not so simple as for the other organs described above. Examination of the data showed that the relation existing during the spring months when the seminal vesicles and prostate were growing rapidly, was different from that exhibited in autumn when the organs were regressing. The data for the months of January to May inclusive, are given in Table VIII. It can be seen that the relation of the weight of the seminal vesicles and prostate to the weight of the testes falls into two clearly defined phases. During the first phase, extending until the testes have attained a weight of approximately 250 mg, the seminal vesicles and prostate do not exhibit any significant increase in weight. In the subsequent phase rapid growth in weight correlated with that of the testes occurs. During both phases the relation evidently approximates to a straight line regression although the spread in the second phase is considerable. It is apparent, therefore, that the growth of the seminal vesicles and prostate relative to that of the testes at the onset of the breeding season exhibits a marked lag, and does not, in fact, begin until the testes have attained a comparatively large size and considerably after the stage at which mature spermatozoa are found both in the testes and epididymides. Since no animals with testes 250 mg in weight and over were obtained before March 24, and all animals obtained after April 16 and before the appearance of young animals of the season had testes over this weight, it shows that the growth of the seminal vesicles and prostate begins during this period.

The data for the months of September and October, when the reproductive organs of mature animals are rapidly regressing at the close of the breeding season, are given in Table IX. It can be seen that the relation of the weights of the seminal vesicles and prostate to the weights of the testes during this period is not divisible into two phases but approximates to a single straight regression line.

A similar type of correlation between the growth and regression of the testis and that of the accessory organs is found in the hedgehog (Allanson, 1934).

e. Prepucial Glands

The relation of the weight of the prepucial glands to the weight of the testes appears to be similar to that of the weight of the seminal vesicles and prostate to the testes and the data are consequently treated in a similar manner. The data for January to May inclusive are given in Table X and exhibit a similar, though less clearly marked, lag in the growth of the gland in relation to the testes. The data for September and October, given in Table XI, are unfortunately scanty but serve to show that the prepucial glands do not regress more rapidly than the testes, as would occur if the relationship was similar to that for the spring months. It is probable, therefore, that the weight of the prepucial glands bears to the weight of the testes during September and October a simple relationship such as that exhibited by the seminal vesicles and prostate.

TABLE VIII—SEMINAL VESICLES AND PROSTATE (JANUARY TO MAY)

Weight of seminal vesicles and prostate in mg	0			0·09	0·1			0·19	0·2			0·29	0·3			0·39	0·4			0·49	0·5			0·59	0·6			0·69	0·7			0·79	0·8			0·89	0·9
																									1												1
500																												1	1								
499																														1		1					
																									1			1			1	1					
																							1							1	2				1		
400																										2				1		1			1		1
399																									1				1				1	2			
																					1			1			1		2	1	1				3		
																										1	1		2	3							
300																					1				3	2	5	2	3	4		1					
299																						1	2			1	3	3	2	1	1		1				
												1				1							2		2	1	5		3		1			1			
																					1		1	1		3	1			1							
200																			1		1	1	4	1	3	1	1	2									
199																			1	1			1	2	1	3	1	2	1	2							
																					2	1	2		3	1				1							
																							2														
100													2				1		1				1														
99																2		1			2																
												2			2		2																				
										1		2			1	1		1																			
0	26	10	7	4	3	1	5	1	1	2	2				1																						

Weight of testes in gm

TABLE IX—SEMINAL VESICLES AND PROSTATE (SEPTEMBER AND OCTOBER)

Weight of seminal vesicles and prostate in mg																						
299																						1
																		1				
																	1					
200																						
199																				2	1	
														1		1						
								1														
100													1					1				
99									1							1						
				1					1			1										
		1		1	1																	
0	46	10	2	3		1																
Weight of testes in gm				0·09	0·1			0·19	0·2			0·29	0·3			0·39	0·4			0·49	0·5	

Table X—January to May (inclusive)

Weight of prepucial glands in mg										
99							1	6		
						1	1			
						1	4	2	1	1
						2	5	6	3	
50				1		4	12	10	2	1
49				1		5	7	8	3	
						4	5	5		
				1	1	5	10	2	1	
			2	3	3	4	7	1	1	
0	3	5	4	2	3	6	4			

0   0·49 | 0·50   0·99 | 1·0

Weight of testes in gm

Table XI—September and October

Weight of prepucial glands in mg										
99										
50										
49			1							
				1	2					
	1				2	1				
	1	1	3	3	1	1				
0	21	1								

0   0·49 | 0·50   0·99 | 1·0

Weight of testes in gm

I am indebted to Professor F. W. Rogers Brambell for the use of the material and to him and Dr. A. S. Parkes, F.R.S., for their advice and criticism. The expenses of this research were defrayed in part by grants from the Government Grant Committee of the Royal Society to Professor Brambell, for which I wish to express my thanks.

VII—Summary

The material consists of 593 male *Evotomys* of which 583 have been employed in describing the seasonal variation in the body-weight and in the reproductive organs.

Sexual activity is more closely correlated with the weight of the testis than with the body-weight, since mature spermatozoa are found in almost all males with testes

weighing 100 mg or more. This is a more accurate criterion of fecundity than the body-weight.

Sexual activity commences early in March and is accompanied by an increase in body-weight and enormous growth of the testes from a winter weight of less than 40 mg to a mean summer weight of 682 mg.

Young males born early in the breeding season become sexually mature before the end of the same season, whereas those born late in the season do not attain sexual maturity until the following spring.

In late August, September, and October the testes are in regression and by November there is complete cessation of spermatogenetic activity.

All male *Evotomys* during the winters 1931–32 and 1932–33 were aspermatic during November, December, and January, and the first three weeks of February. During this period two types of testes could be distinguished histologically; those of young animals that had not bred and those of adults which had atrophied.

The size of the spermatic tubules and interstitial cells were found to be directly and simply related to the size of the testes.

Seasonal changes occur at the same time in the accessory organs. When correlated with testis weight they appear to fall into two groups. The epididymides, penis, and probably the Cowper's glands exhibit a straight line regression throughout the year, while the seminal vesicles, together with the prostate and the prepucial glands in the spring, do not increase in weight until the testes have attained a weight of 250–300 mg. Subsequent growth in these organs is very rapid and is correlated with testis growth.

The male accessory organs resemble those of the common mouse (Disselhorst, 1904) except in details. A glandular urethral sinus is present in the bulbus which resembles that of the mouse in structure and position.

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IX—Description of Plates

Key to Lettering

a.g. = ampullary gland ; *b.u.* = bulbo-urethral muscle ; *ca.e.* = cauda epididymis ; *ct.e.* = caput epididymis ; *c.g.* = Cowper's gland ; *c.p.* = crus of penis ; *p*1 = ventral lobes of prostate gland ; *p*2 = ventro-lateral lobes of prostate gland ; *p*3 = dorsal lobes of prostate gland ; *p*4 = dorso-lateral lobes of prostate gland ; *p.d.* = duct of prepucial gland ; *p.g.* = prepucial gland ; *s.v.* = seminal vesicle ; *t.* = testis ; *u.m.* = membranous part of urethra ; *u.s.* = urethral sinus ; *v.d.* = vas deferens.

Plate 12.

Fig. 7—Dissection of the reproductive organs of the male *Evotomys* during the breeding season. Dorsal view. × 2·7. The organs are untouched but for the removal of fat from the right epididymis and the removal of the bulbo-urethral muscles so as to expose the urethral sinus.

Fig. 8—Dissection of the reproductive organs of the male *Evotomys* during the breeding season. Ventral view of same. × 2·7.

