VII. *The Reproductive Processes of Certain Mammals.* VII.—*Seasonal variation in the Reproductive Organs of the Male Hedgehog.*

By MARJORIE ALLANSON, *Department of Zoology, King's College, London.*

(*Communicated by* A. S. PARKES, *F.R.S.*)

(Received September 26, 1933—Read February 15, 1934.)

[PLATES 34-37.]

CONTENTS.

		Page.
I.	Introduction	278
II.	Material and technique	278
	(*a*) Source of material	278
	(*b*) Methods	279
	(*c*) Histological treatment	279
	(*d*) Measurement of tissues	279
III.	General morphology of the reproductive organs	280
IV.	Breeding season	280
V.	Seasonal variation in the testis	282
	(*a*) Gross size	282
	(*b*) Spermatogenesis	283
	(*c*) Diameter of the seminiferous tubules	284
	(*d*) Interstitial tissue	286
VI.	Seasonal variation in the accessory organs	287
	(*a*) Epididymis	287
	(*b*) Vas deferens	288
	(*c*) Seminal vesicles	289
	(*d*) Prostate glands	291
	(*e*) Cowper's glands	291
	(*f*) Penis	291
VII.	Correlation between the testis and accessory organs	291
	(*a*) Correlation with testis weight	291
	(*b*) Correlation with interstitial tissue	293
VIII.	Discussion	294
	(*a*) Age of puberty	294
	(*b*) Initial infertility of the hedgehog	295
	(*c*) Comparison with ferret	295
	(*d*) Effect of captivity	296
	(*e*) Use of accessory organs	296
IX.	Summary	296
	References	297
	Description of Plates	298
	Appendix	299

The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to
Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character.
www.jstor.org

I. *Introduction.*

The seasonal changes in the genital tract of the male hedgehog, notably the enormous hypertrophy of the accessory sexual glands in the spring and summer, early attracted the attention of biologists. The first important account of the reproductive cycle was given by MARSHALL (1911) who described the histological condition of the testis at different seasons and found that the production of spermatozoa commenced as early as January and continued to the end of September. The summer and winter appearance of the prostate and Cowper's glands was described by GRIFFITHS (1890), and in 1926 PELLEGRINI published observations on the secretory cycle in the interstitial cells of the testis. COURRIER (1927) studied the cyclic changes in the various organs and gave a full bibliography of work on the male hedgehog.

Animals with restricted reproductive activity have already proved valuable for experimental research (HILL and PARKES, 1932; BISSONNETTE, 1932), and earlier workers recognized the suitability of the hedgehog in this connection. MARSHALL (1911), by castrating hedgehogs at various phases of the reproductive cycle, showed that the periodic hypertrophy and continued activity of the accessory glands was controlled by the testes, and COURRIER extended and confirmed his findings. The hedgehog should prove useful in a wide range of experimental work, for, besides possessing remarkable accessory glands, it is probably the only mammal with abdominal testes that can be easily obtained in England and kept in captivity. Although the general nature of the reproductive cycle has been described, previous authors have been content to examine a few animals only, and it was therefore thought desirable to examine a series sufficiently large to provide an adequate quantitative basis for experimental work. In addition, the large number of immature animals obtained supplied information on the rate of development of the genital tract before the first breeding season.

II. *Material and Technique.*

(*a*) *Source of Material.*—The material consists of the males of the hedgehog collection described in Part VI. This account of the cycle is based on 135 males (see Appendix I) killed and dissected immediately after, or within a few days of, trapping, and therefore deals with the animal in the wild state. Several animals were kept in the laboratory or in an outdoor enclosure for periods up to ten months, but these became sexually active at least two months before animals from the field, and they are not included in this account.

Much of the material was received from Bangor already dissected and fixed, but it was generally possible to judge from the body weight and the condition of the accessory organs if the animals had been definitely immature. Animals dissected in London were more easily classified owing to the skull and teeth being available. The term "immature" in this paper is used for animals not yet sexually active for the first time. During the autumn and winter there is no difficulty in distinguishing such young first-year animals from the anœstrous adults, but with the onset of the breeding season the separation becomes increasingly difficult. Many of the animals approaching full sexual activity in April and May and classified as adults are probably just at the end of their first year. 31 animals collected from July to May were distinguished as definitely immature.

The distribution of the material throughout the year is uneven, but this was unavoidable owing to the greater difficulty of obtaining animals during the winter months.

(*b*) *Methods*.—Animals received alive from the field were killed with chloroform, and the genital tract was dissected out and fixed entire within twenty minutes. A few animals were obtained several hours *post mortem*, and were used for macroscopic examination only. Date, district, body weight and appearance of the accessory glands were recorded. Care was taken during dissection to avoid expulsion of the liquid secretion of the accessory glands, and the ducts of Cowper's glands were ligatured, but some loss of fluid in handling was often unavoidable. After fixation and transference to 70% alcohol, the organs were cleaned of fat and connective tissue, drained and weighed on a chemical balance. A constant degree of dissection was possible for all organs except the penis, which presented considerable difficulty. The weights of penes can be considered comparable only to within about 0·5 gm. The results are shown in Appendix I. For paired organs the combined weights of the two are given. In many animals a fragment of testis was subjected to different fixation and only one testis was weighed. Since no significant difference was noted in the size of right and left testes, the weight of the intact one was doubled in these instances.

(*c*) *Histological Treatment*.—Bouin's picro-formol-acetic fluid was used as a routine fixative. Sections of the testis were cut at 7μ, and of the epididymis and vas deferens at 10μ. Representative vasa deferentia were sectioned serially at 15μ. Histological examination was confined to animals with well-fixed organs, and a further selection was made of the April and May animals to avoid sectioning large numbers of the same type. Seminal vesicles, prostate, and Cowper's glands from certain anœstrous and breeding animals were examined, but no attempt was made to obtain a complete histological series of these glands. The Bouin-fixed material was stained in Ehrlich's or Mayer's hæmatoxylin and counterstained with eosin.

From several animals in each phase of the cycle, a fragment of testis was fixed in Flemming's strong fluid. Sections were cut at 5μ and mounted unstained in Farrant's glycerine medium for study of the fat content of the seminiferous tubules and interstitial cells.

(*d*) *Measurement of Tissues*.—Measurements were made of the diameters of seminiferous tubules and epididymis tube, with the aid of a Leitz projector, at a magnification of either 95 or 175; the figures given for each animal (see Appendix I) are the average of measurements of ten tubules. Interstitial cells were drawn by means of a camera lucida at a magnification of 1,500.

Testis tubules were measured at the periphery of approximately median transverse sections, since shrinkage of the tubules often occurs in the centre of a large testis. Measurements of the epididymis tube were all taken in the body region and the diameters given include the surrounding muscle layers.

III. *General Morphology of the Reproductive Organs.*

DISSELHORST (1904) gives a full account of the reproductive tract of the male hedgehog. Many workers have described the comparative anatomy of the accessory glands and controversy has occurred over their homologies and nomenclature. This account is concerned only with seasonal changes in these glands and no attempt has been made to examine the contentions of the various authors. The terms current in comparative anatomy, seminal vesicles, prostate and Cowper's glands, have therefore been used.

The genital apparatus of the male during rut is enormous in relation to the body size. Fig. 15, Plate 34, shows a photograph of the tract during the breeding season. The testes are abdominal throughout life, lying on each side of the bladder just beneath the body wall to which they are attached by the gubernaculum. Two many-lobed seminal vesicles lie dorsal to the bladder, the lobes being supported by connective tissue. Separate ducts run from each of the lobes and become invested in a common sheath. These multiple ducts from the two seminal vesicles disappear into the muscular wall of the urethra immediately behind the neck of the bladder. Right and left prostate glands lie ventral to the bladder, and a duct from each runs back within the urethral muscles. Two large Cowper's glands lie outside the pelvis, behind the ischia and embedded in the fascia of the thigh. Long ducts run from them to the urethral bulb.

The vasa deferentia, seminal vesicle ducts, and prostate ducts do not open into the urethra before the region of the bulb but run alongside the urethral tube within the thick coat of urethral muscle. The ducts from Cowper's glands enter the urethra by a common opening a short distance below (fig. 1). Embedded in the muscle in the region of the bulb, and only discernible in sections, are two masses of glandular tissue with several ducts leading to the urethra, which MARSHALL called the Cowper's glands, fig. 29, Plate 37. Glands in a comparable situation are found in the female.

IV. *Breeding Season.*

The first litters are born in June (see Part VI, DEANESLY, p. 239), so that young males begin to appear in field material about the end of July. Second litters may be born later in the year, and these, together with delayed first litters, provide a continuous supply of young throughout the late summer and the autumn. Although no pregnant female was taken in September, it is probable that litters are born in this month, and young males of 250 gm. body weight and under may be found until the end of the year.

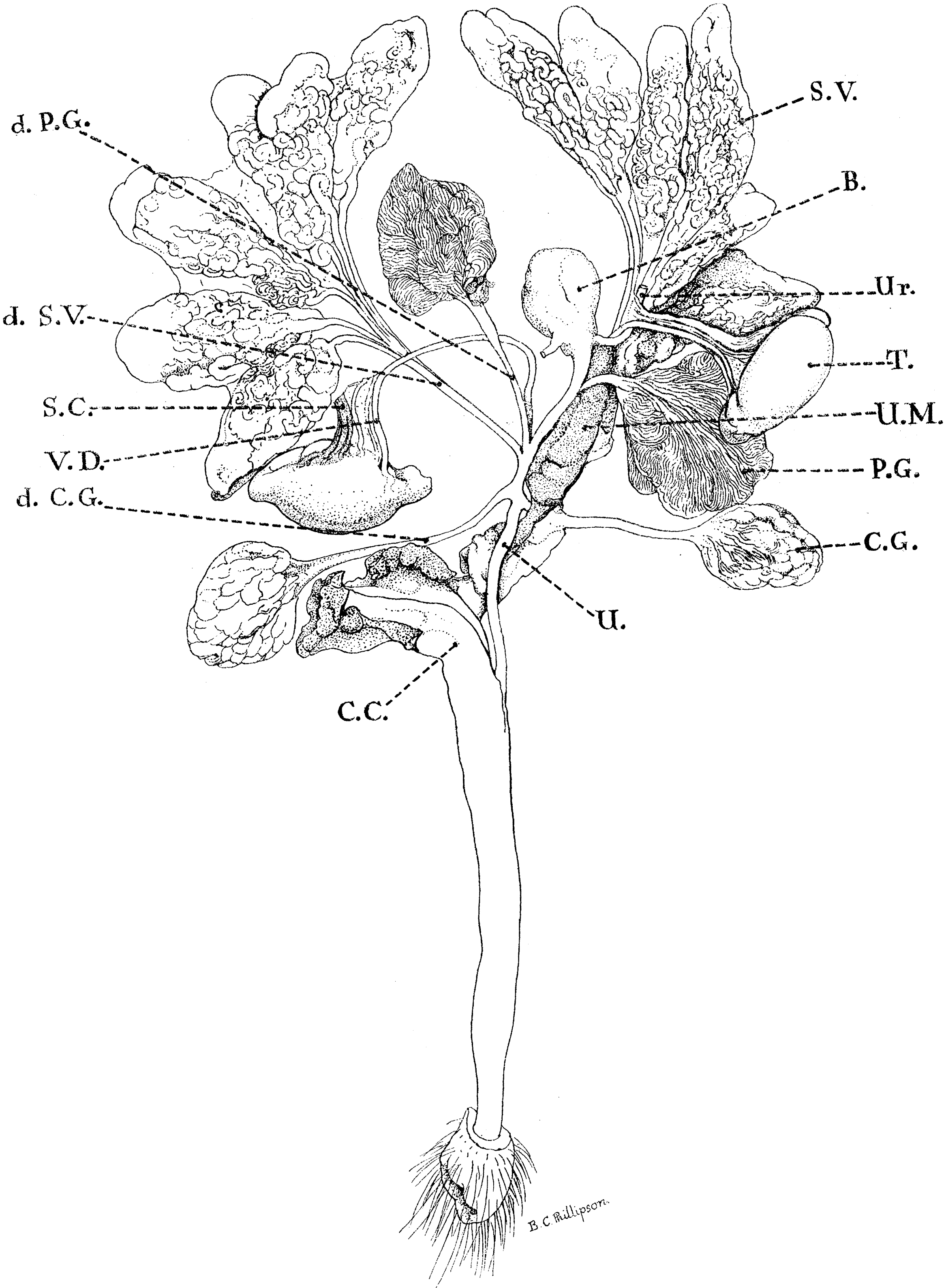

FIG. 1.—Dissection of genital tract of adult male hedgehog killed in July. The urethral muscle has been removed on one side, and the vas deferens and ducts from the seminal vesicle, prostate and Cowper's glands displayed. The corpus cavernosum has been freed from the proximal end of the penis and turned to the side.

B., bladder; *C.C.*, corpus cavernosum; *C.G.*, Cowper's gland; *d.C.G.*, duct of Cowper's gland; *d.P.G.*, duct of prostate gland; *d.S.V.*, duct of seminal vesicle; *S.C.*, spermatic cord; *S.V.*, seminal vesicle; *T.*, testis; *U.*, urethra; *U.M.*, urethral muscle; *Ur.*, ureter; *V.D.*, vas deferens.

The weight of the adult male may reach a little over 1,000 gm., but the majority of animals caught weighed between 500 and 700 gm. There is no constant seasonal variation in body weight; heavy animals, *i.e.*, above 700 gm., were obtained in all seasons. Body weight distinguishes the small half-grown animals from the adults during the summer months, but is not always significant in the remaining seasons owing to the variable condition of the animals.