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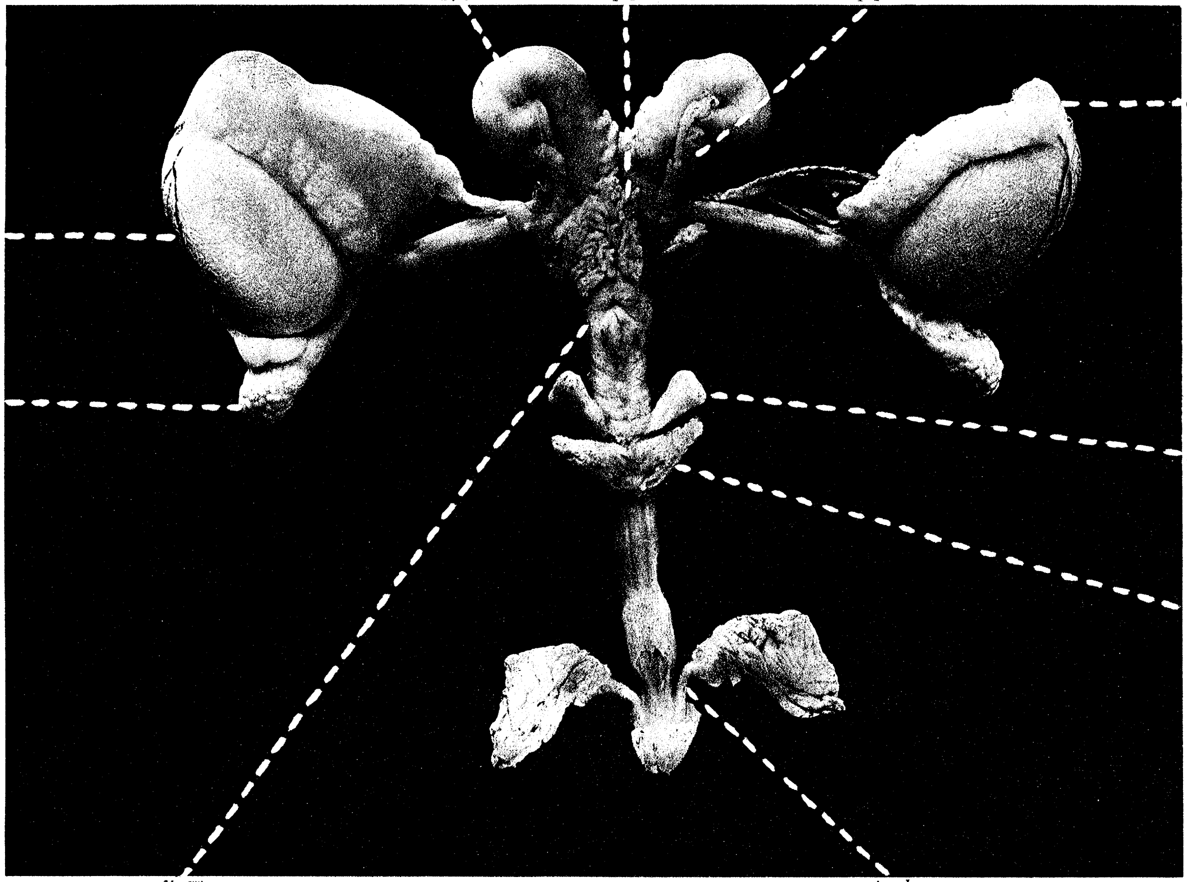

FIG. 7.

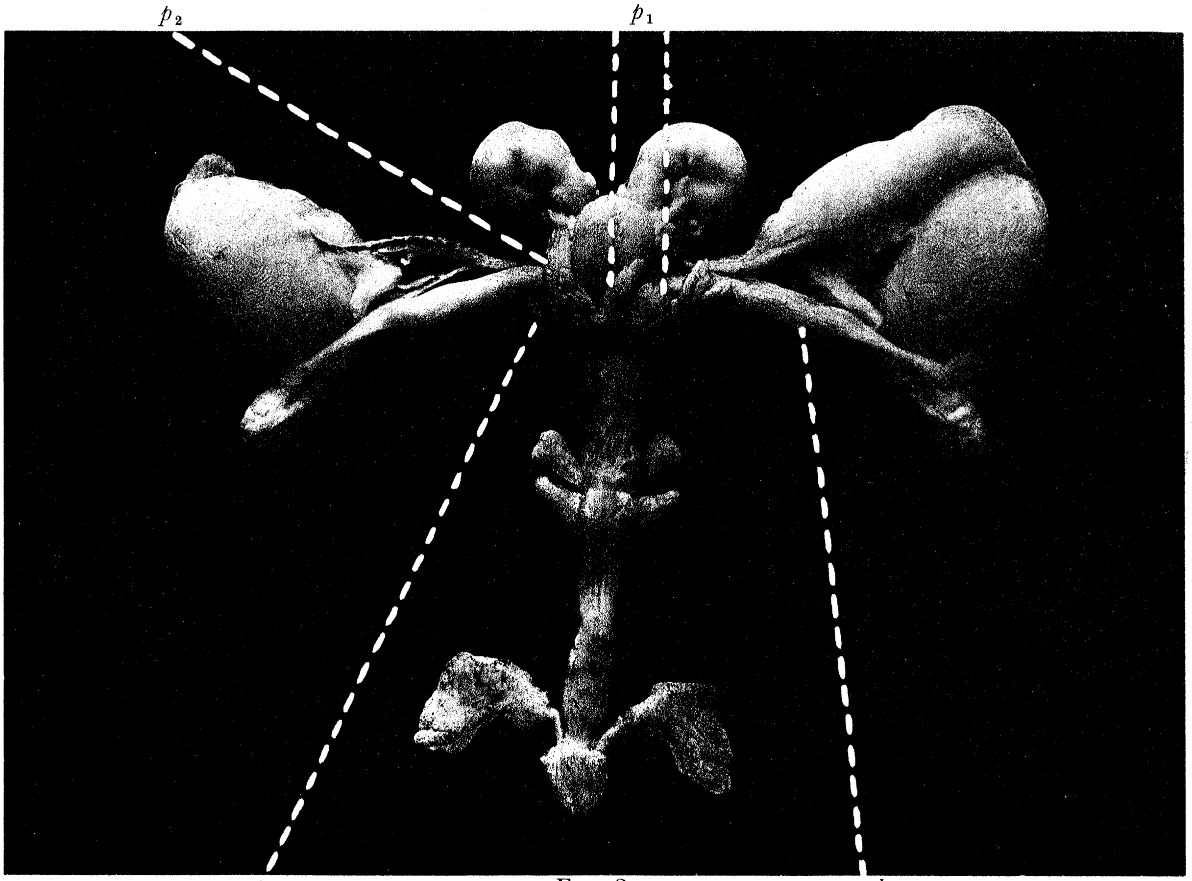

FIG. 8.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PLATE 13.

FIG. 9—Dissection of the reproductive organs of the male *Evotomys* during the breeding season. Ventral view. × 3·0. The bladder has been pulled backwards so as to show the ampullary glands at the base of the vasa deferentia. The large mass of bulbo-urethral muscle is seen partly obscuring the Cowper's gland on the right side.

FIG. 10—Transverse section of the testis of immature *Evotomys* (E 306) in winter (3 Jan. '32). The large number of closely packed spermatic tubules, surrounded by a thin tunica albuginea, is characteristic of this stage. × 68.

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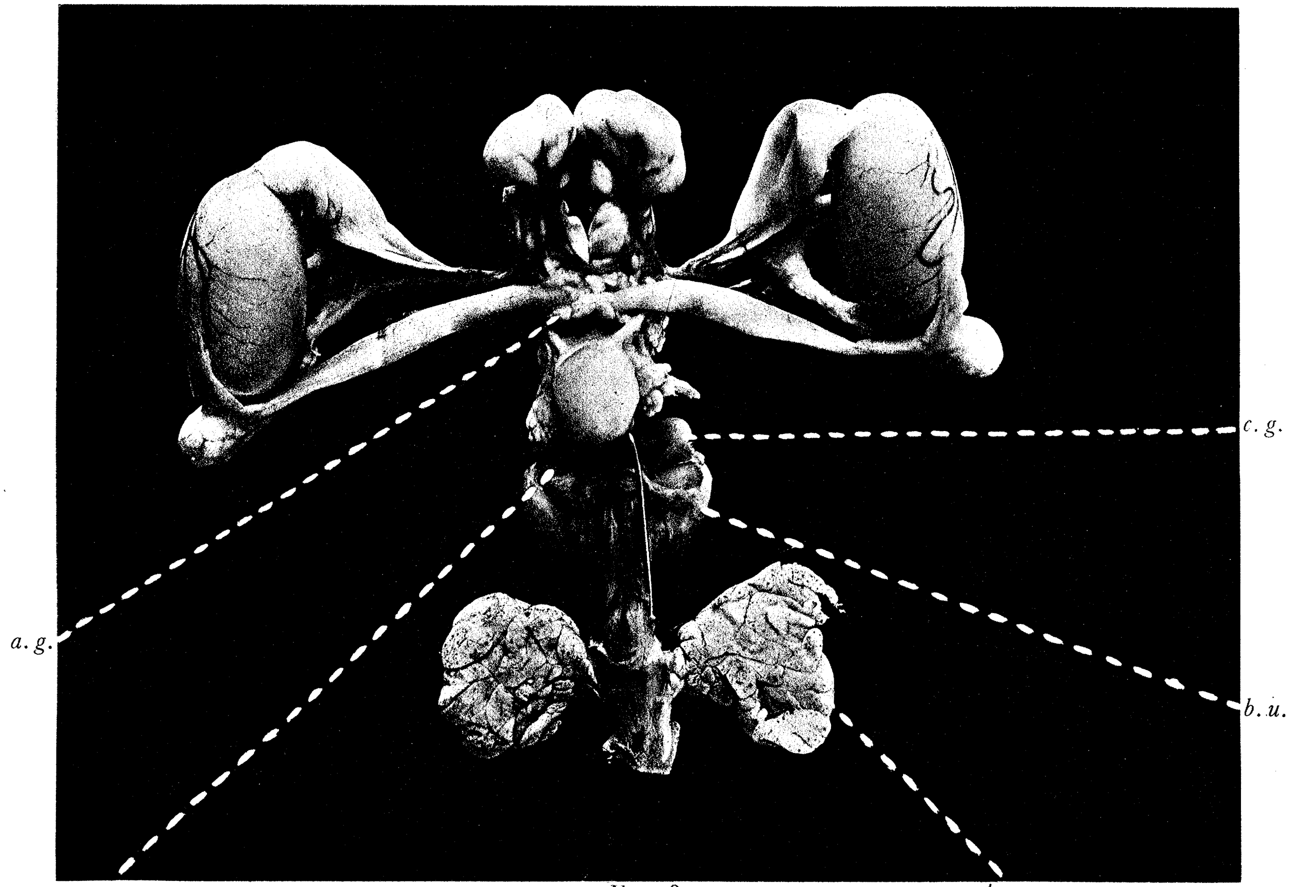

Fig. 9.