V. *Seasonal Variation in the Testis.*

(*a*) *Gross Size.*—Differences in the general condition of animals caught in the field, fluctuations in body weight as a result of periods of hibernation, and absence of a regular relation between testis and body weight in immature animals, make it undesirable to express the testis weight as a percentage of the total weight. In fig. 2 the weight

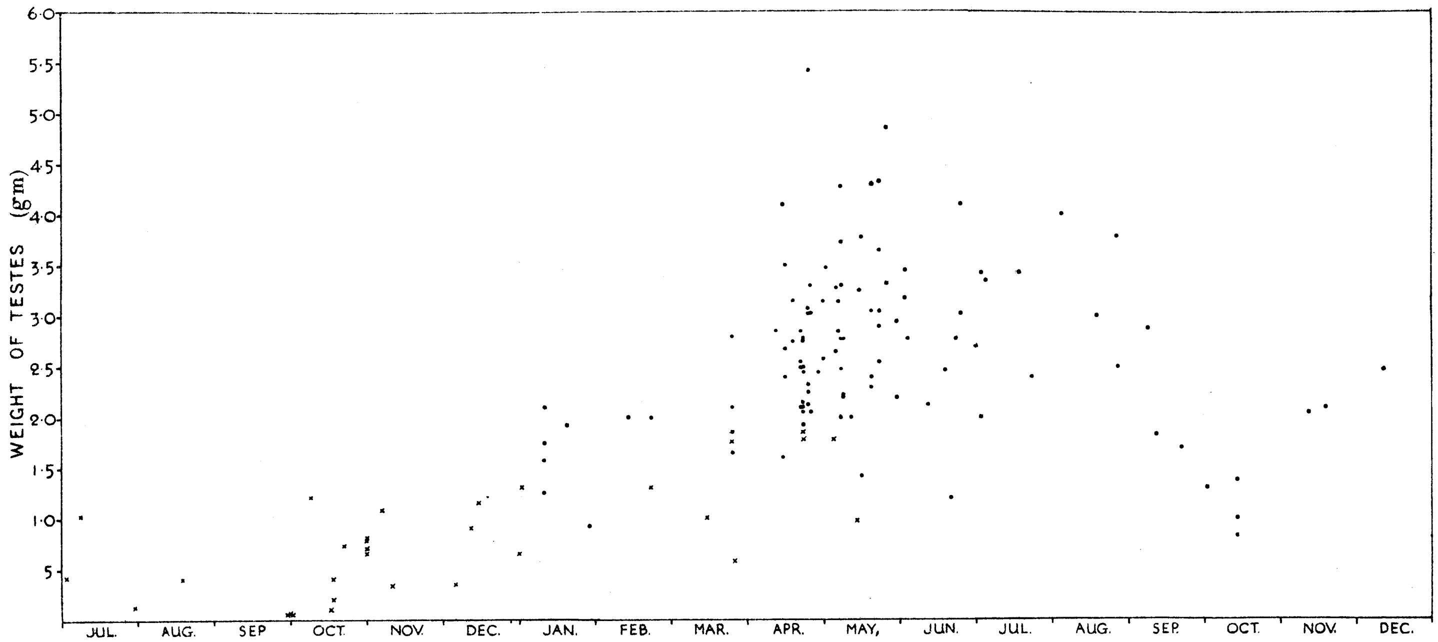

FIG. 2.—Seasonal variation in weight of testes. • Adult animal. × Immature animal.

of the two testes is plotted throughout the year. From October to February the weight is between 0·9 gm. and 2·5 gm. In March one animal had testes of 2·83 gm., but the other animals showed no change from the winter condition. In the latter half of April the testes of 60% of the adults weighed 2·5 gm. or over; in May the number over 2·5 gm. had risen to 75%. Testis weight remains high throughout June, July and August, falling below 2·5 gm. in only four of the nineteen animals caught. In September a decrease is evident.

The weight of the testis cannot be taken as an index of its activity, except within wide limits, since in November and December inactive testes of 2·0–2·5 gm. occur, while in the breeding season testes of 1·5–2·0 may be in full activity. It seems certain, therefore, that the testes of individual animals do not show such marked seasonal variation in weight as has been observed in some mammals, *cf.* figs. 15 and 16, Plate 34. The extreme limit of variation, as shown by our material, would be an increase during the breeding season of about five times, but it is more likely that in animals that have experienced a breeding season the testes do not usually fall much below 2 gm., so that the increase during the breeding season may be only about 200%. Other male mammals with seasonal activity show more striking weight changes, *e.g.*, the ferret, in which the active testis reaches over ten times its anœstrous weight (ALLANSON, 1932), and the mole, where the increase may be as much as five times.

In the diagram, immature animals in the period July-December have been separated from the adults. The testes in males born early in the season have reached 1 gm. in July; those born later have reached this weight in October and increase gradually, to merge with the adults in March and April. The second litter males have testes of under 0·5 gm. until December and probably do not approximate to the adult condition until May or June. The rate of development obviously differs greatly in individual animals, and a large number with light testes in April and May are probably in their first breeding season although, since their accessory glands were well developed, they could not definitely be classed as first-year animals.

(*b*) *Spermatogenesis.*—From the beginning of April to the end of August the testes of all animals examined, except two (hedgehogs 204 and 219) were in full spermatogenesis. Hedgehog 204, killed in May, had recently been fertile. The seminiferous tubules were large, and although the germinal epithelium contained no stages later than primary spermatocytes, the testes were heavy and the epididymis was crowded with spermatozoa. Hedgehog 219, killed in June, had not previously been in spermatogenesis that season, and was probably born late in the preceding year. In September, the production of spermatozoa slows down and rapid retrogression sets in. The seminiferous tubules vary in an individual testis: spermatozoa are present in some, while others contain no stage later than primary spermatocytes. The lumen of the seminiferous tubules in September and October often contain loose masses of degenerating cells. In October, November and December the seminiferous tubules are in their most quiescent state and contain spermatogonia, Sertoli nuclei and primary spermatocytes, figs. 18 and 20, Plate 35. Active production of spermatogonia and spermatocytes is continuing throughout these months, so that the majority of tubules in a testis contains two or three rows of cells, and a lumen is nearly always apparent. There is evidence that many of these spermatocytes are eventually destroyed, since from December to February the tubules are often filled with loose spermatocytes clumped together in degenerating masses, and in March spermatocytes appear in the tube of the epididymis. From January to the end of March the seminiferous tubules are more active. In this phase, as in regression, there is much individual variation: testes producing spermatids and occasional spermatozoa are found in January (hedgehog 250), though spermatids may still be absent in March.

The testes of immature animals from July to December show all stages, from a completely inactive condition where the seminiferous tubules are lined with one row of cells consisting of Sertoli nuclei and an occasional spermatogonium, to a condition resembling that of the anœstrous testes of the adult. Many of the first-litter young have reached the stage typical of the anœstrous adult in October, and their further development is retarded until the following spring. In the winter months it is sometimes possible to distinguish the immature testis from that of the adult by the smaller number of spermatocytes and the absence of a lumen in the tubule, but as the spring approaches this distinction is no longer apparent.

(*c*) *Diameter of the Seminiferous Tubules.*—The size of the seminiferous tubules varies with the degree of activity of the germinal epithelium, so that the seasonal fluctuations can be represented graphically. In fig. 3 the mean tubule diameter is plotted throughout the year.

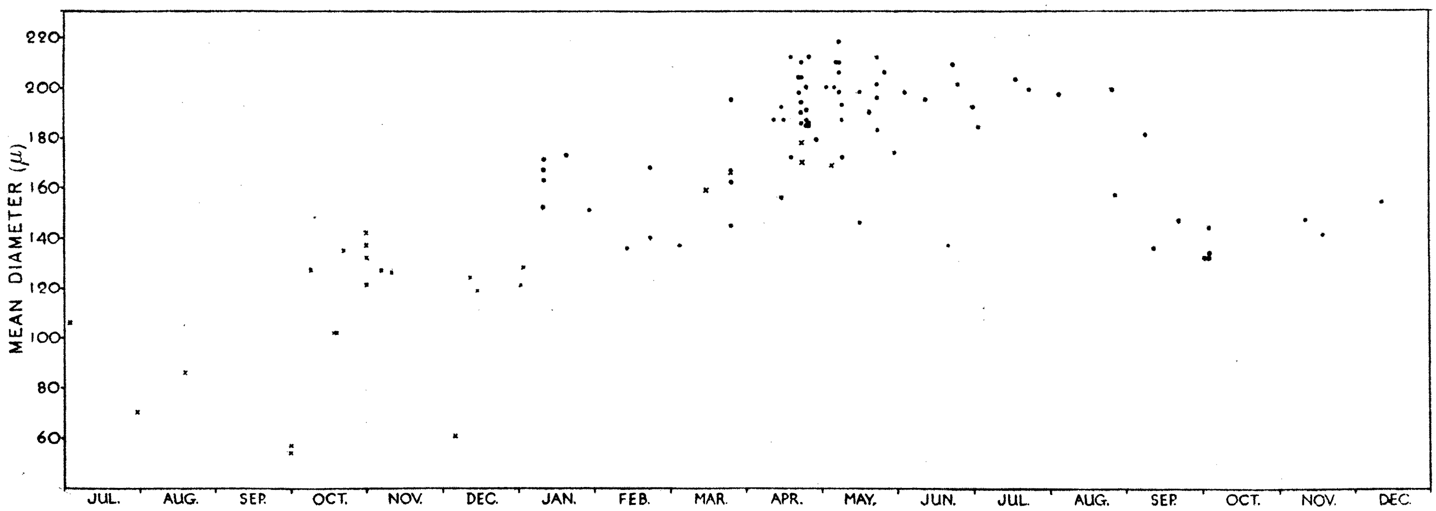

FIG. 3.—Seasonal variation in diameter of seminiferous tubules.

The diameter of the testis tubules of the early-born young approximates to that found in anœstrous adults in October, and falls little behind in the spring growth period. In later young the diameter is still low in December, and the seminiferous tubules would probably not overtake those of the adults until late in May or June, thus accounting for the low figures found in these months. In the adult, the tubules are at their maximum size from April to early August, measuring 190–210 μ, fig. 19, Plate 35. In late August and September they decrease rapidly to a diameter of 130–150 μ, and remain within these limits throughout October and November. From December to the end of March there is a gradual increase, and by April the breeding season condition is reached in most animals. Testes with smaller tubules occur throughout April, May and June, showing that there is much individual variation in the attainment of full breeding activity.

Consideration of the relation between the diameter of the testis tubule and the weight of the testis is complicated by the fact that the material, taken as a whole, includes three groups :—

(*a*) Immature animals developing for their first breeding season.

(*b*) Adult animals recovering from anœstrus for another breeding season.

(*c*) Animals declining into anœstrus.

As pointed out above, the first two of these groups cannot be distinguished as the breeding season approaches, but in plotting the diameter of testis tubule against testis weight, group (*c*) above has been segregated roughly by considering adults in June–

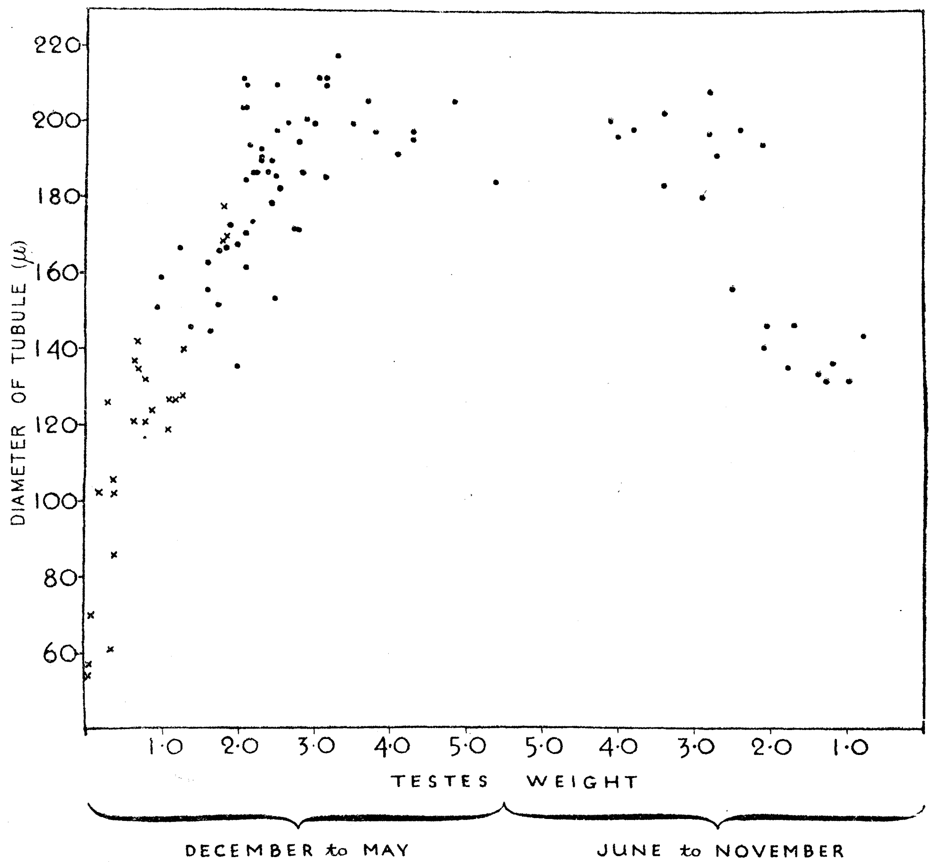

FIG. 4.—Weight of testis and diameter of seminiferous tubule.

November separately. For graphical purposes this latter material is arranged in descending order of testis weight, while the remaining animals, immature and adults approaching œstrus are arranged in ascending order. In fig. 4, diameter of testis tubule is plotted against testis weight in this manner. It is evident that the tubules increase rapidly in diameter from about 140μ to 170μ as the testis increases from 1 gm. to 2 gm. If the ratio of tubular to intertubular tissue remains the same during this period, some increase in tubule length is obviously indicated. The maximum tubule size may be found in 2 gm., and is always found in 3 gm. testes. With increase of testis weight up to 5 gm. there is no corresponding increase in tubule size, so that the further growth of the organ must be due to lengthening of the seminiferous tubules (as found by ROWLANDS and BRAMBELL, 1933, in the mouse, and ALLANSON, 1933, in the grey squirrel), or to increase in the intertubular elements. The decrease in diameter of the tubules after the breeding season (from 200μ to 140μ) would represent a volume decrease to one-half if the tubule length remained unaltered, or to one-third if the length decreased equally. The available data show a decrease in testis weight during anœstrus to between one-half and one-third, but are not adequate to show how far the change could be accounted for by tubule diameter decrease only.

In the ferret, where the testes undergo greater annual size fluctuations and the anœstrous testis is more completely quiescent, the tubules show greater seasonal size changes (80μ to 150–190μ), and tubule size is correlated more obviously with testis weight.

(*d*) *Interstitial Tissue.*—PELLEGRINI (1926) and COURRIER (1927) have described the interstitial tissue in the winter and summer testis of the hedgehog, and have noted that the volume of the interstitial cells is greatest in the breeding season and least in anœstrus. Study of a larger number of stages shows that in the interstitial tissue development starts later and is more rapid than in the seminiferous tubules. The area of the interstitial cells is greatest in April, May and June, when it may be as much as 250–260 sq. μ, and is seldom less than 200 sq. μ, fig. 21, Plate 35. During July and August the area is decreasing, although spermatogenesis is still in progress, and by early October it is 100 sq. μ or less, fig. 22, Plate 35. There is gradual growth of the cells from January to March to an area of 120–140 sq. μ, but in the first weeks of April a more rapid growth occurs, so that the maximum size was found in animals killed on 15th April (hedgehogs 38, 251, etc.). In fig. 5 the mean area is plotted throughout the year; the cycle roughly corresponds with that shown by testis weight.