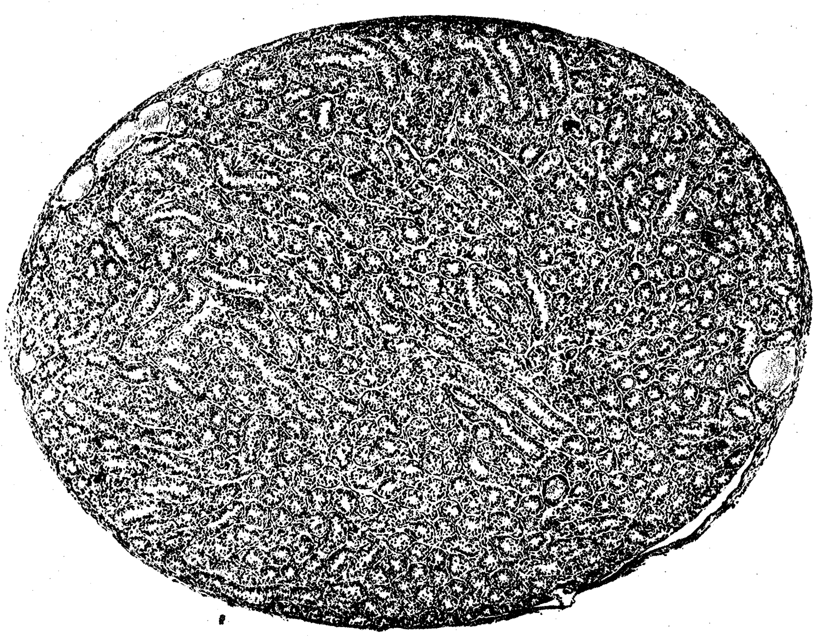

Fig. 10.

PLATE 14.

FIG. 11—Part of section of testis shown in fig. 10. The tubules contain few spermatogonial nuclei and a large number of Sertoli nuclei. × 260.

FIG. 12—Part of a transverse section of the testis of an adult *Evotomys* (E 469) at the onset of the breeding season (26 Feb. '32). Primary spermatocytes in pachynema are again to be seen. This shows that the male *Evotomys* can breed in one season, spend the winter in a state of regression and again become active in the following breeding season. × 150.

FIG. 13—Part of section of testis shown in fig. 15. The characteristic zone of eosinophil cytoplasm between the wall of the tubule and the ring of Sertoli nuclei is seen. × 300.

FIG. 14—Part of a transverse section of the testis of an immature *Evotomys* (E 412) at the onset of the breeding season (11 Mar. '32). Primary spermatocytes in pachynema are seen in all the tubules. × 150.

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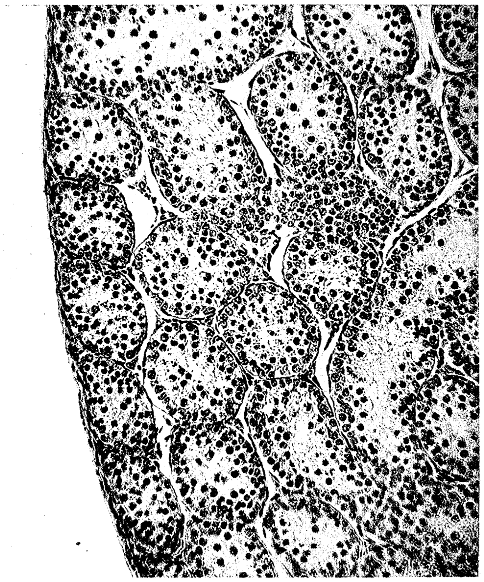

FIG. 14.

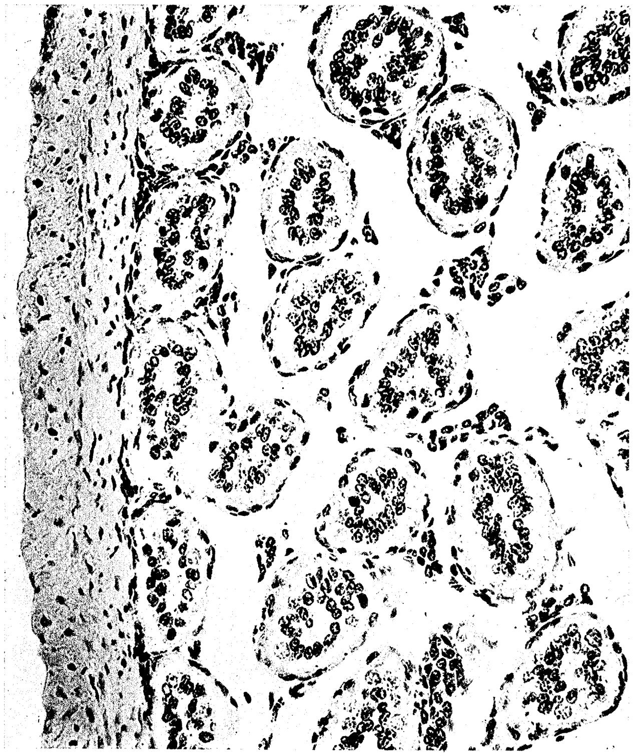

FIG. 13.

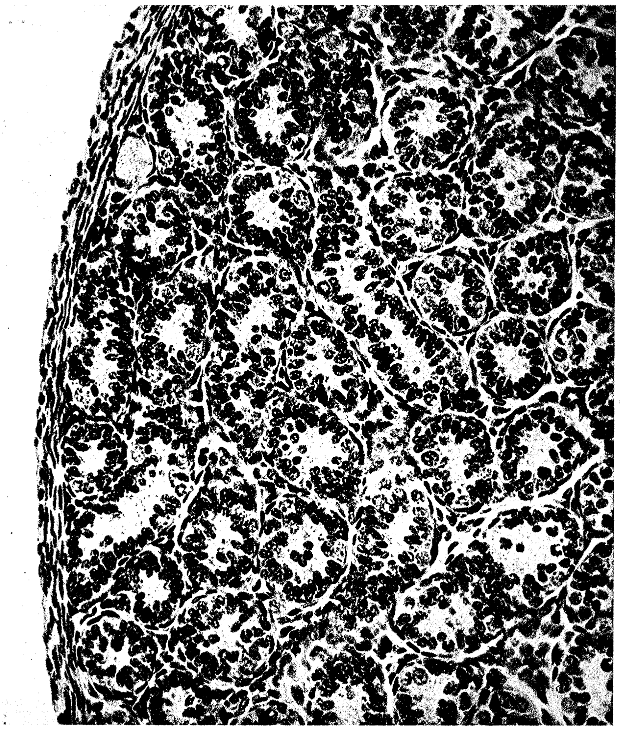

FIG. 11.

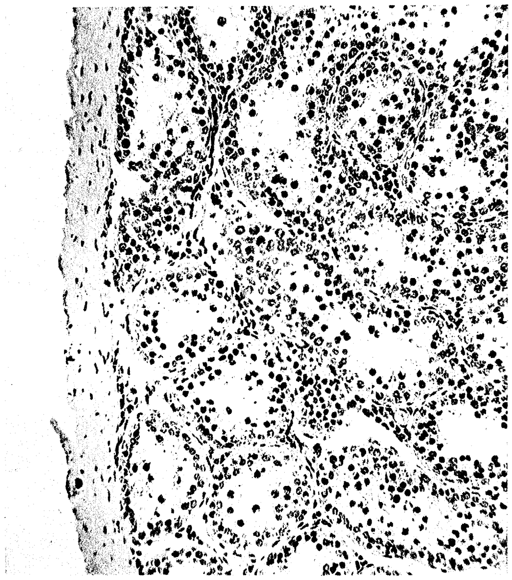

FIG. 12.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PLATE 15.

FIG. 15—Transverse section of testis of an adult *Evotomys* (E 1025) during aspermatogenesis (12 Nov. '34). The loose arrangement of the tubules is clearly shown. The tunica albuginea is very much thickened and contracted. × 72.

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FIG. 18—Part of section of the testis shown in fig. 17. Photograph of a few of the central tubules in which spermatozoa are still found. × 300.

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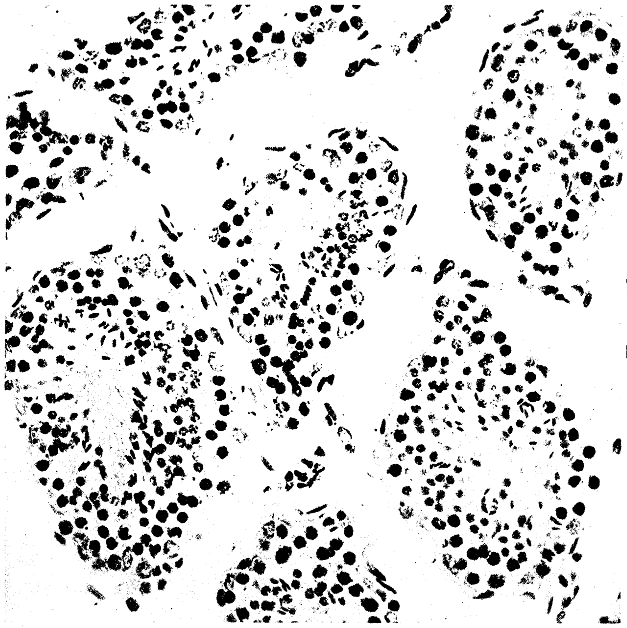


Fig. 18.

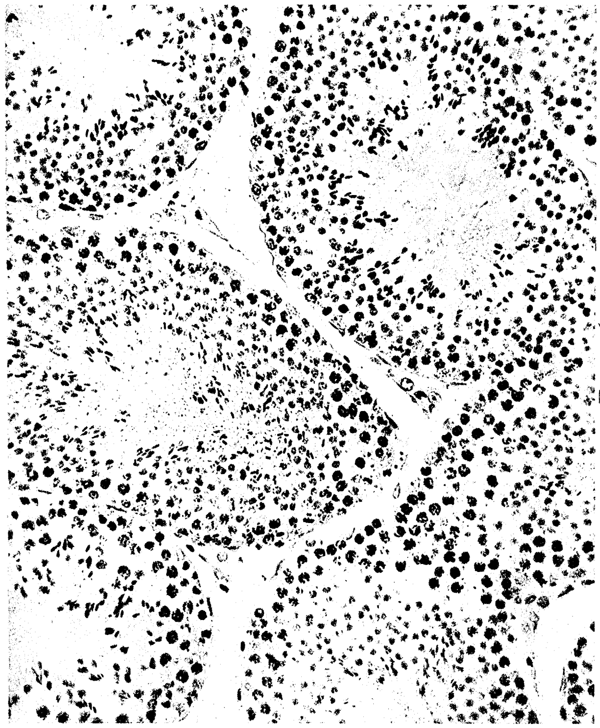
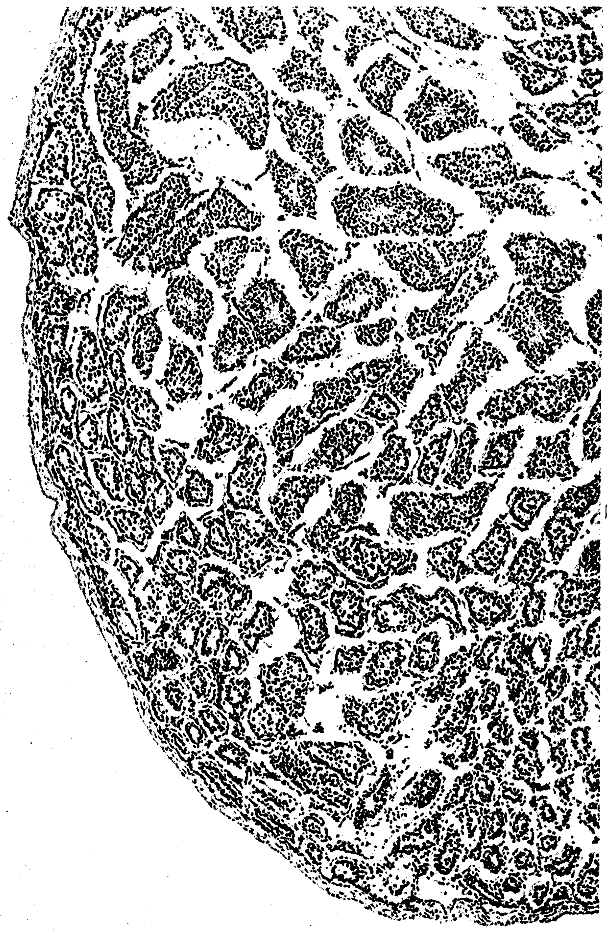


Fig. 16.

Fig. 15.



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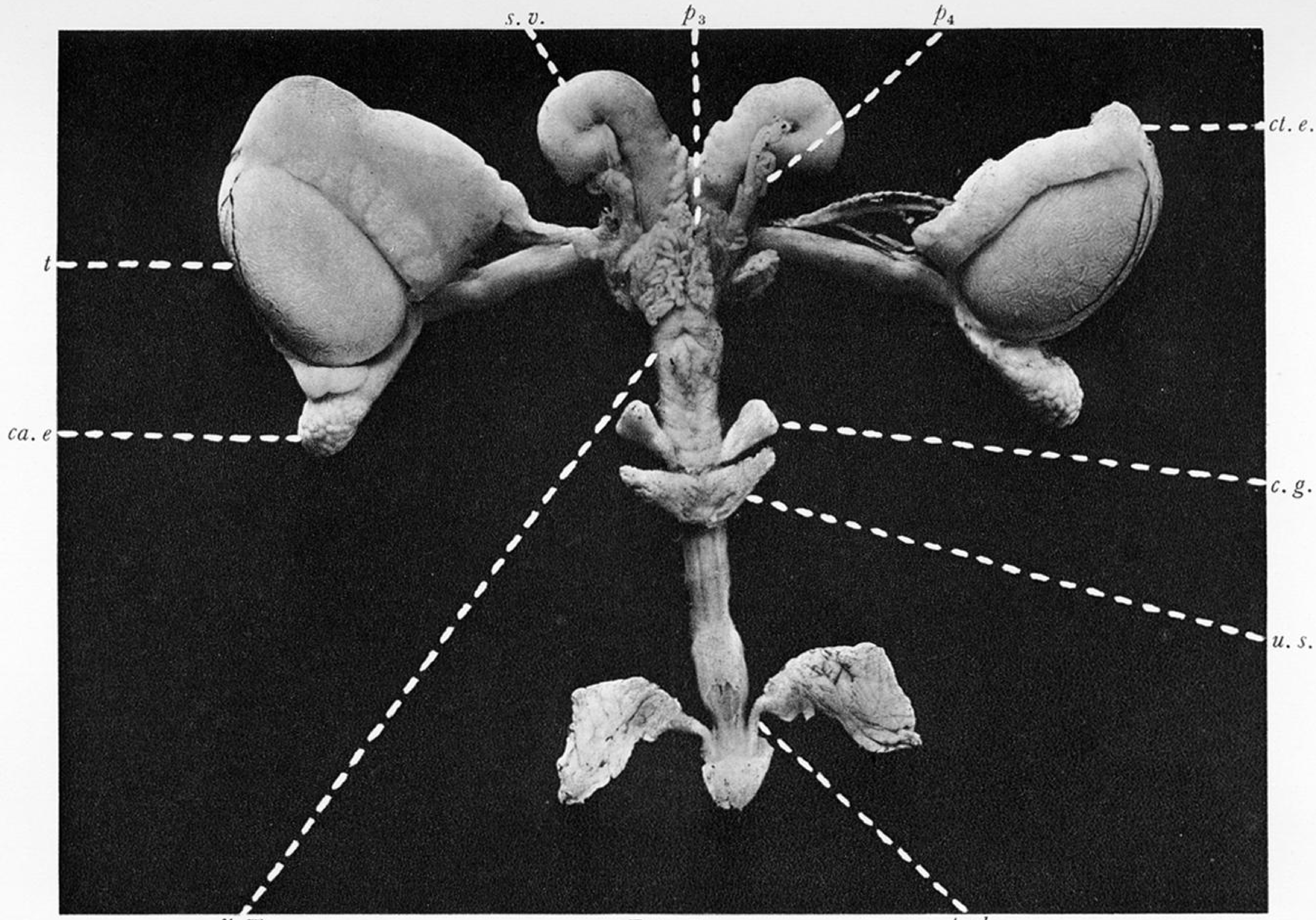
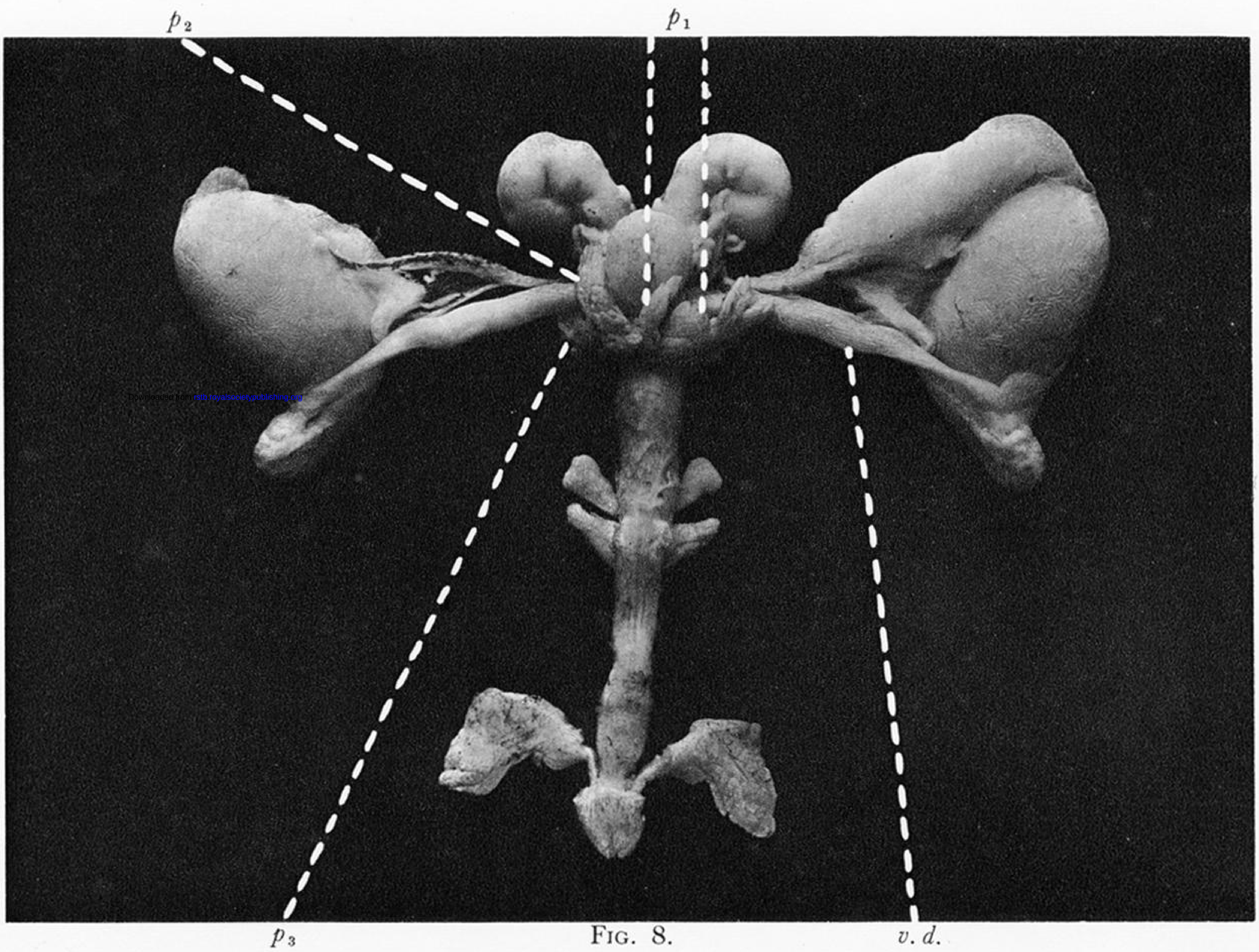