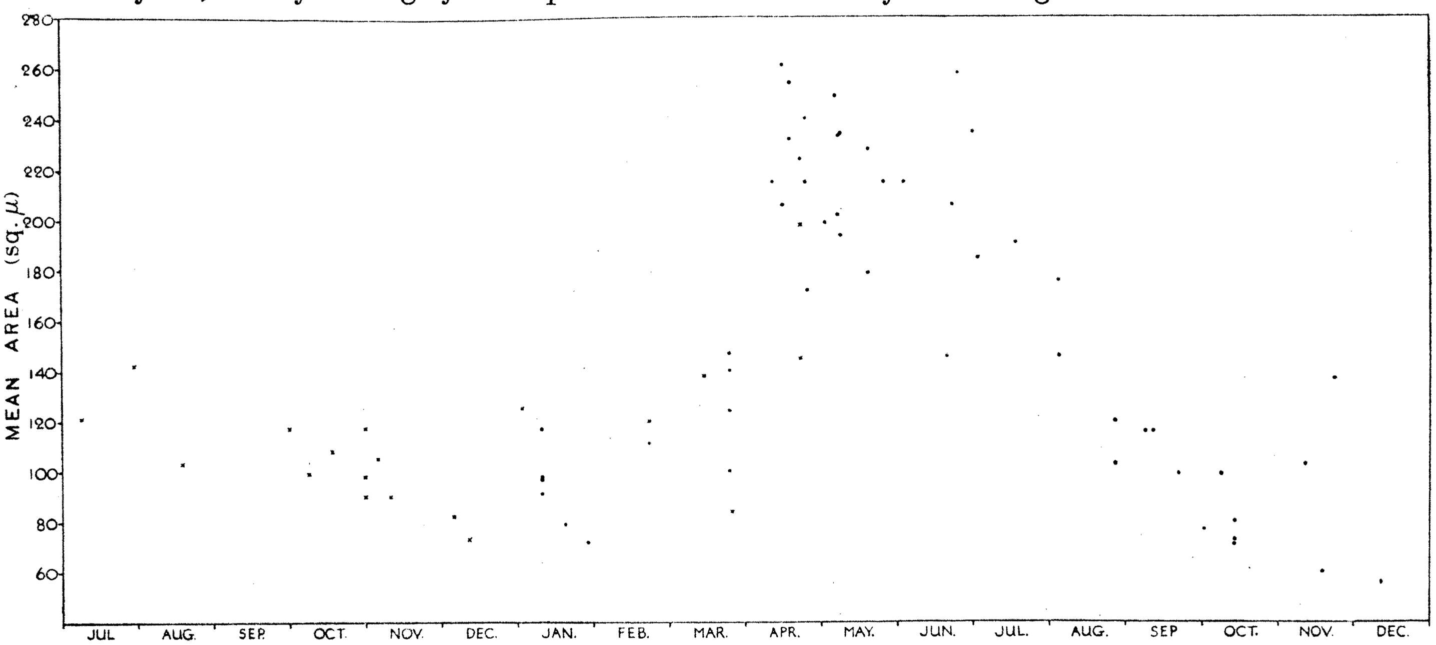

FIG. 5.—Seasonal variation in size of interstitial cells.

In immature animals, the size of these cells is little different in first and second-litter animals for a certain period of development. In October and November, when there are considerable differences in body weight, testis weight, etc., the interstitial cells measure 90–110 sq. μ in an animal of 110 gm. body weight (hedgehog **174**) and also in one of body weight 600 gm. (hedgehog 227). Often the interstitial cells are larger than those of anœstrous adults, *e.g.*, in December and January. Interstitial cell size, therefore, is not correlated closely with the size of the testis during initial growth.

Fat content.—PELLEGRINI and COURRIER studied the fat content of the cells at the different phases of the cycle, but further observations are recorded here for comparison with other species showing periodic activity. Fine fat granules can be found in the cytoplasm at all stages. From January to May there are in addition larger droplets, and sometimes coarse masses. In June large numbers of the cells are heavily charged with fat, and fat accumulation in decreasing amounts is found until October. The presence of these fat masses is, however, not so constant a feature of the summer and autumn testes as it is in the ferret.

Fat appears in the immature testes of about 1 gm. and is similar in quantity and distribution to that found in the anœstrous testes.

Pigment.—Pigment was entirely absent from the interstitial cells at all phases of the cycle.

VI. *Seasonal Variation in the Accessory Organs.*

(*a*) *Epididymis.*—There is a close correlation between the size and activity of the testis and that of the epididymis, so that the seasonal variation is very similar in the two organs, fig. 6. The two epididymides weigh between 0·3 and 0·5 gm. from October to late March. In early April the majority are between 0·5 and 0·65 gm., and later in the month are 0·75 gm. and over. The weight remains high until the end of August

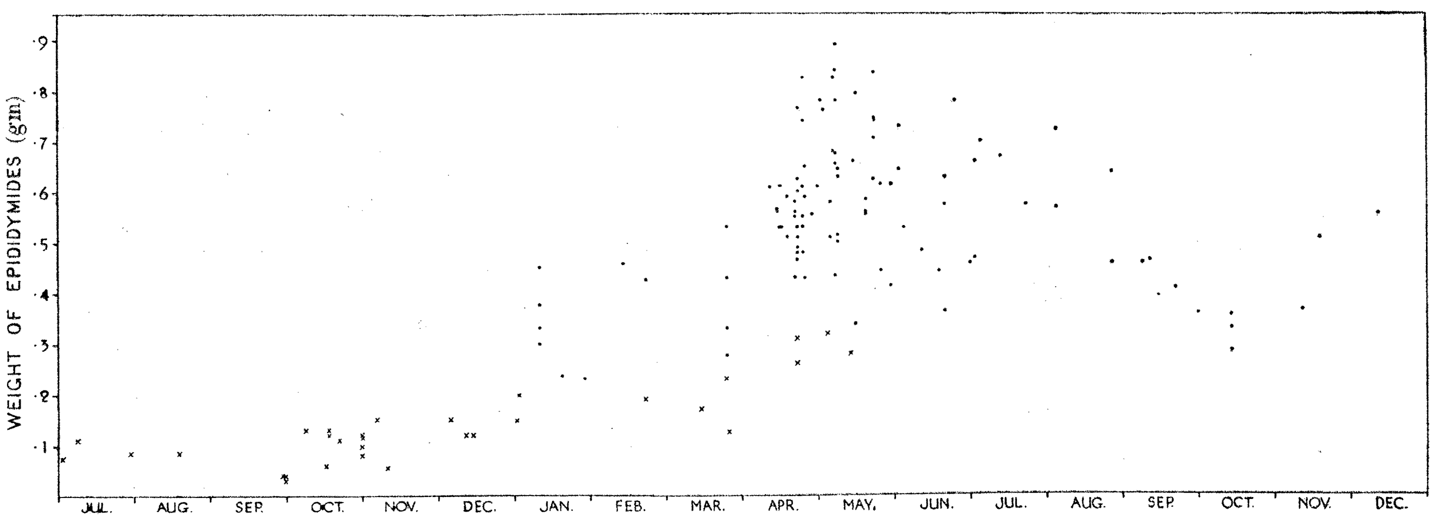

FIG. 6.—Seasonal variation in weight of epididymides.

and then falls gradually to 0·3–0·4 gm. in October. Spermatozoa do not appear in the epididymal tube until after the middle of April, and later persist in the tube for 2–3 weeks after spermatogenesis has stopped (see Appendix I).

The development of the epididymis of the immature animals is slower than that of the testis, since they are still well below adult weight in April and May of the year following their birth.

The diameter of the epididymis tube, including the surrounding muscle layers, is 180–220 μ from May to August, fig. 7. In September there is a gradual shrinkage, and from October to the end of the year the tube remains between 120 and 140 μ. In January growth for the next breeding season commences, so that by the end of March the tube may measure 160 μ. It continues to enlarge throughout April. As in the seminiferous tubules, growth from the winter to the breeding condition lasts over five months, while regression is rapid and takes place in about a month.

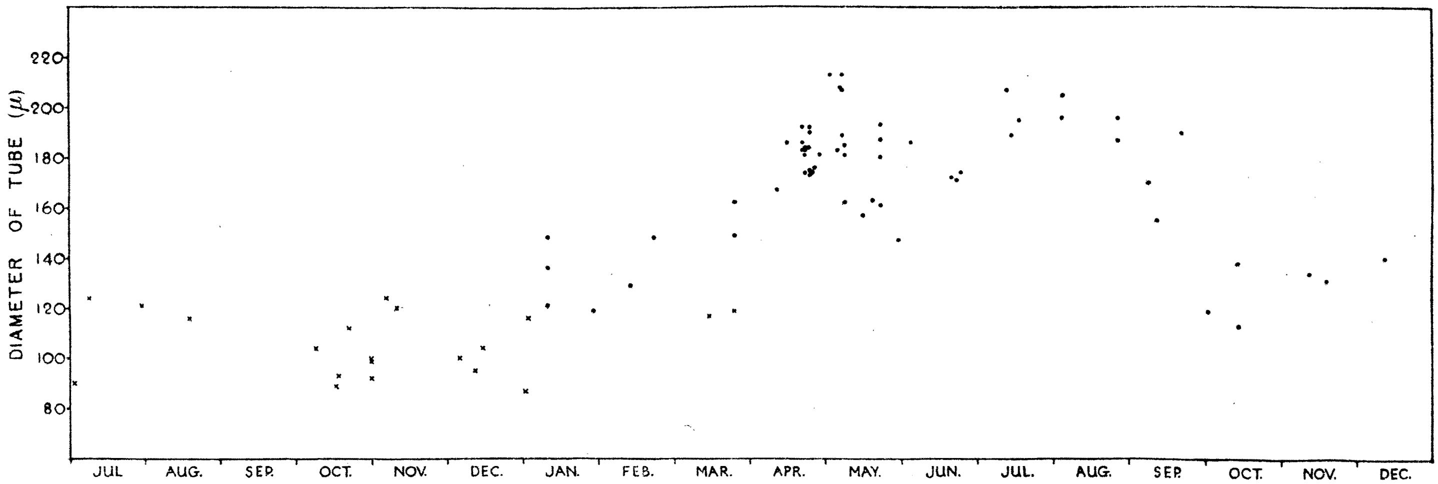

FIG. 7.—Seasonal variation in diameter of epididymal tube.

The epididymal tube in the early young is about 120 μ in diameter from July to December, while in the later animals it is 90–100 μ and reaches 120 μ in March.

In the winter condition of the epididymal tube the surrounding muscle layer measures 15–17 μ in thickness. As the tube enlarges, the muscle layers are stretched so that in the breeding season they are only 8–9 μ thick. The epithelium lining the tube increases in height at the onset of the breeding season and measures 45–50 μ from April to August. In the inactive condition, November to March, it sinks to 30–35 μ. The non-vibratile threads of the epithelial cells do not show in the hedgehog the striking involution that they undergo in the ferret. They remain at much the same state of development in anœstrus as in the breeding season.

(*b*) *Vas Deferens*.—Sections of the vas deferens, from approximately the middle of its length, were studied and measured to find whether the muscular coats increased in thickness during the breeding season. Two diameters were taken at right angles to each other in several sections, and the mean diameter calculated. This was found to range from 500–600μ in the anœstrous condition to 900–1000μ in rut, but a variation of about 200μ occurred for individual animals at each season. Several vasa deferentia were therefore sectioned serially, and measurements taken at intervals throughout the length. It was then obvious that the mean diameter of the tube gradually increases from the epididymal to the urethral end: figures for typical animals in anœstrus and in the breeding season are as follows:—

	October.	May.
	μ	μ
Epididymal end to urethral end	485	741
	561	865
	665	969
	774	1074
	793	1121

The figures obtained by the first method were therefore discarded because random selection of a region to be measured could lead to large errors.

Since the difference between the winter and summer diameter of the tube is comparatively small, it is possible that the amount of muscular tissue does not increase during the breeding season, and the greater width of the layer may be due to increased vascularity. By contrast, the diameter of the tube itself and the height of the epithelial lining definitely increases during the breeding season.

Apart from descriptions of the presence or absence of ampullæ on the vas deferens, no reference has been found to gradual increase in diameter along the length of the vasa deferentia of other animals. It is possible that, where the testes are scrotal and the vasa deferentia are consequently longer, the diameter of the tube is more constant.

(*c*) *Seminal Vesicles*.—These glands reach a relatively enormous size in the breeding season, often weighing 20–30 gm. The largest obtained were from animals caught in late April and in May, but heavy specimens occur until August. The presence of large quantities of secretion makes the weights of these organs vary greatly, but most adults from late April to late September possessed seminal vesicles of over 4 gm. From October to March, with one exception, they weighed less than 4 gm. and often less than 2 gm. In fig. 8, the weights are plotted throughout the year, and the rapid rise is shown from the winter condition in March to the fully active condition in April. The size and macroscopical appearance of these glands afford a useful guide in distinguishing the well-grown immatures from the adult animals in the period October–April, when they often resemble the adults in other particulars, figs. 16 and 17, Plate 34. It is possible at the beginning of the breeding season to find animals with active testes in which the seminal vesicles weigh 0·2–0·3 gm. In animals which have experienced a breeding season, the lobes of the seminal vesicles, although they are thin and contain practically no secretion, are still extensive as the result of previous activity. In April and May, however, when the seminal vesicles are developing rapidly in both types, this distinction disappears.

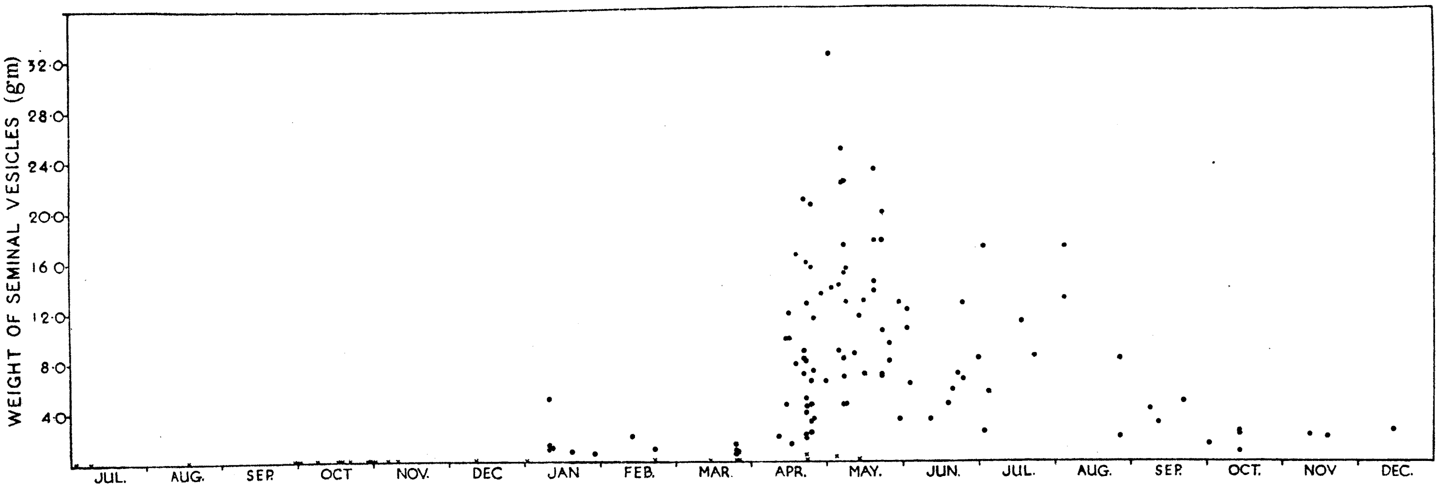

FIG. 8.—Seasonal variation in weight of seminal vesicles.

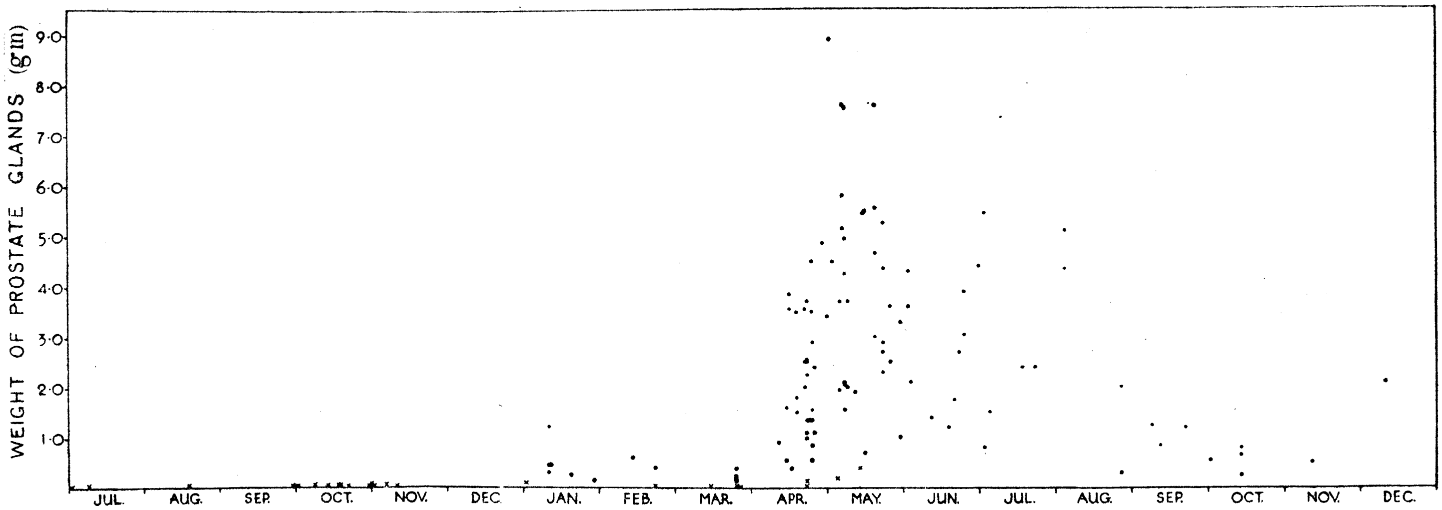

FIG. 9.—Seasonal variation in weight of prostate glands.

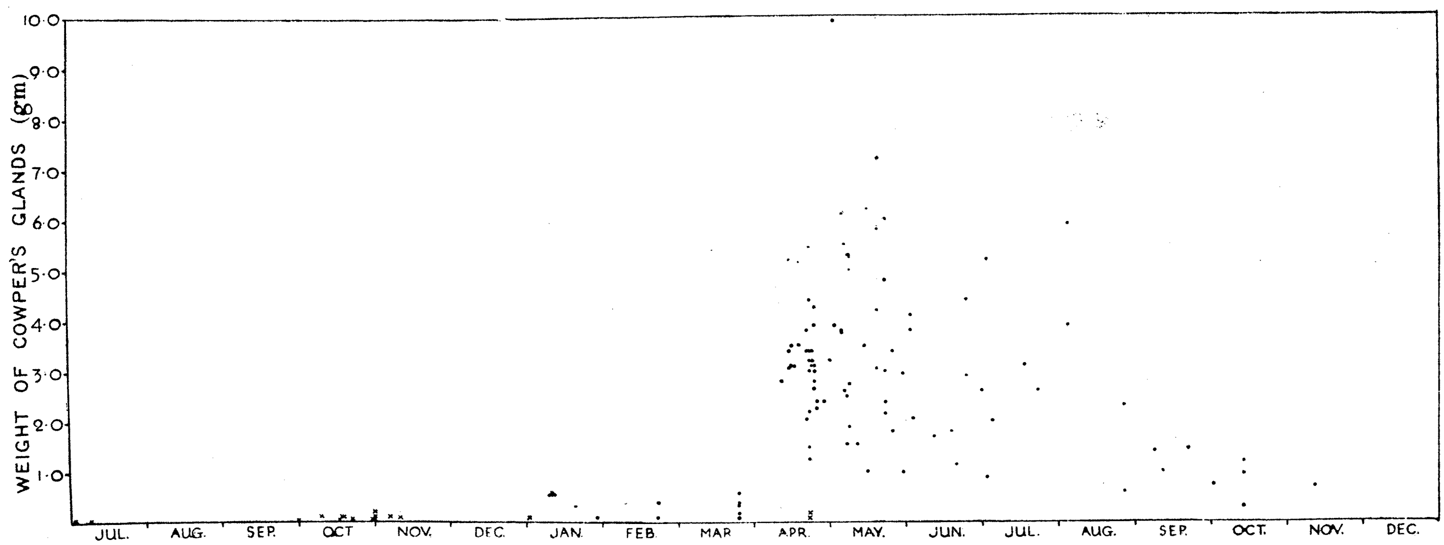

FIG. 10.—Seasonal variation in weight of Cowper's glands.

The histology of the accessory glands has been studied by several earlier workers, and COURRIER has described the seasonal changes in secretory activity. The present study has therefore been confined to size variation in these glands in the adult animals and to their condition in the immatures. Figs. 23 and 24, Plate 36, show the appearance of the gland in quiescence and in full activity. It will be noticed that secretion is not completely absent in the winter gland.

(*d*) *Prostate Glands.*—The seasonal changes in the size of the prostate glands are similar to those of the seminal vesicles, fig. 9, but the annual variation is not so great. Their weight varies from 1–2 gm. in anœstrus to 9 gm. in the breeding season. This maximum was approached by only four animals; in most the prostate glands weighed between 3 and 6 gm. As in the seminal vesicles there is rapid development during the first weeks of April, and more gradual retrogression to quiescence in September. In immature animals the prostates weigh 0·1 gm. or less throughout the winter and early spring.

The quiescent and active appearance of the glands is shown in figs. 25 and 26, Plate 36.

(*e*) *Cowper's Glands.*—The weight of these glands lies between 0·1 gm. and 1 gm. from November to March. In April there is the sudden growth typical of the accessory glands, and from the middle of April to early August most of them weigh 3–6 gm., but some reach 9·0 gm. In immature animals the weight remains below 0·2 gm. until well into April, fig. 10.

Figs. 27 and 28, Plate 37, show the typical histological appearance in quiescence and in activity. The secretion is characterized by the presence of large numbers of pycnotic nuclei from desquamated cells.

(*f*) *Penis.*—There appears to be no marked seasonal fluctuation in the size of the penis. In the adult animal, the penis weighs from 2·5 gm. to over 6 gm., and since heavy penes (4–5 gm.) were found in all months, the weight is apparently more closely correlated with age than with the phases of the reproductive cycle.

The weight of the penis therefore is useful, in conjunction with other criteria, in distinguishing the immatures from the adults in the spring. It weighs 1·0 gm. or less in immatures caught in the autumn, 1·0–1·5 gm. in January, and in March, April and May it reaches 1·8 gm. The occurrence of animals with light penes (2·0–2·5 gm.) in early spring is added evidence that several animals classed as adults are really young males born in the preceding breeding season (see p. 283).

VII. *Correlation between the Testis and the Accessory Organs.*

(*a*) *Correlation with Testis Weight.*—It is obvious, from the diagrams of the seasonal changes in the testes and accessory organs, that in all parts of the reproductive tract, with the exception of the penis, the periods of maximum activity and quiescence roughly correspond. The weight of the accessory organs is therefore correlated with that of the testes, but, owing to the more extended preparation for the breeding season in the testis as compared with the accessory organs, and the more rapid regression, the relation of testis size to accessory organ size differs according to whether preparation for, or regression from, the breeding season is taking place. An attempt has been made to compare the growth rates by separating the "coming-up" animals (December to May) from those which have passed the peak of breeding activity (June to August) and from the obviously regressing animals (September to November). Definitely immature animals have been considered as representing initial growth stages and have been placed with the "coming-up" animals irrespective of the date of trapping. Treated thus there is a close correlation between testes weight and accessory organ weight.

The relation between the weight of the epididymis and the weight of the testis is obviously linear, both in the "coming-up" and the "going down" phase; moreover, the two organs develop proportionately at the same rate, fig. 11. In the accessory glands the state of affairs is rather different, figs. 12-14. Taking progress towards full development as the criterion, the initial growth in the immature animal lags behind that of the testis. When the testes have reached 1 gm. (20% maximum) the

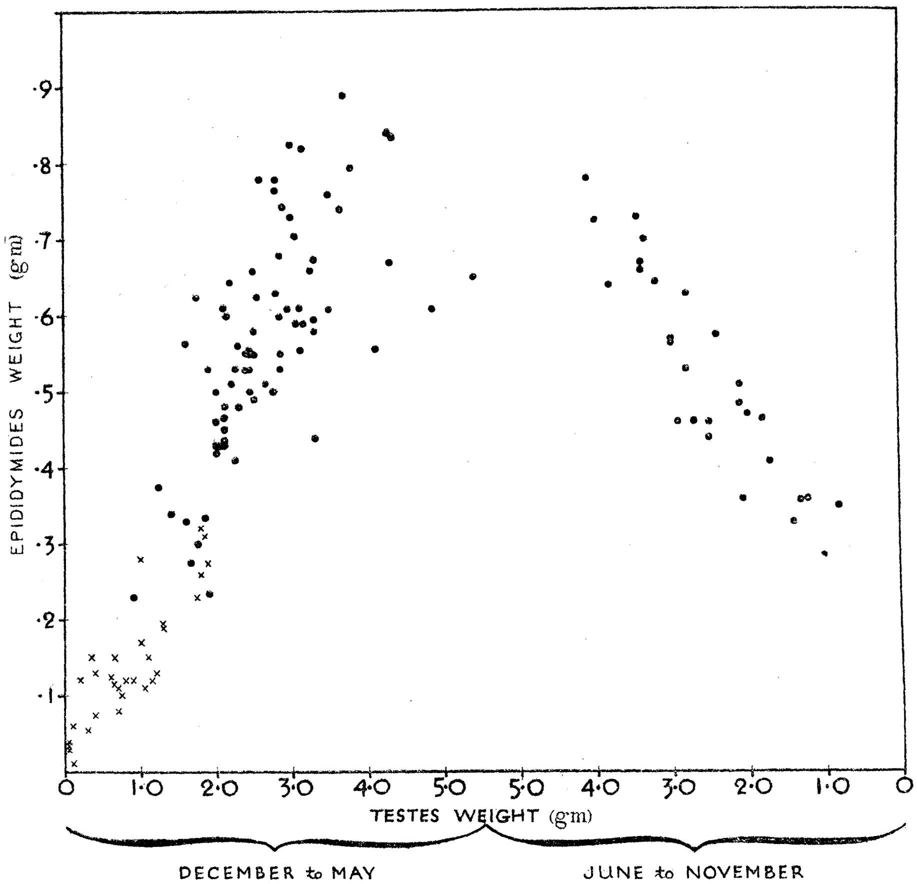

FIG. 11.—Weight of epididymides and weight of testes.

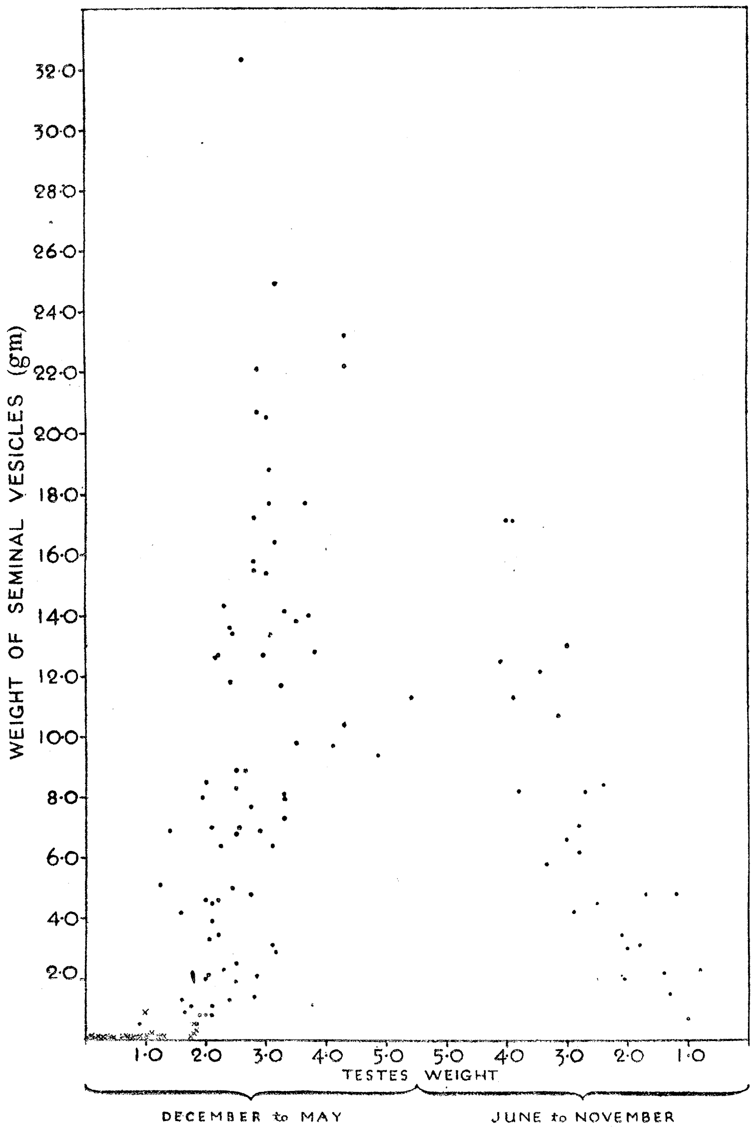

FIG. 12.—Weight of seminal vesicles and weight of testes.

accessory glands have barely started to develop. At this point the growth-rate becomes greater than that of the testis, and fully-developed accessory glands are usually found in animals with testes of over 3 gm. The relation between the gland weights and testis weights during regression appears to be linear in each case, although the percentage decrease is much greater than in the testis. There is less "fanning out" of the points in the regression phase than in the preparation phase in which two types of animal (old males and young males) are represented.

(*b*) *Correlation with Interstitial Tissue.*—A comparison of the cycle in the interstitial cells, fig. 5, and in the accessory organs, figs. 6–9, shows that the period of maximum development of the former corresponds with that in the accessory organs; in both there is a rapid period of growth in April, and a rapid fall in August. COURRIER maintained that the cycles in the tubules, in the interstitial tissue and in the accessory organs are synchronized, but the present data point to a dissociation of the spermatogenic cycle from that of the interstitial tissue and accessory organs.