FIG. 7.



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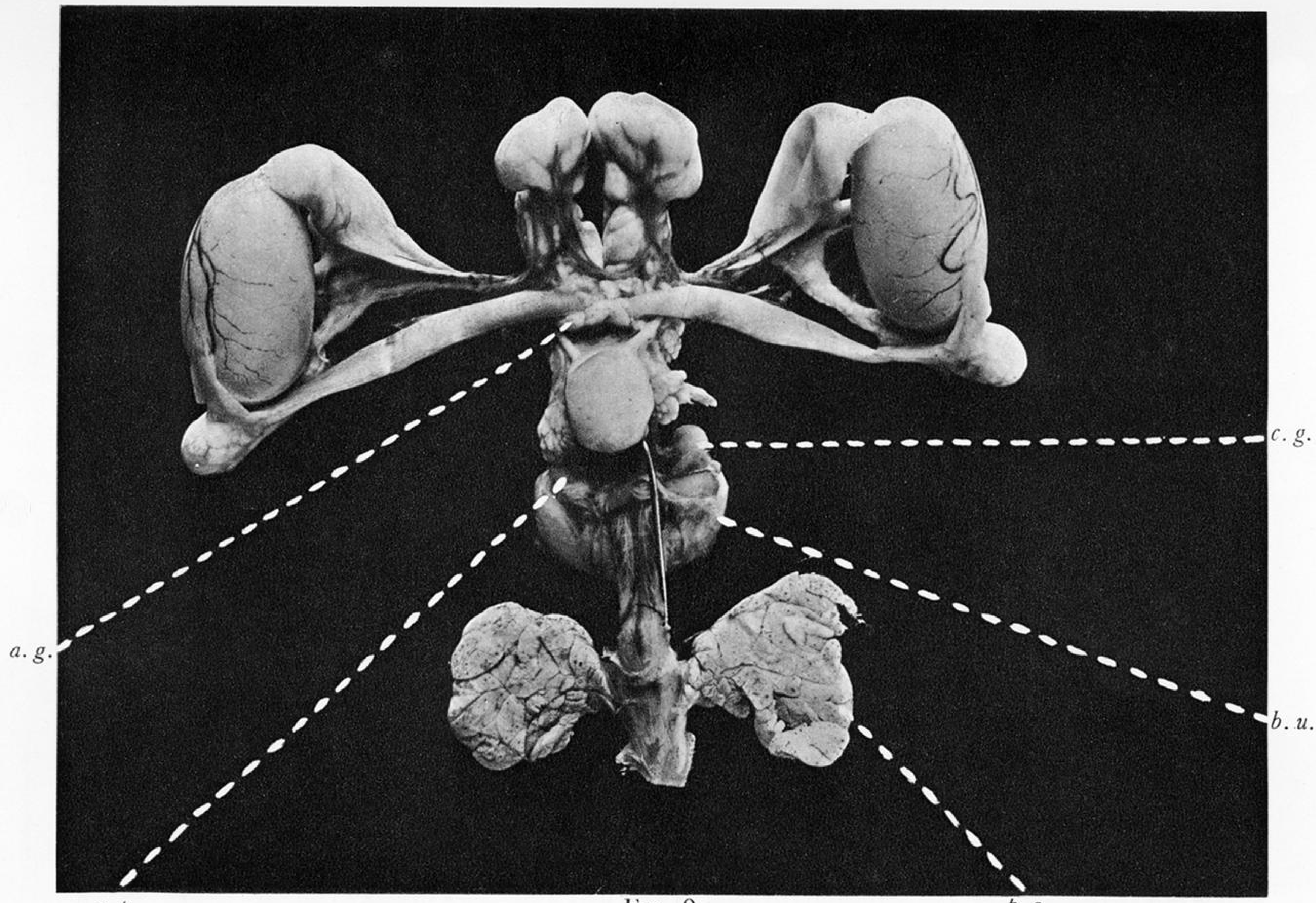

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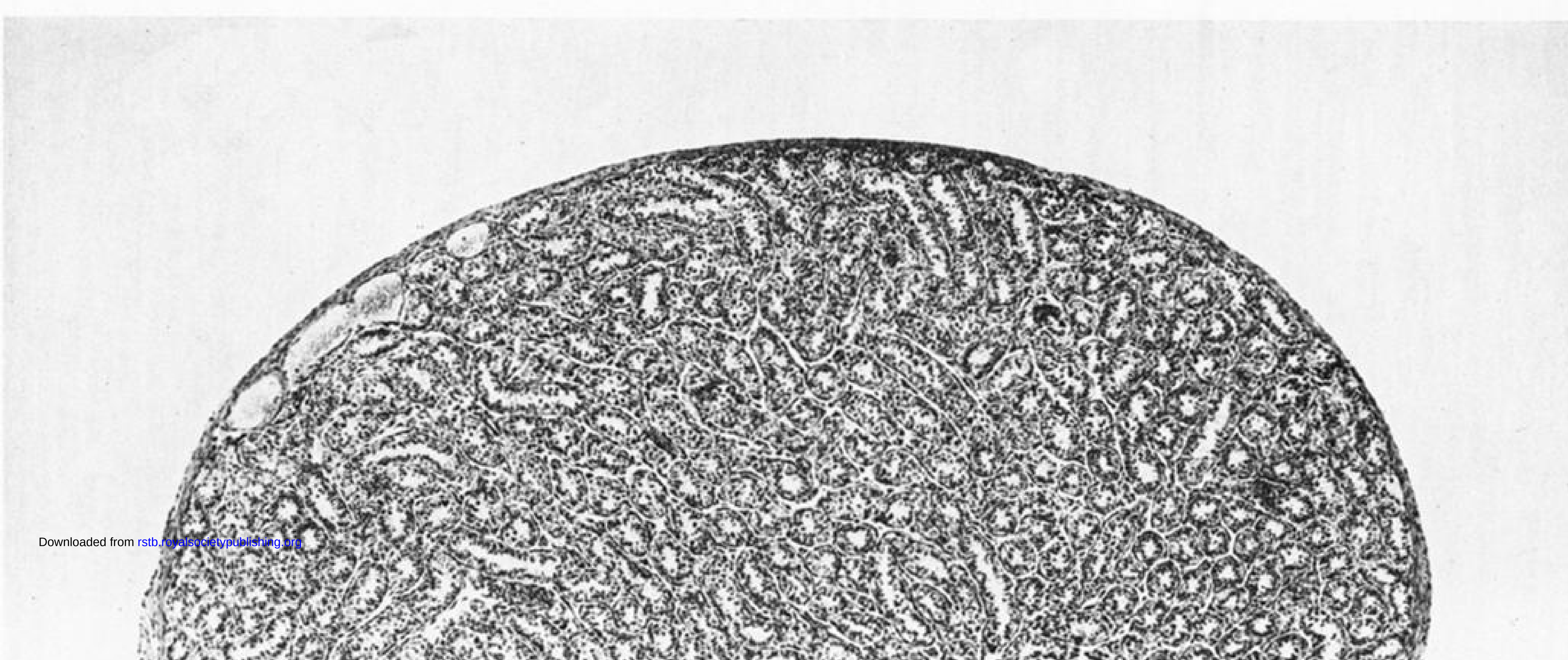