VIII. *Discussion.*

(*a*) *Age of Puberty.*—From a study of the immature animals in this collection it seems evident that males of the first litters do not breed in the same season, so that the period of immaturity in the male hedgehog is not less than nine months, and probably not more than eleven months. An animal such as hedgehog 209, which in early July is

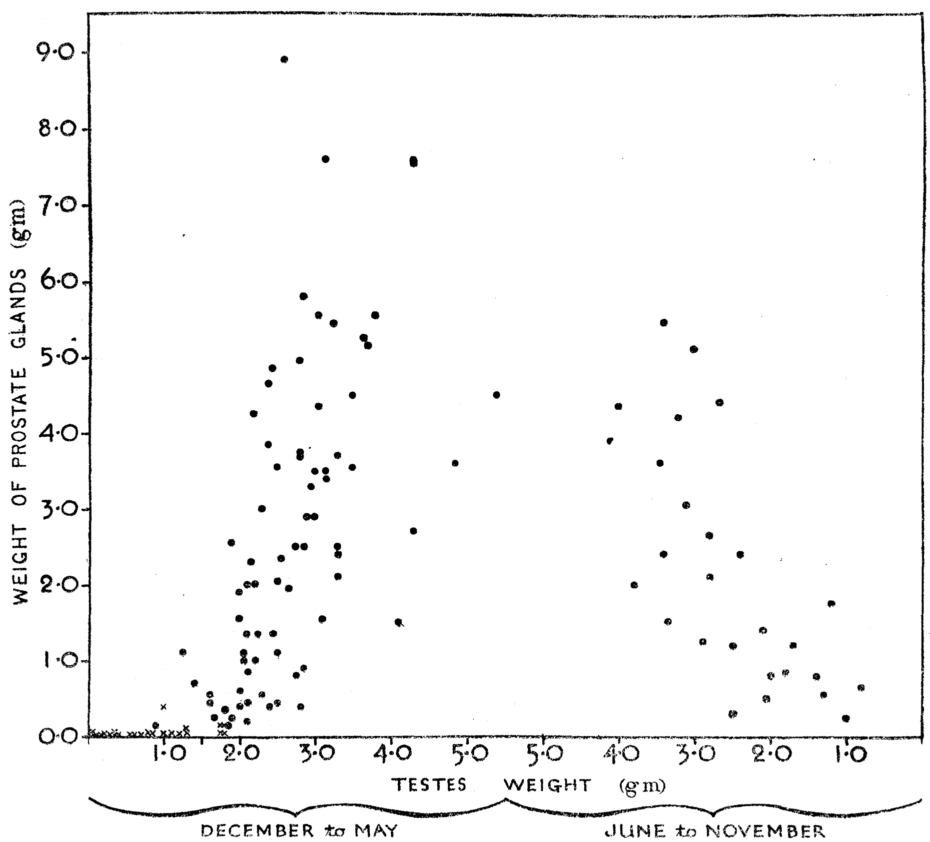

Fig. 13.—Weight of prostate glands and weight of testes.

producing spermatids, might possibly be ready for breeding in August, but since animals with testes at a similar stage were caught in January and February it is more likely that the autumn regression sets in before the production of spermatozoa commences. In addition, the accessory organs could scarcely develop to full activity in time. The males born early in the breeding season would therefore regress with the adults in the autumn and would not be ready for breeding until the following April. Those born later would lag behind the adult condition throughout the winter and probably not reach full development until May, although spermatogenesis may commence in April.

(*b*) *Initial Infertility of the Hedgehog.*—The data recorded in this paper show that the failure of the female to mate at the first periods of œstrus in early May is not due to delayed development of the male, and it seems likely that the initial failure to mate, as well as the failure to get pregnant after the first copulation, must be due to some factor affecting the female (see Part VI, *loc. cit.*).

(*c*) *Comparison with Ferret.*—The reproductive cycle of the hedgehog differs from that of the ferret in some interesting particulars. While the season of full spermatogenic

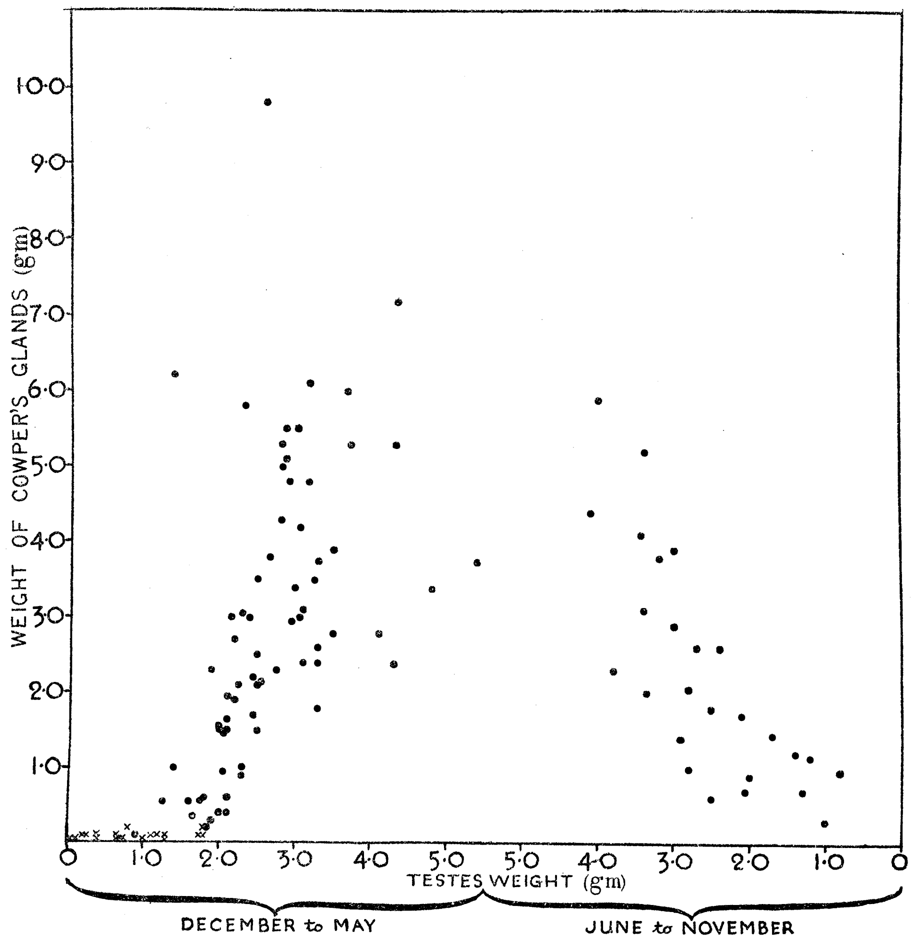

FIG. 14.—Weight of Cowper's glands and weight of testes.

activity is roughly of the same duration (April to August) in the two forms, the period of quiescence in the hedgehog is extremely short, and probably at no time does the testis cease the active production of spermatocytes. The testis of the anœstrous ferret is composed mainly of tubules containing Sertoli nuclei and spermatogonia only, and the latter are of the resting or "winter" type. Only occasional tubules have scattered spermatocytes. In the anœstrous hedgehog, however, it is the exception to find tubules without several rows of primary spermatocytes, fig. 20, Plate 35. It follows that the seminiferous tubules do not decrease in size to the same degree as in the ferret, and it is rare to find tubules in which the lumen has been obliterated. The size decrease in the hedgehog testis is correspondingly less.

In the ferret the degree of atrophy of the anœstrous testis is extreme, and it is known that the anterior pituitary body is inactivated, or practically so, during this period (HILL and PARKES, 1933). As regards the hedgehog, it seems likely that the anterior lobe is partially active throughout the winter. This difference is more remarkable since the hedgehog becomes extremely torpid during winter even if true hibernation does not occur, while the ferret shows no appreciable lethargy. A comparison of the testis of the anœstrous and of the hypophysectomized hedgehog should throw light on this point. It is possible, also, that the more active condition of the anœstrous testis in the hedgehog is connected in some way with the fact that the testes are abdominal throughout the cycle. The testes of the mole, however, which are almost abdominal, are described by COURRIER (1926) and by TANDLER and GROSZ (1911, 1912) as extremely atrophic in winter.

(*d*) *Effect of Captivity.*—A small number of animals were kept in captivity at room temperature, and it is of interest to note that the normal rhythm had been disturbed and that animals killed in January, February and March all possessed completely active testes though the accessory organs did not differ materially from those of animals in the field. This disturbance of the normal cycle is important from the point of view of experimental work and will be dealt with later.

(*e*) *Use of Accessory Organs.*—In the fully active hedgehog, the reproductive organs weigh over 50 gm., often approaching 10% of the body weight. Four-fifths or more of the weight is due to the accessory glands, which must be the largest in relation to body weight so far described. The upper vagina of the female is designed to hold a large volume of fluid, but the utility of the very large amount of secretion produced is not obvious. So far as can be determined, no solid vaginal plug, such as is found in the mouse, occurs in the hedgehog.

I wish to express my gratitude to Dr. A. S. PARKES for supplying the material and for assistance and advice during the progress of the investigation. My thanks are due also to Professor F. W. R. BRAMBELL for dissecting many of the animals and for his generous advice.

The histological expenses were defrayed by a grant from the Medical Research Council, for which I am grateful.

Fig. 1 is the work of Miss B. C. PHILLIPSON. Photographs by Mr. D. KEMPSON.

IX.—Summary.

1. One hundred and thirty-five male hedgehogs were collected during 1930-1933. The seasonal changes in the reproductive organs have been investigated with special reference to individual variation.

2. Thirty-one of the animals, caught from July to May, were classed as definitely immature. In the spring the more developed immatures merge with the adults recovering from anœstrus. It is estimated that sexual maturity is reached at not less than nine months old, *i.e.*, in the breeding season following the year of birth.

3. The testes in adults are fully active from April to the end of August. Retrogression is rapid, and a comparatively quiescent condition, which lasts until the end of the year, is reached by the beginning of October. At no time does the active production of spermatogonia and spermatocytes cease. Anœstrous quiescence is, therefore, less marked than in the ferret. From January to March the testes are preparing actively for the breeding season.

4. Seasonal variation in the size of the testis is not so great as in the ferret and there is less change in the diameter of the seminiferous tubules. It is probable, therefore, that in the hedgehog the anterior pituitary is not so inactive during anœstrus as it is known to be in the ferret.

5. There is a definite cycle in the size of the interstitial cells. From April to the end of June they are large and in the fully active condition. They gradually decrease in size to the inactive condition in October : growth for the next breeding season begins in January, but the most rapid growth takes place at the end of March.

6. The accessory sexual organs undergo enormous hypertrophy in the breeding season. The cycle in the epididymis is closely related to that in the testis, but in the seminal vesicles, prostate glands and Cowper's glands development is first slow and then rapid in relation to that of the testis.

REFERENCES.

ALLANSON (1932). 'Proc. Roy. Soc.,' B, vol. **110**, p. 295.

—— (1933). 'Phil Trans.,' B, vol. **222**, p. 79.

BISSONNETTE (1932). 'Proc. Roy. Soc.,' B, vol. **110**, p. 322.

COURRIER (1927). 'Arch. Biol. Paris,' vol. **37**, p. 173.

DISSELHORST (1904). OPPEL's "Lehrbuch der vergleichenden mikroskopischen Anatomie," Teil IV. Jena.

GRIFFITHS (1890). 'J. Anat. Physiol.,' vol. **24**, p. 27.

HILL and PARKES (1932). 'Proc. Roy. Soc.,' B, vol. **112**, p. 138.

—— —— (1933). 'Proc. Roy. Soc.,' B, vol. **113**, p. 530.

MARSHALL (1911). 'J. Physiol.,' vol. **43**, p. 247.

PELLEGRINI (1926). 'C. R. Ass. Anat.,' p. 464.

ROWLANDS and BRAMBELL (1933). 'Proc. Roy. Soc.,' B, vol. **112**, p. 200.

TANDLER and GROSZ (1911). 'Arch. EntwMech. Org.,' vol. **33**, p. 297.

—— —— (1912). *Ibid.*, **35**, p. 132.

DESCRIPTION OF PLATES.

Abbreviations.

c, capillary; *ic*, interstitial cell; *it*, interstitial tissue; *s*, secretion; *sn*, Sertoli nucleus; *spc*, spermatocyte; *spg*, spermatogonium; *spz*, spermatozoa; *u*, urethra; *ug*, urethral gland; *um*, urethral muscle.

PLATE 34.

See fig. 1 for legend.

FIG. 15.—Dissection of adult male hedgehog killed 19 May. The penis has been stretched backwards and the prostate glands have been turned back from the ventral surface of the bladder. $\frac{3}{4}$ natural size.

FIG. 16.—Dissection of adult male killed 10 January. $\frac{3}{4}$ natural size.

FIG. 17.—Dissection of immature male killed in April. Testes nearly full size but accessory glands little developed. $\frac{3}{4}$ natural size.

PLATE 35.

FIG. 18.—Testis of No. 237, killed 11 November. Tubules in anœstrous condition with no stages later than primary spermatocytes. Interstitial cells small. $\times$ 100.

FIG. 19.—Testis of No. 80, killed 7 May. Tubules in full activity, interstitial cells large. $\times$ 100.

FIG. 20.—Seminiferous tubule of No. 237, killed 11 November, showing large numbers of spermatogonia and primary spermatocytes. $\times$ 430.

FIG. 21.—Interstitial tissue of No. 237, killed 11 November. Nuclei crowded, cytoplasm scanty. $\times$ 650.

FIG. 22.—Interstitial tissue of No. 80, killed 7 May. Cells larger, cytoplasm intensely eosinophil. $\times$ 650.

PLATE 36.

FIG. 23.—Seminal vesicle of No. 9, killed 18 November. Tubules shrunken, little secretion. $\times$ 40.

FIG. 24.—Seminal vesicle of No. 252, killed 18 April. Tubules filled with secretion. $\times$ 40.

FIG. 25.—Prostate of No. 25, killed 13 February. $\times$ 40.

FIG. 26.—Prostate of No. 252, killed 18 April. $\times$ 40.

PLATE 37.

FIG. 27.—Cowper's gland of No. 240, killed 28 January. $\times$ 40.

FIG. 28.—Cowper's gland of No. 88, killed 6 May. $\times$ 40.

FIG. 29.—Urethra from animal killed in July, showing the two masses of glandular tissue ventral to the uro-genital tract.

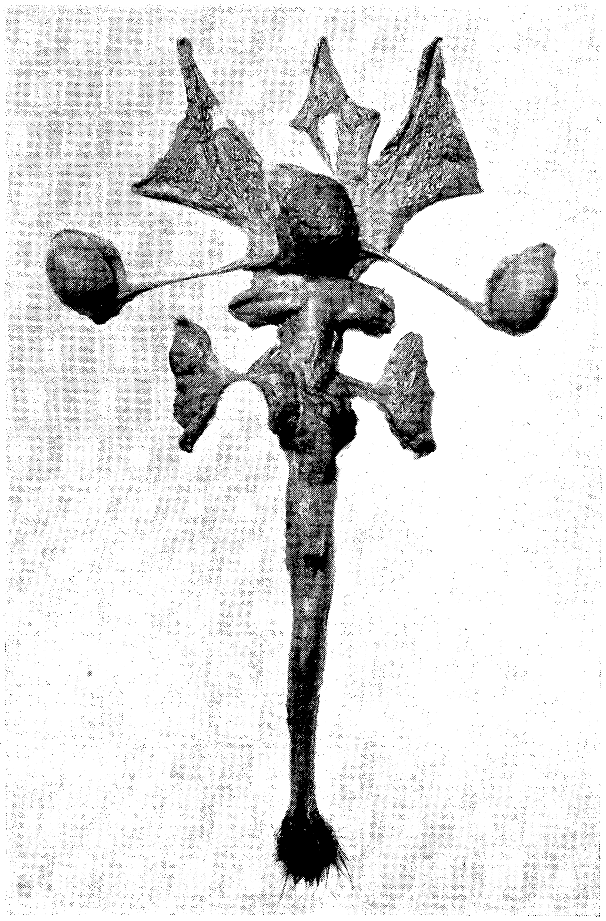

Fig. 16.