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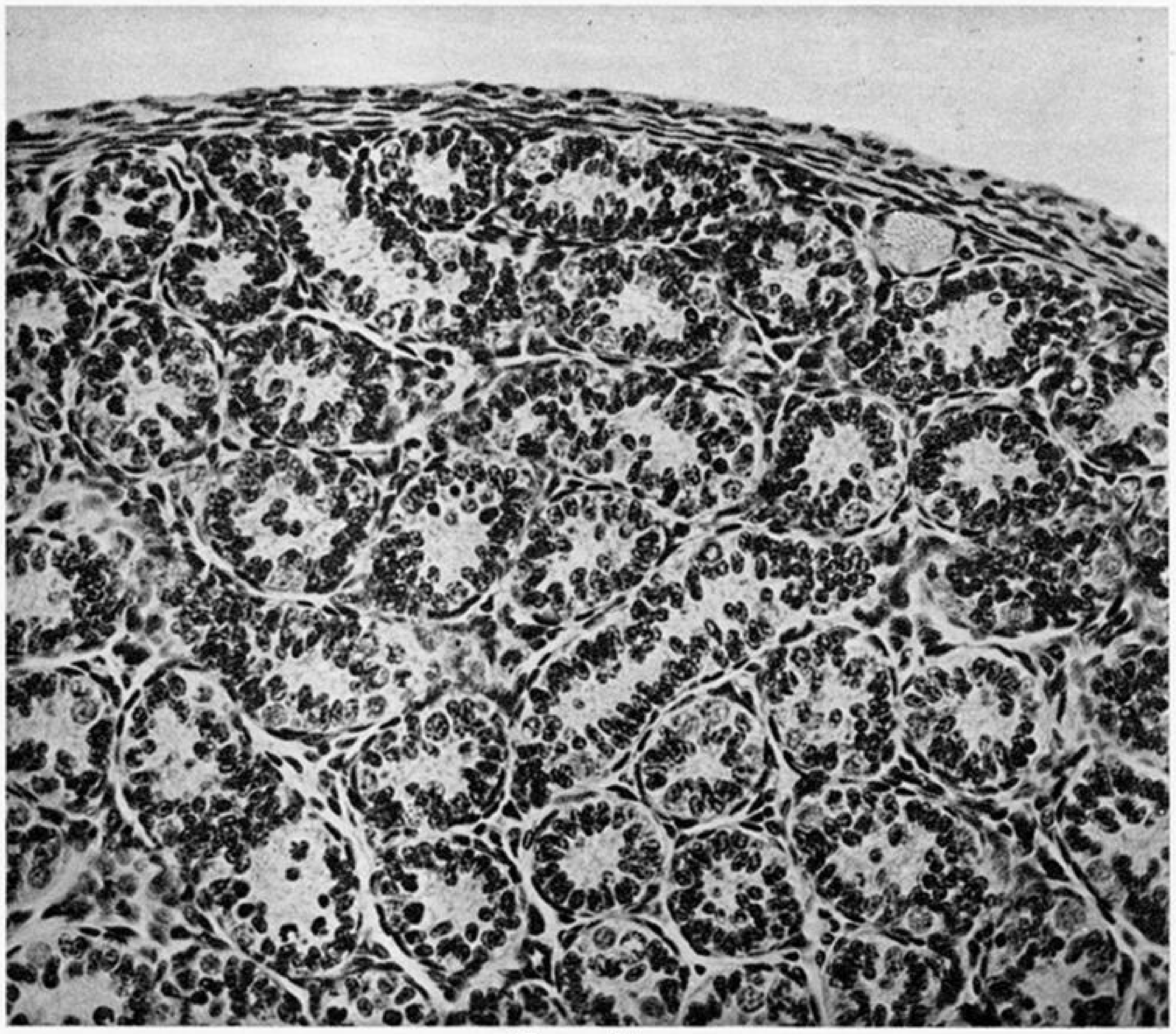

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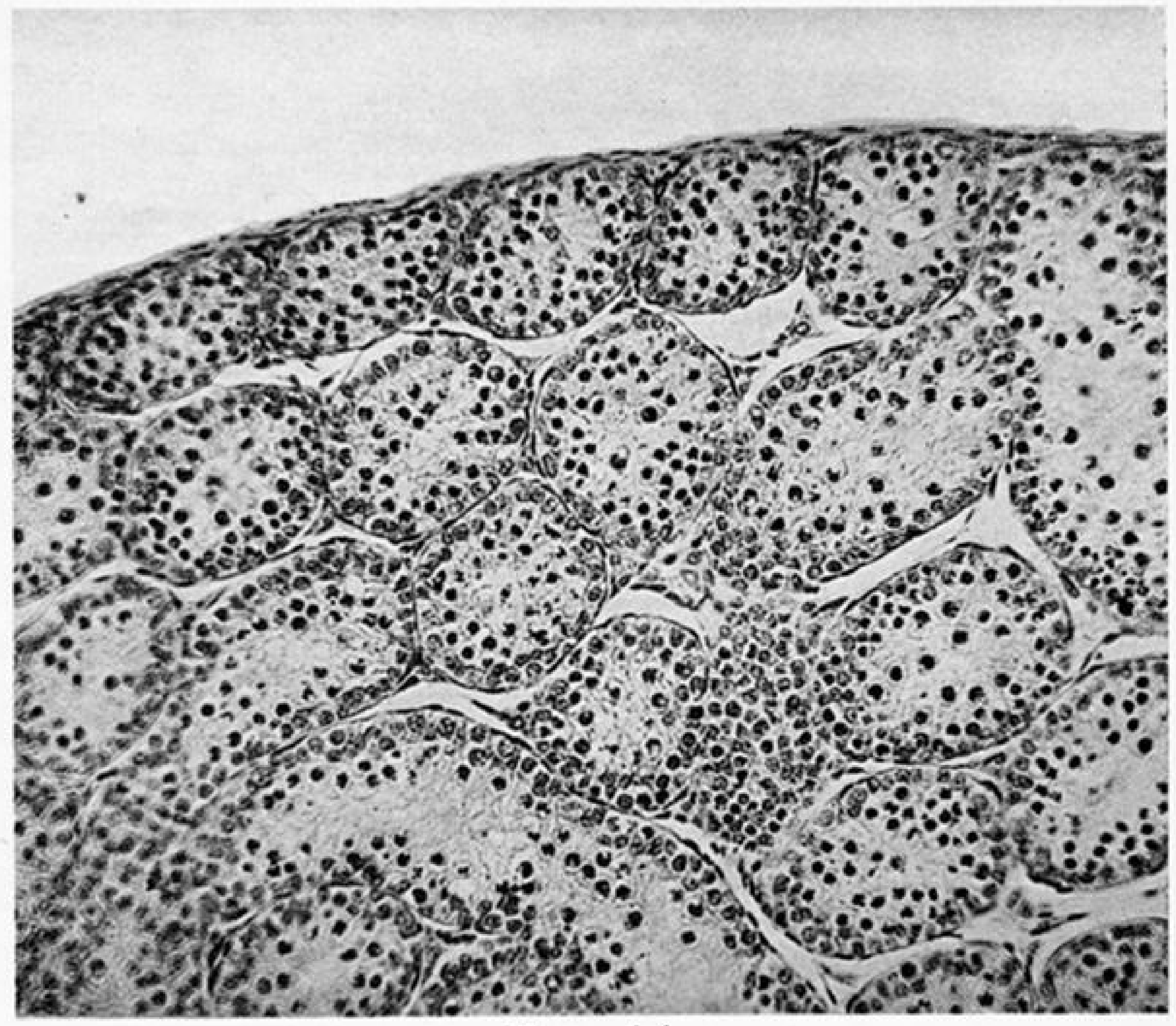