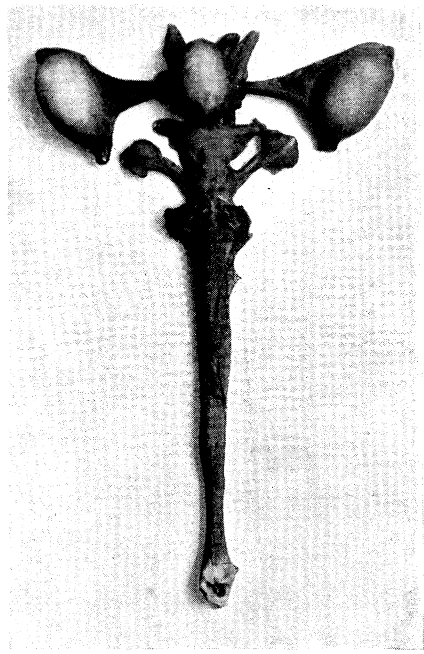

Fig. 17.

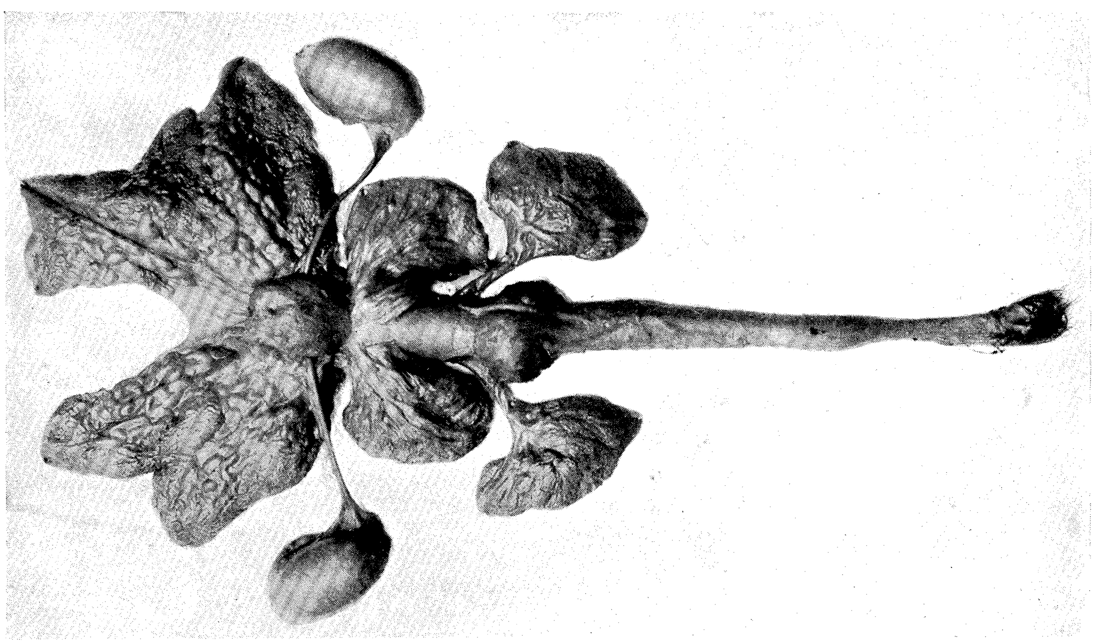

Fig. 15.

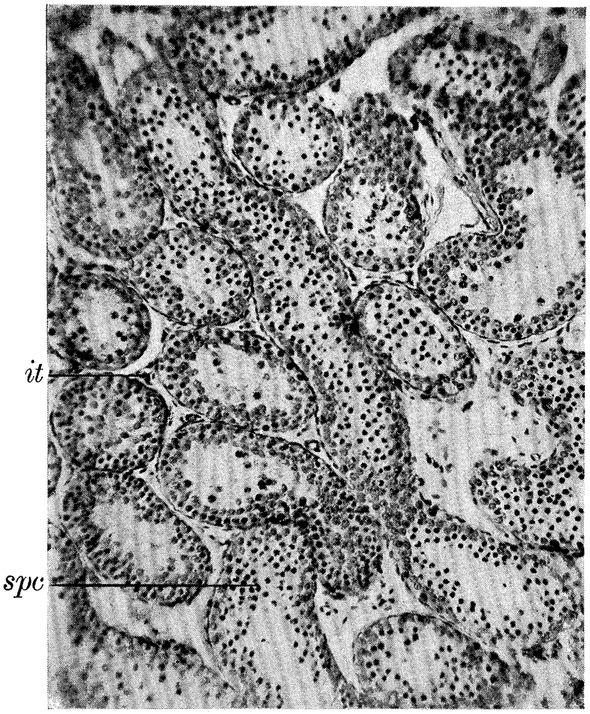

Fig. 18.

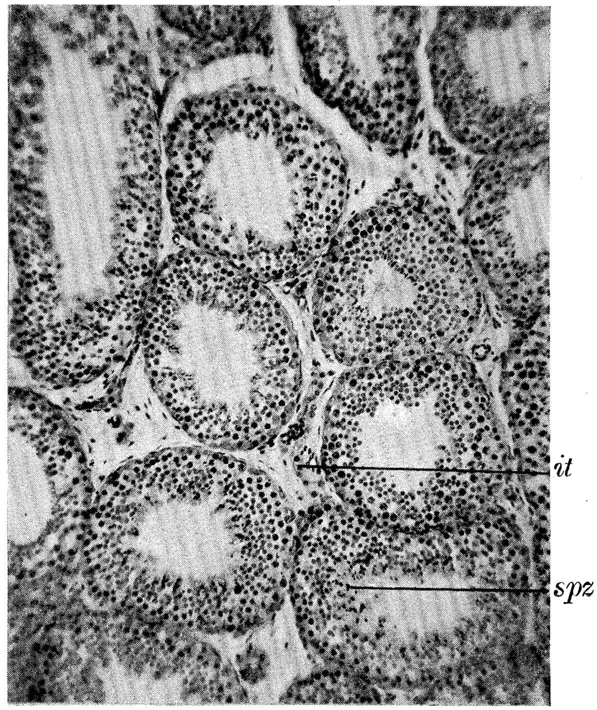

Fig. 19.

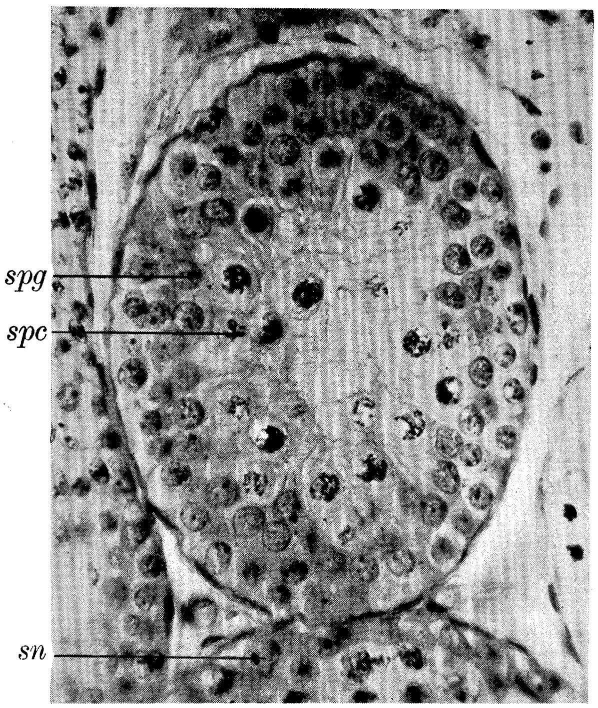

Fig. 20.

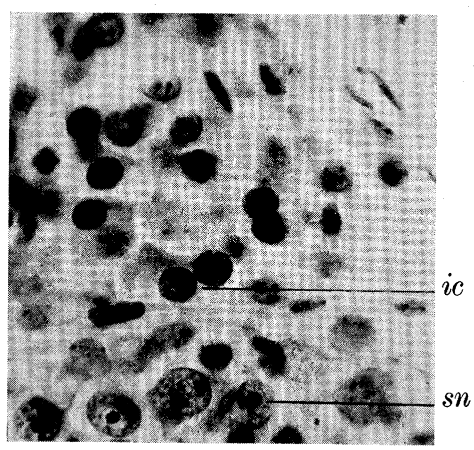

Fig. 21.

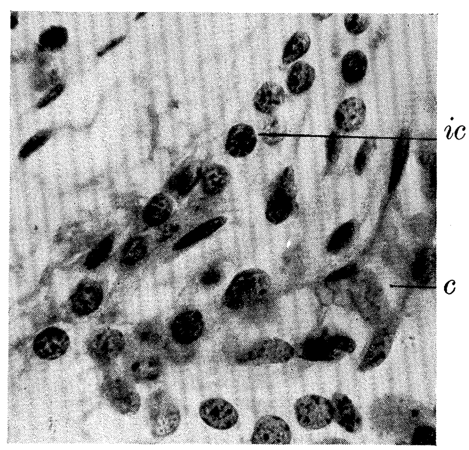

Fig. 22.

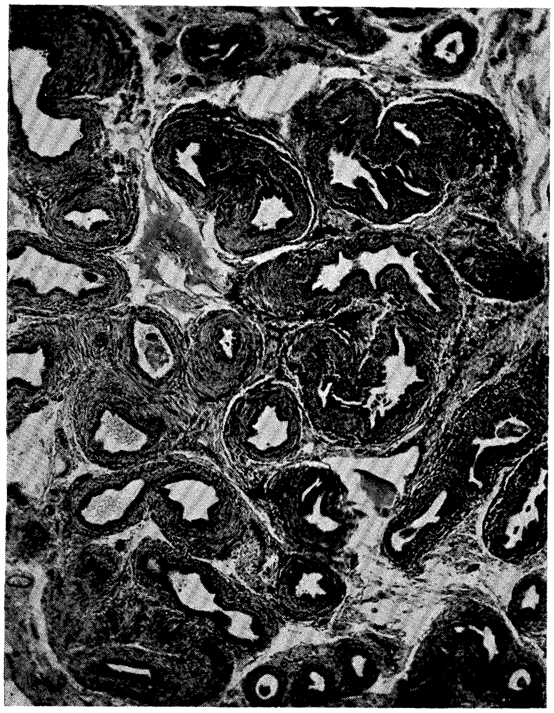

Fig. 23.

Fig. 24.

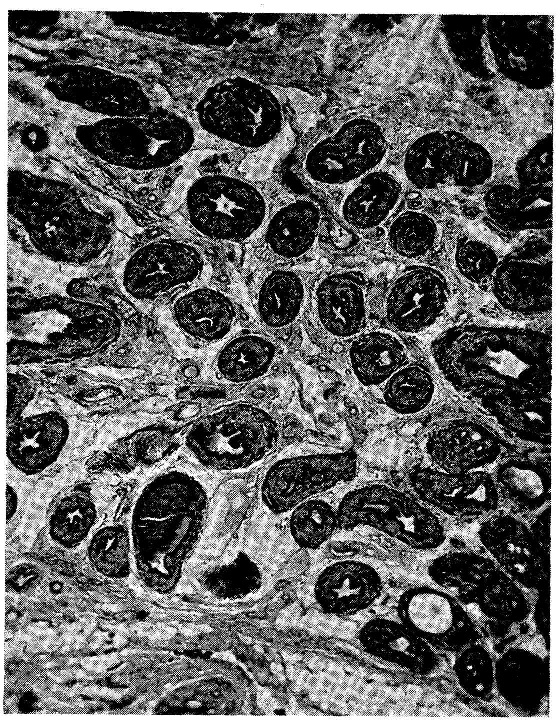

Fig. 25.

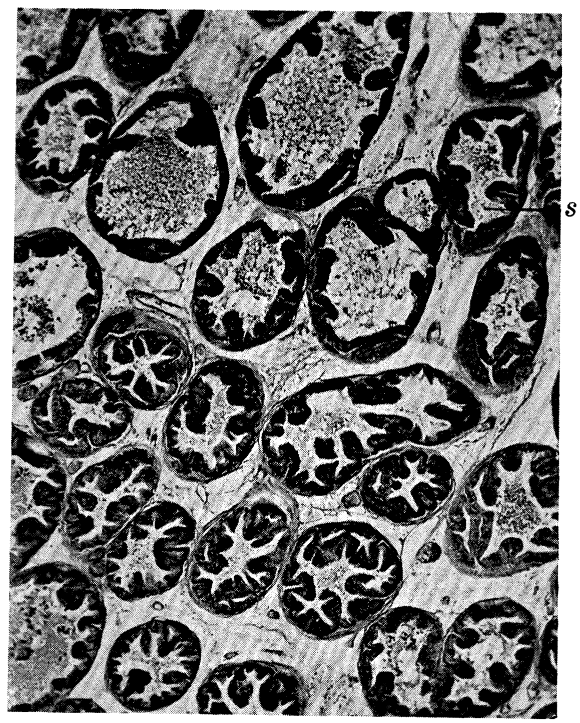

Fig. 26.

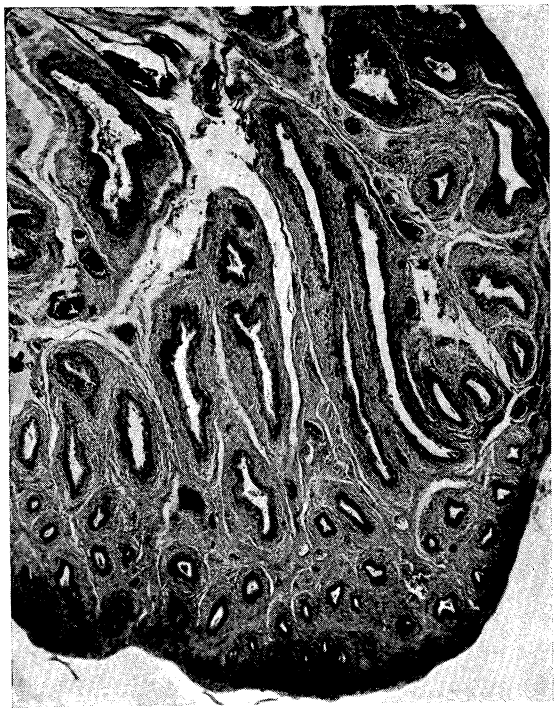

FIG. 27.

FIG. 28.

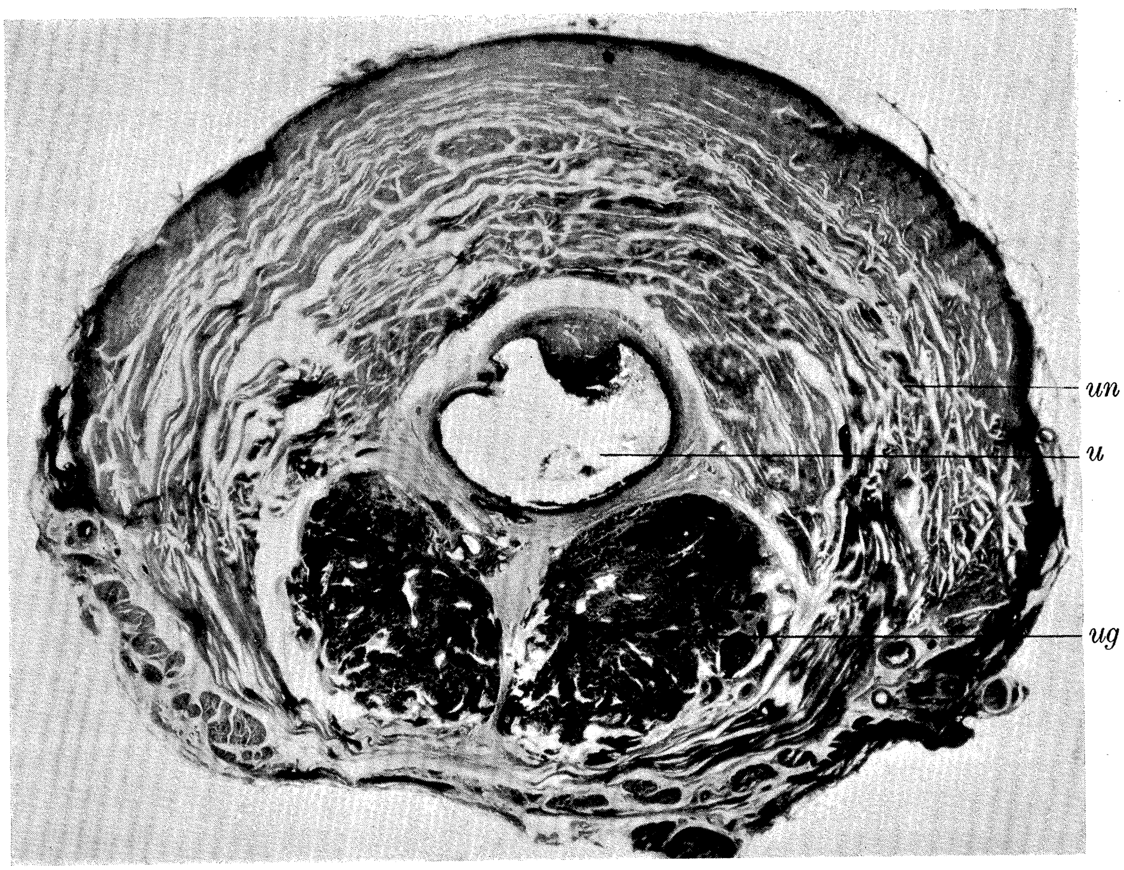

FIG. 29.

Appendix.

Number of hedgehog.	Date.	Body weight.	Testis. Weight (pair).	Testis. Spermatozoa.	Testis. Mean diameter of tubules.	Testis. Mean area of interstitial cells.	Epididymis. Weight (pair).	Epididymis. Spermatozoa.	Epididymis. Mean diameter of tube.	Weight of seminal vesicles (pair).	Weight of prostate glands (pair).	Weight of Cowper's glands (pair).	Weight of penis.
		gm.	gm.		μ	sq. μ	gm.		μ	gm.	gm.	gm.	gm.
12*	January 1 ...	250	0·65	—	121	...	0·15	—	87	...	...	...	0·51
240	„ 28 ...	440	0·93	—	151	82	0·22	—	119	0·55	0·14	0·12	2·85
276	„ 10 ...	800	1·25	—	167	117	0·37	—	...	5·15	1·10	0·56	4·62
239*	„ 2 ...	610	1·30	—	128	125	0·19	—	116	0·13	0·07	0·07	1·60
274	„ 10 ...	700	1·57	—	163	98	0·33	—	148	1·31	0·46	0·55	3·90
275	„ 10 ...	620	1·76	—	152	97	0·29	—	121	1·08	0·33	0·55	3·60
250	„ 19 ...	420	1·92	few	173	79	0·23	—	...	0·80	0·25	0·33	2·65
277	„ 10 ...	800	2·10	—	171	91	0·45	—	136	1·15	0·45	0·59	4·70
289*	February 22 ...	480	1·30	—	140	120	0·19	—	...	0·13	0·05	0·07	1·25
288	„ 22 ...	586	2·00	—	168	111	0·42	—	148	0·93	0·37	0·41	2·78
25	„ 13 ...	520	2·00	—	136	...	0·45	—	129	2·03	0·59	...	2·35
11*	March 25 ...	200	0·59	—	...	84	0·12	—	...	0·11	0·02	...	0·47
248*	„ 14 ...	520	1·00	—	159	138	0·17	—	117	0·11	0·06	...	1·75
294	„ 24 ...	460	1·65	—	145	...	0·27	—	...	0·87	0·25	0·36	3·05
290*	„ 24 ...	300	1·75	—	166	147	0·23	—	119	0·10	0·04	0·10	1·00
291	„ 24 ...	380	1·85	—	167	140	0·33	—	149	0·56	0·14	0·20	2·30
293	„ 24 ...	500	2·10	—	162	100	0·42	—	...	0·86	0·21	0·37	2·88
292	„ 24 ...	600	2·83	—	195	124	0·53	—	162	1·40	0·38	0·62	3·55
36	April 14 ...	650	1·61	+	156	...	0·56	—	...	4·26	0·54	...	3·04
29*	„ 22 ...	450	1·77	+	178	198	0·26		...	0·17	0·06	0·13	1·22
47*	„ 22 ...	300	1·86	+	170	125	0·31		...	0·54	0·20	0·21	1·50
52	„ 22 ...	480	1·92	+	...	...	0·53	+	184	8·02	2·55	2·30	3·41
48	„ 22 ...	450	2·06	+	204	...	0·46	+	181	2·12	0·98	1·49	3·02
83	„ 25 ...	600	2·06	+	212	...	0·43	+	176	3·30	1·10	0·95	2·26

* Immature Animal.

APPENDIX (continued).

Number of hedgehog.	Date.	Body weight.	Testis. Weight (pair).	Testis. Spermatozoa.	Testis. Mean diameter of tubules.	Testis. Mean area of interstitial cells.	Epididymis. Weight (pair).	Epididymis. Spermatozoa.	Epididymis. Mean diameter of tube.	Weight of seminal vesicles (pair).	Weight of prostate glands (pair).	Weight of Cowper's glands (pair).	Weight of penis.
		gm.	gm.		μ	sq. μ	gm.		μ.	gm.	gm.	gm.	gm.
51	April 22 ...	400	2·09	+	210	...	0·48	+	183	3·92	1·35	1·50	2·19
86	,, 21 ...	500	2·10	—	204	...	0·43	+	186	6·98	2·00	1·65	2·06
56	,, 24 ...	480	2·12	+	185	...	0·60	+	175	4·51	0·85	1·94	3·12
30	,, 22 ...	500	2·16	+	194	...	0·60	+	184	12·60	2·26	3·00	3·37
57	,, 24 ...	426	2·26	+	187	...	0·53	+	192	6·46	1·36	2·09	2·81
58	,, 24 ...	480	2·32	+	191	215	0·48	+	173	2·31	0·55	0·90	3·12
38	,, 15 ...	630	2·39	+	187	261	0·53	+	186	11·84	3·85	3·00	3·50
28	,, 16 ...	520	2·42		...	...	0·53		...	1·36	0·39	...	3·09
31	,, 22 ...	400	2·45	+	190	224	0·50	+	183	5·03	1·35	1·71	3·23
89	,, 28 ...	535	2·45	+	179	...	0·55	+	181	13·39	4·86	2·23	2·38
78	,, 21 ...	580	2·49	+	198	...	0·55	+	192	8·80	1·45	2·08	3·50
49	,, 22 ...	370	2·50	+	186	...	0·48	+	174	1·92	1·12	1·48	3·19
90	,, 21 ...	670	2·53		...	...	0·58		...	8·25	3·55	3·53	3·40
251	,, 18 ...	480	2·75	+	172	254	0·50		...	7·72	1·82	2·28	3·12
253	,, 22 ...	540	2·75	+	...	...	0·62		...	4·42	2·48	1·45	4·40
50	,, 22 ...	590	2·78		...	...	0·76		...	15·80	3·70	4·31	5·45
34	,, 11 ...	700	2·84	+	187	215	0·60	—	167	2·11	0·93	...	2·80
40	,, 21 ...	600	2·85		...	...	0·55		...	20·70	2·52	5·12	3·79
61	,, 24 ...	480	3·02		...	...	0·73		...	15·38	3·53	3·42	3·92
59	,, 24 ...	580	3·02	+	200	240	0·82	+	190	20·47	2·92	5·52	4·52
60	,, 24 ...	370	3·08	+	188	...	0·55	+	174	3·16	1·56	3·12	2·66
92	,, 30 ...	530	3·14		...	...	0·60		...	6·40	3·40	2·40	3·19
252	,, 18 ...	600	3·15	+	212	232	0·59		...	16·46	3·47	4·77	5·15
93	,, 25 ...	558	3·30		...	...	0·59		...	7·27	2·37	2·42	2·42
37	,, 15 ...	650	3·49	+	...	...	0·61		...	9·77	3·55	3·81	3·42
265	,, 14 ...	643	4·10	+	192	206	0·55		...	9·70	1·63	2·83	5·18
74	,, 25 ...	524	5·42	+	185	172	0·65		...	11·35	4·49	3·74	2·99
73*	May 13 ...	360	0·97	—	...	...	0·28		...	0·92	0·42	...	2·84

210	„ 15	...	413	1·42	—	146	...	0·34	—	157	6·95	0·71	1·01	2·75
63*	„ 4	...	430	1·77	few	169	...	0·32		...	0·34	0·18	...	1·75
76	„ 11	...	513	1·99		...	...	0·50		...	8·55	1·88	1·55	2·76
84	„ 7	...	430	2·00		...	...	0·43		...	4·61	1·56	1·55	2·39
77	„ 8	...	580	2·20	+	193	194	0·51	+	162	12·72	4·25	2·73	4·45
124	„ 29	...	400	2·20	+	174	...	0·41	+	147	3·45	1·01	1·02	2·97
75	„ 8	...	550	2·23	+	187	234	0·64	+	185	4·65	2·02	1·88	2·88
108	„ 19	...	430	2·30	+	190	228	0·56		...	14·33	3·03	3·06	3·65
111	„ 19	...	440	2·40	+	...	179	0·55	+	163	13·62	4·65	5·82	4·30
80	„ 7	...	480	2·47	+	210	...	0·65	+	189	6·76	2·05	2·48	3·65
118	„ 22	...	373	2·54	+	183	...	0·62	+	187	7·00	2·34	2·16	3·10
62	„ 1	...	800	2·58		...	...	0·78		...	32·30	8·91	9·87	5·51
87	„ 5	...	427	2·65	+	200	...	0·51	+	183	8·89	1·94	3·77	2·55
113	„ 8	...	453	2·77	+	172	...	0·62	+	181	15·48	3·70	5·32	3·13
85	„ 7	...	640	2·78		...	...	0·78		...	17·25	4·96	5·00	4·65
112	„ 6	...	507	2·86		...	...	0·68		...	22·15	5·79	5·49	3·38
119	„ 22	...	533	2·91	+	201	...	0·74	+	180	6·90	2·90	4·78	4·13
123	„ 29	...	520	2·96		...	...	0·61		...	12·70	3·30	2·96	4·14
116	„ 22	...	453	3·06	+	212	...	0·70	+	193	18·80	4·36	3·02	4·69
109	„ 19	...	600	3·06		...	...	0·58		...	17·68	5·55	4·20	4·35
88	„ 6	...	651	3·15	+	210	249	0·82	+	208	24·89	7·57	6·08	4·26
212	„ 14	...	685	3·25		...	...	0·65		...	11·73	5·45	3·47	4·45
72	„ 5	...	520	3·28		...	...	0·58		...	14·09	3·71	3·75	4·70
79	„ 7	...	580	3·30	+	218	...	0·67	+	207	8·15	2·12	2·62	3·27
206	„ 25	...	419	3·32	+	...	...	0·44		...	7·95	2·50	1·80	3·10
94	„ 2	...	701	3·48	+	200	199	0·76	+	213	13·79	4·48	3·90	4·07
117	„ 22	...	547	3·65		...	...	0·74		...	17·70	5·25	6·00	5·60
82	„ 7	...	590	3·72	+	206	233	0·89	+	213	13·97	5·15	5·31	5·48
200	„ 15	...	700	3·78	+	198	...	0·79		...	12·83	5·55	6·22	4·33
81	„ 7	...	704	4·27	+	198	202	0·84		...	22·19	7·57	5·33	4·16
110	„ 19	...	720	4·30		...	...	0·67		...	23·20	7·62	7·20	6·37
204	„ 22	...	652	4·32	—	196	...	0·83	+	161	10·43	2·70	2·40	5·08
205	„ 25	...	537	4·85	+	206	215	0·61		...	9·40	3·60	3·40	5·00
219	June 20	...	520	1·21	—	137	146	0·36	—	172	5·85	1·74	1·15	3·42
211	„ 11	...	425	2·12	+	195	...	0·48		...	3·45	1·37	1·73	2·65
208	„ 18	...	422	2·48	+	...	...	0·44		...	4·63	1·23	1·80	2·75
216	„ 30	...	475	2·70	+	192	235	0·45		...	8·21	4·38	2·60	3·37
207	„ 3	...	482	2·77	+	198	215	0·52	+	186	6·20	2·08	2·05	3·25
214	„ 22	...	555	2·78	+	209	206	0·63	+	171	7·05	2·70	...	4·40
201	„ 22	...	590	3·02		...	...	0·57		...	6·60	3·06	2·93	4·10

* Immature Animal.

Appendix (continued).