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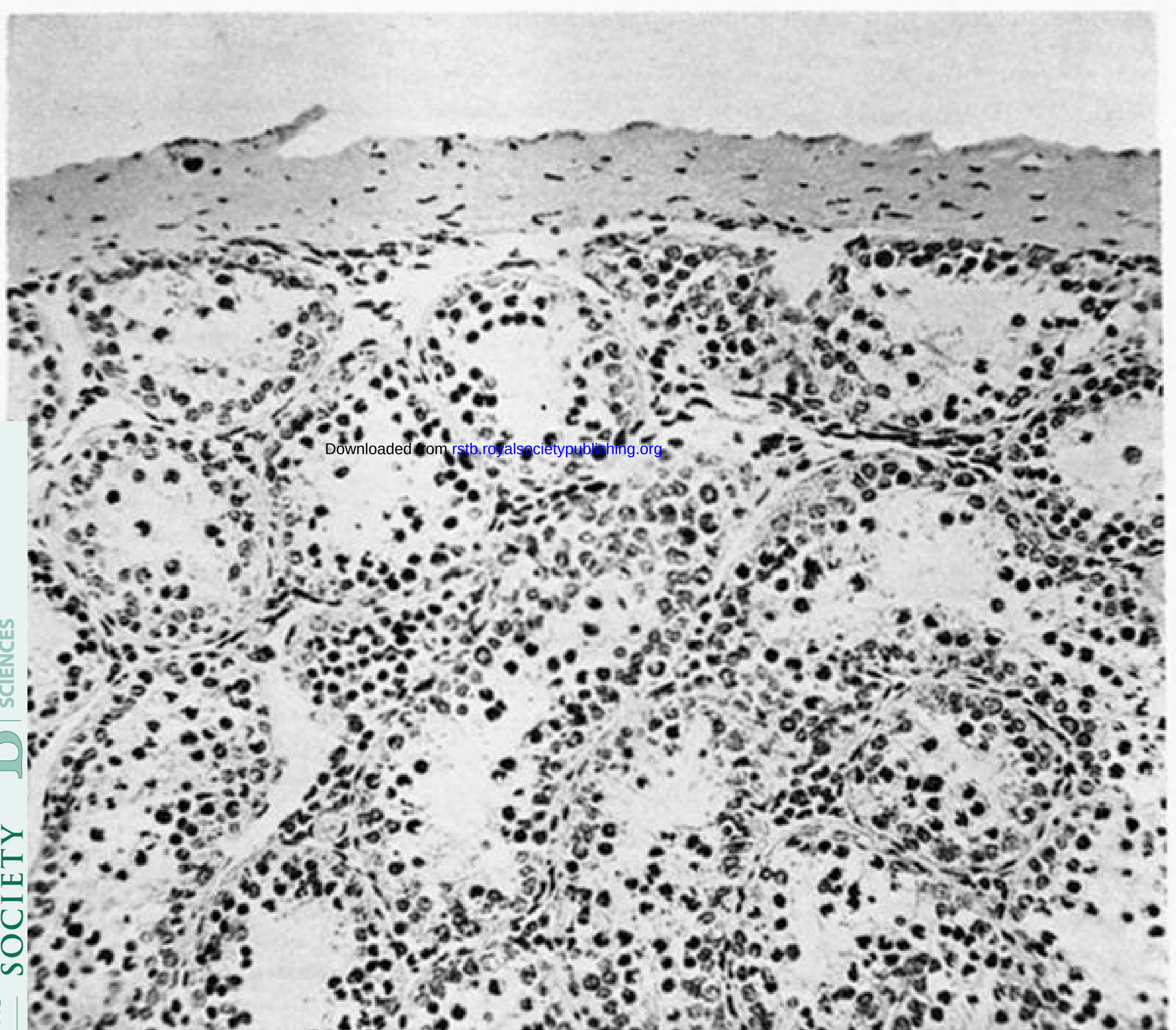

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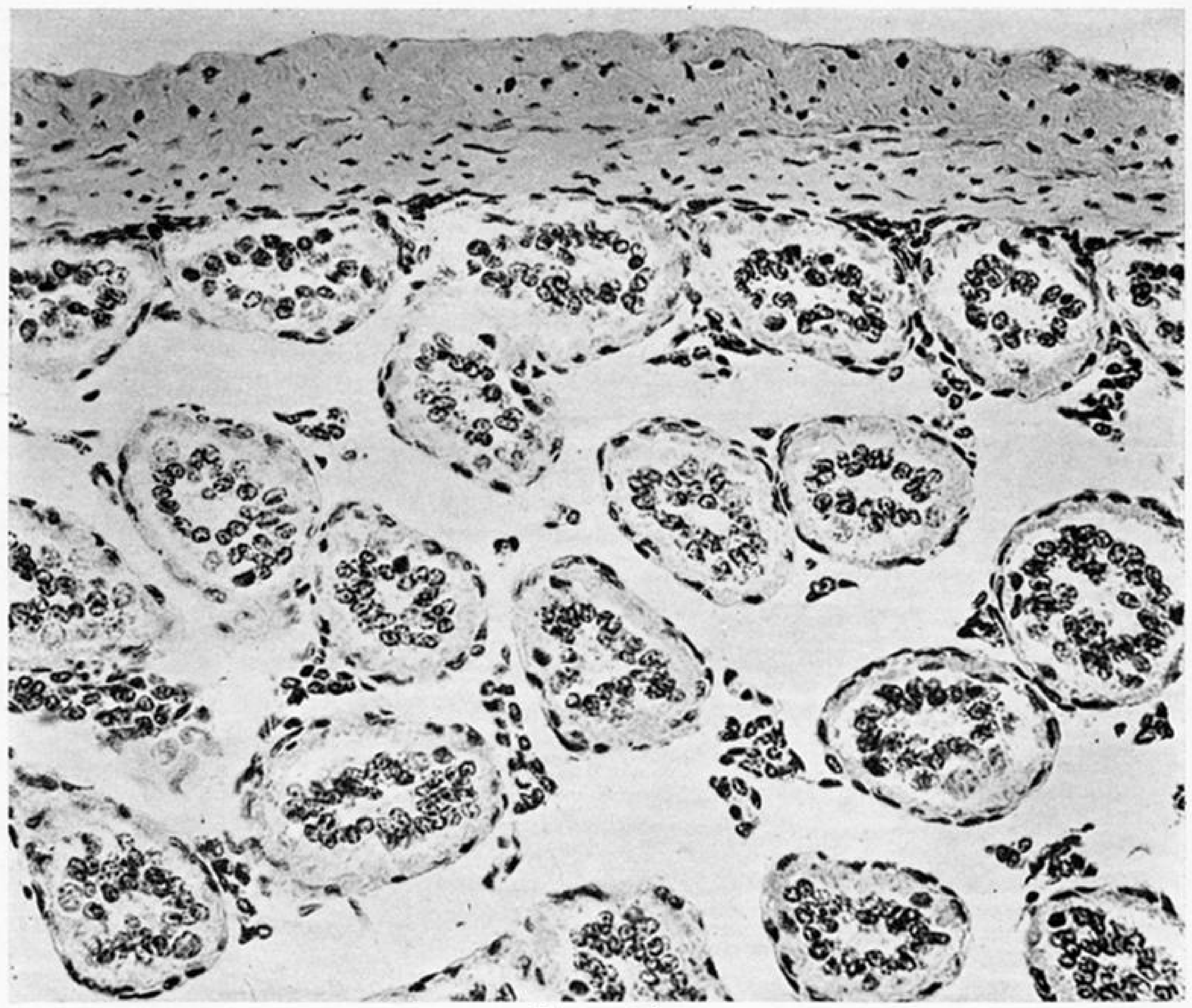

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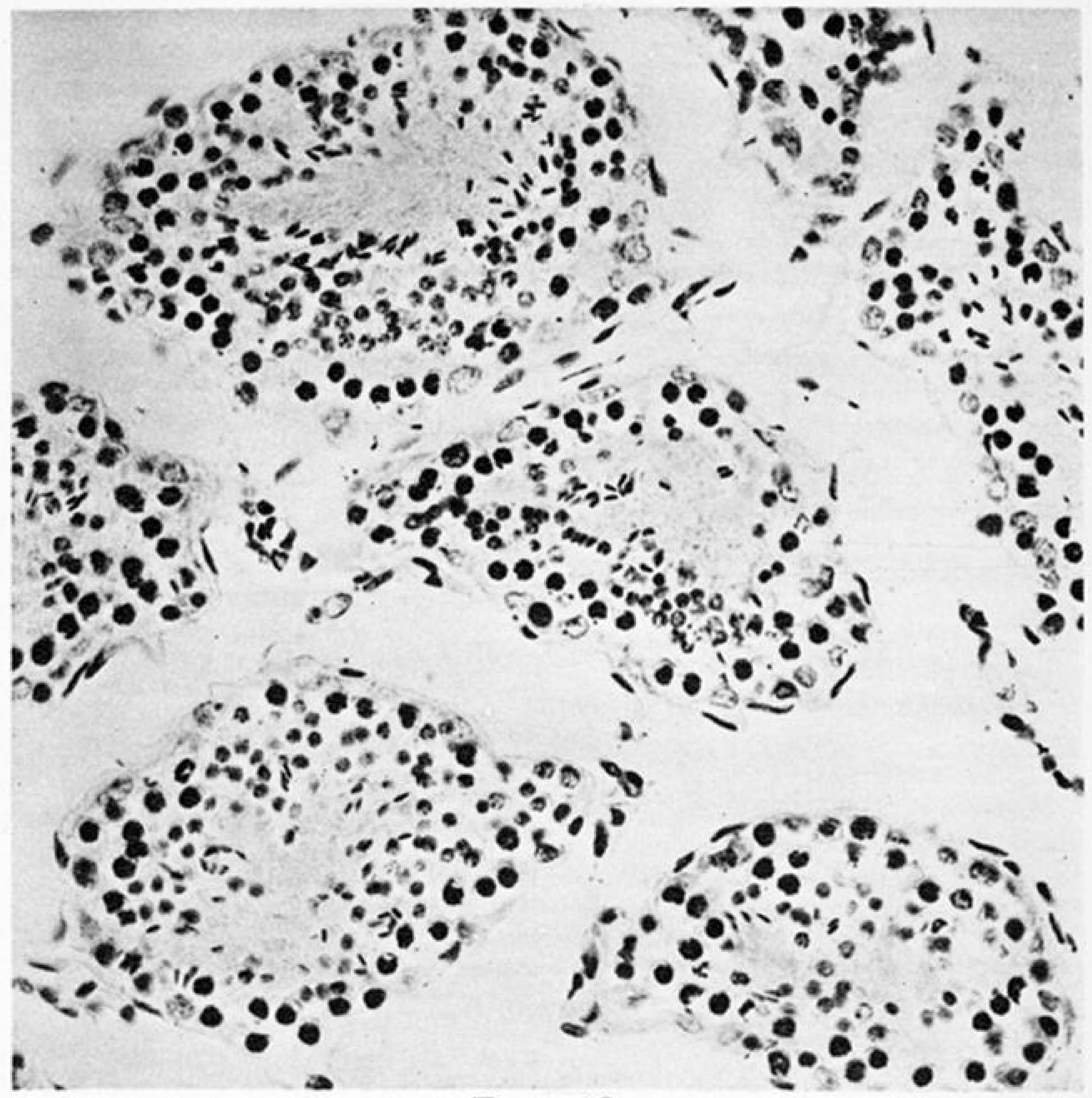

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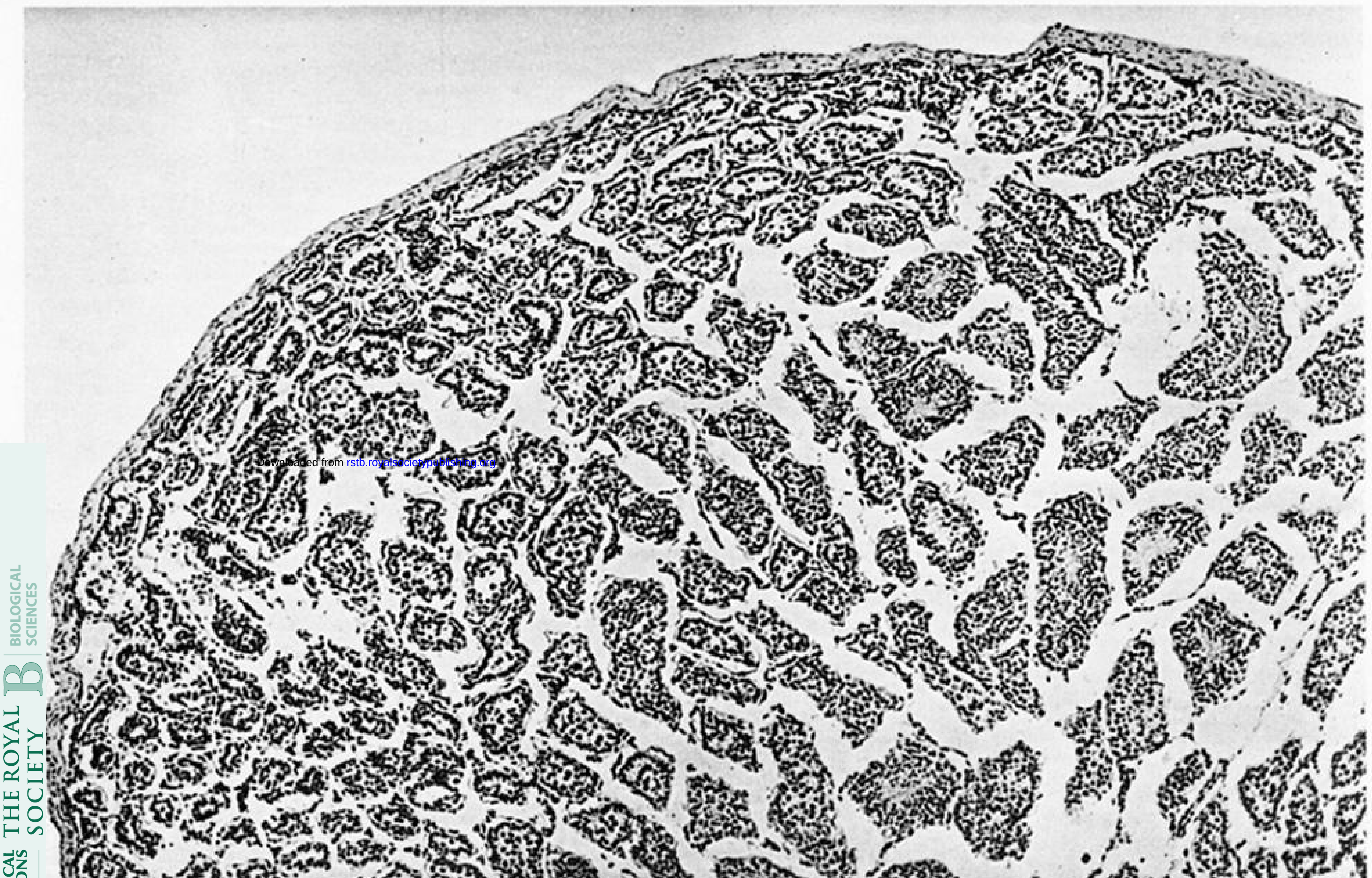

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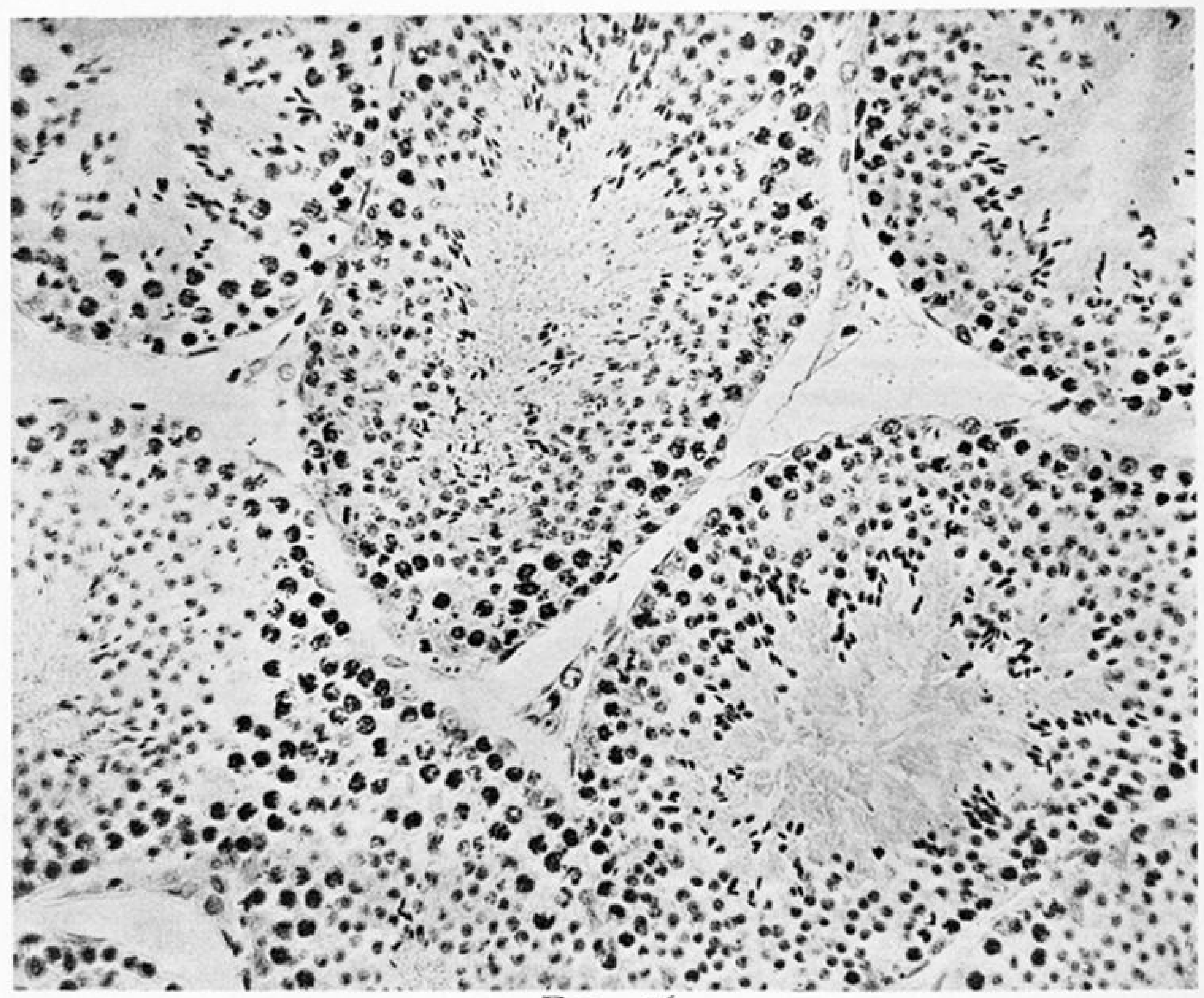

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