Number of hedgehog.	Date.	Body weight.	Testis. Weight (pair).	Testis. Spermatozoa.	Testis. Mean diameter of tubules.	Testis. Mean area of interstitial cells.	Epididymis. Weight (pair).	Epididymis. Spermatozoa.	Epididymis. Mean diameter of tube.	Weight of seminal vesicles (pair).	Weight of prostate glands (pair).	Weight of Cowper's glands (pair).	Weight of penis.
		gm.	gm.		μ	sq. μ	gm.		μ	gm.	gm.	gm.	gm.
202	June 2 ...	590	3·17		...	...	0·64		...	10·68	4·23	3·83	4·09
215	,, 2 ...	570	3·45		...	...	0·73		...	12·15	3·63	4·12	4·72
203	,, 24 ...	585	4·10	+	201	258	0·78	+	174	12·52	3·93	4·43	4·52
137*	July 29 ...	175	0·13	—	70	142	0·08	—	121	...	...	...	0·53
218*	,, 2 ...	244	0·42	—	106	...	0·07	—	90	0·05	0·02	0·05	0·54
209*	,, 8 ...	245	1·03	—	...	121	0·11	—	124	0·11	0·03	0·05	0·54
127	,, 2 ...	420	2·00	+	...	...	0·47		...	2·47	0·79	0·87	3·70
199	,, 22 ...	595	2·40	+	199	...	0·57	+	...	8·35	2·37	2·57	4·42
217	,, 4 ...	520	3·35	+	...	...	0·70	+	189	5·77	1·53	2·02	3·52
213	,, 2 ...	536	3·42	+	184	185	0·65	+	207	17·15	5·45	5·20	4·15
134	,, 17 ...	770	3·43	+	203	191	0·67	+	195	11·28	2·40	3·07	5·32
142*	August 18 ...	250	0·40	—	86	103	0·08	—	116	0·06	0·02	...	0·60
146	,, 26 ...	700	2·50	+	157	120	0·46	+	196	1·98	0·33	0·62	3·03
140	,, 4 ...	550	3·00	+	...	176	0·56	+	196	13·02	5·10	3·90	4·55
148	,, 26 ...	600	3·78	+	199	103	0·64	+	187	8·22	2·00	2·30	5·57
141	,, 4 ...	700	4·00	+	197	146	0·72	+	205	17·15	4·35	5·90	6·26
175*	September 30...	110	0·05	—	54	...	0·04	—	...	0·03	0·02	...	0·16
174*	,, 30...	110	0·05	—	57	117	0·03	—	...	0·04	0·01	...	0·13
171*	,, 30...	110	0·06	—	...	...	0·03	—	...	0·04	0·01	0·03	0·17
151	,, 21...	700	1·70	—	147	99	0·41	few	190	4·80	1·19	1·44	5·12
149	,, 11...	700	1·82	few	136	116	0·46	few	155	3·15	0·85	0·98	4·80
150	,, 8...	600	2·87	—	181	116	0·46	+	170	4·22	1·25	1·40	3·85
245*	October 16 ...	190	0·08	—	...	...	0·05	—	89	0·07	0·02	0·03	0·30
220*	,, 17 ...	400	0·21	—	102	...	0·12	—	93	0·11	0·06	0·07	1·01

221*	,, 17 ...	373	0·40	—	102	108	0·13	—	...	0·08	0·05	0·07	0·78
227*	,, 30 ...	600	0·66	—	137	117	0·11	—	92	0·08	0·03	0·08	1·18
226*	,, 30 ...	240	0·70	—	142	...	0·07	—	...	0·08	0·03	0·05	0·67
225*	,, 21 ...	450	0·73	—	135	...	0·11	—	112	0·09	0·03	0·06	1·07
231*	,, 30 ...	373	0·76	—	121	90	0·09	—	100	0·10	0·05	0·05	1·08
232*	,, 30 ...	480	0·78	—	132	98	0·12	—	99	0·13	0·04	0·19	1·17
189	,, 13 ...	760	0·82	—	144	71	0·35	—	138	2·31	0·65	0·94	4·19
187	,, 13 ...	380	1·00	—	132	73	0·28	—	113	0·75	0·25	0·27	2·27
186*	,, 8 ...	453	1·20	—	127	99	0·13	—	104	0·07	0·05	0·08	1·20
176	,, 1 ...	640	1·30	—	132	77	0·36	—	119	1·48	0·55	0·68	4·31
188	,, 13 ...	640	1·37	—	134	80	0·33	—	...	2·19	0·80	1·21	3·82
236*	November 10...	400	0·33	—	126	90	0·05	—	120	0·06	0·02	0·07	0·77
234*	,, 6...	600	1·07	—	127	105	0·15	—	124	0·18	0·06	0·10	1·31
237	,, 11...	880	2·06	—	147	103	0·36	—	134	2·13	0·53	0·69	3·87
9	,, 18...	950	2·09	—	141	60	0·51	—	131	2·07	...	...	4·94
10*	December 5 ...	200	0·36	—	61	82	0·15	—	100	...	...	...	...
19*	,, 11 ...	460	0·90	—	124	73	0·12	—	95	0·09	...	...	1·00
14*	,, 14 ...	300	1·15	—	119	...	0·12	—	104	...	...	...	0·39
21	,, 11 ...	700	2·47	—	154	56	0·55	—	140	2·47	...	...	4·11

* Immature Animal.

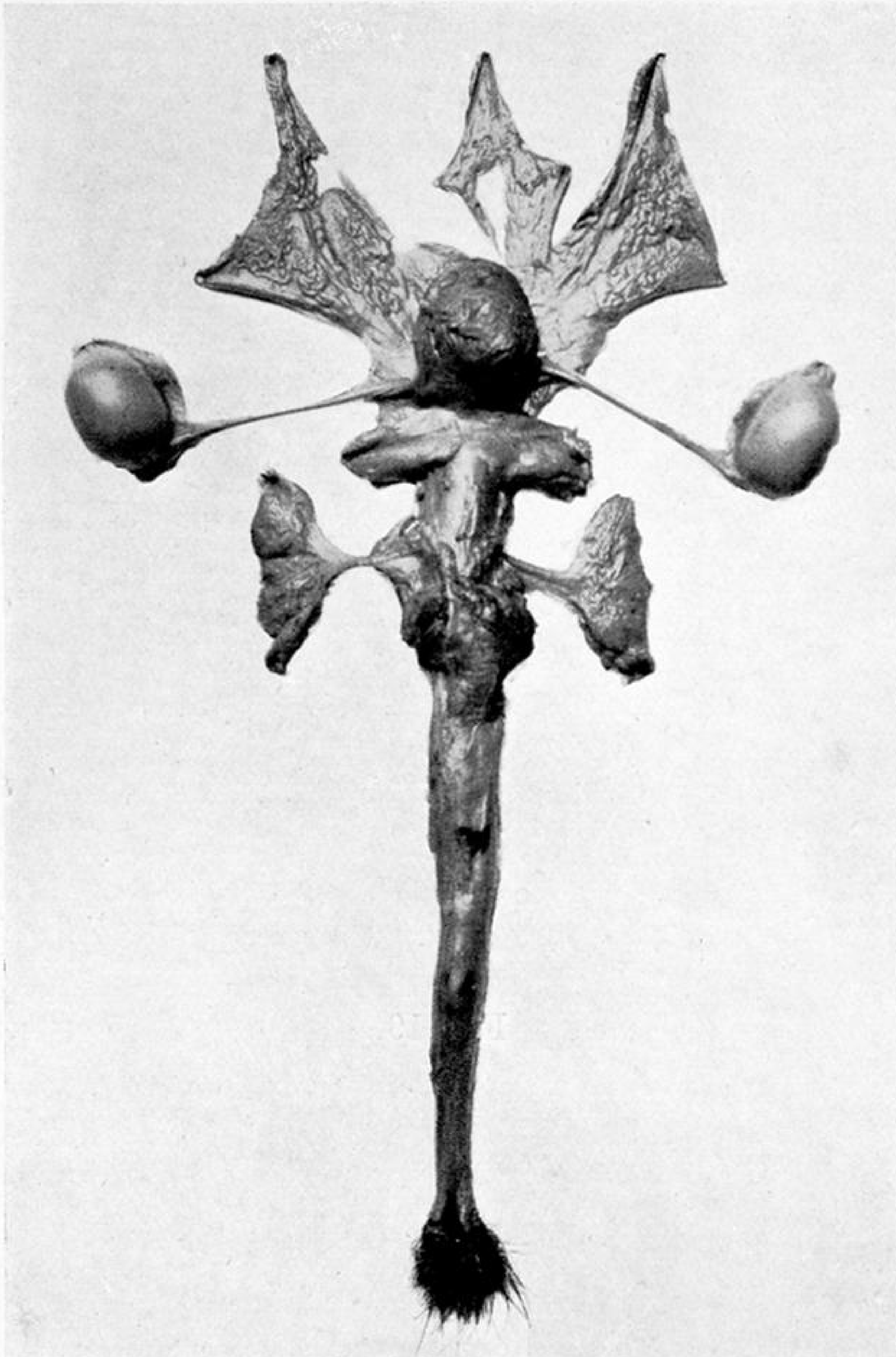

Fig. 16.

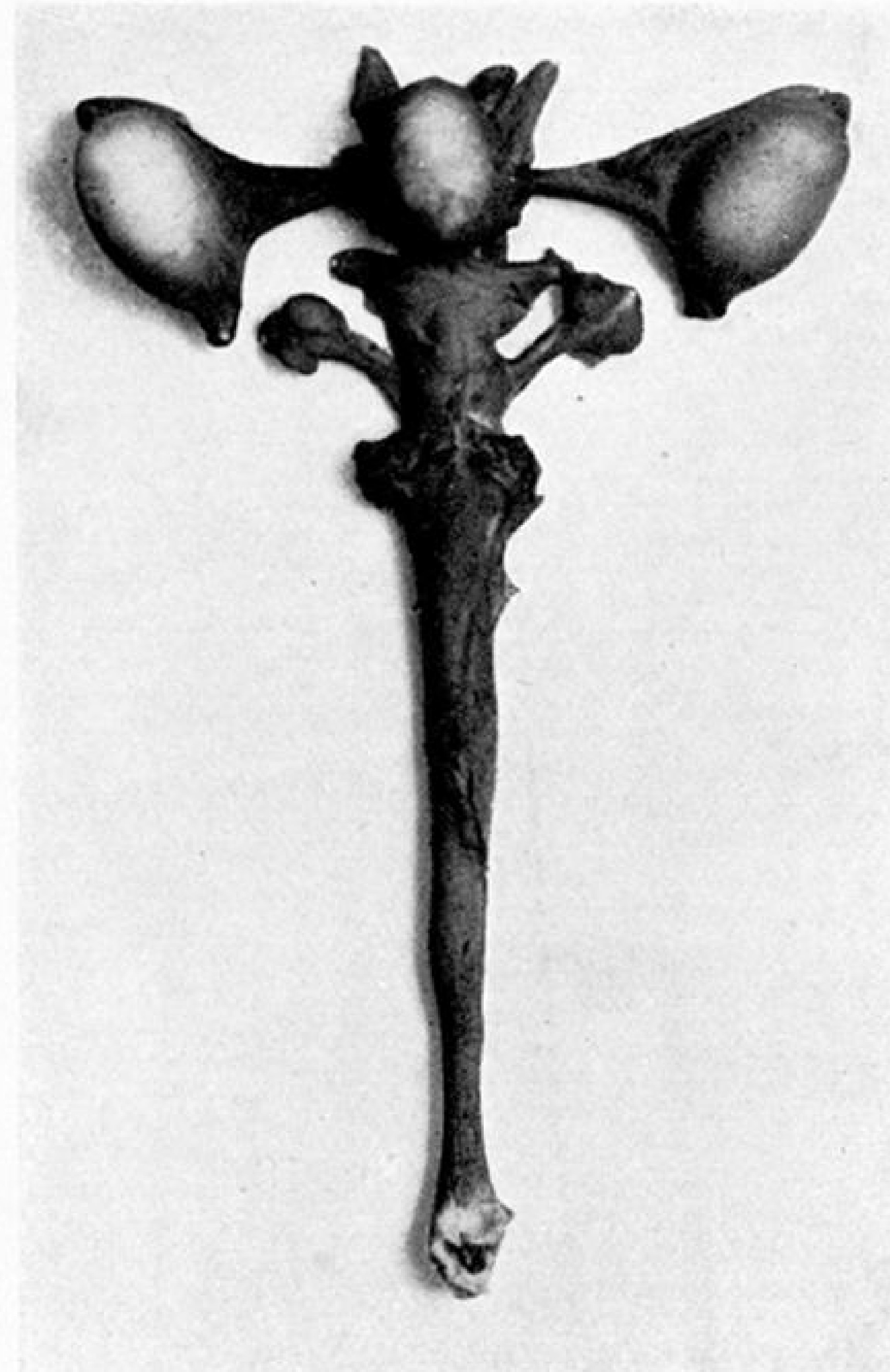

Fig. 17.

Fig. 15.

Plate 34.

See fig. 1 for legend.

Fig. 15.—Dissection of adult male hedgehog killed 19 May. The penis has been stretched backwards and the prostate glands have been turned back from the ventral surface of the bladder. $\frac{3}{4}$ natural size.

Fig. 16.—Dissection of adult male killed 10 January. $\frac{3}{4}$ natural size.

Fig. 17.—Dissection of immature male killed in April. Testes nearly full size but accessory glands little developed. $\frac{3}{4}$ natural size.

Fig. 18.

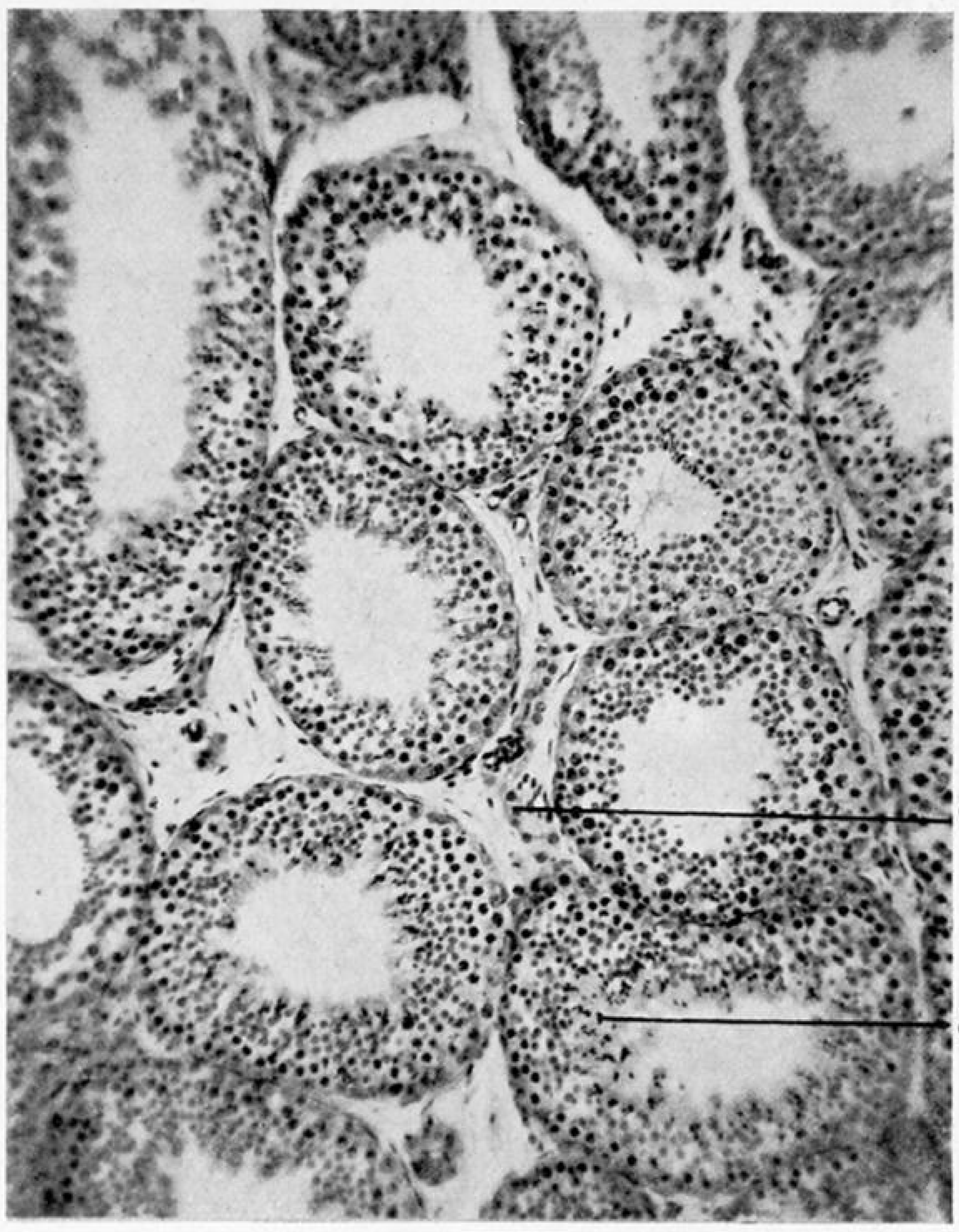

Fig. 19.

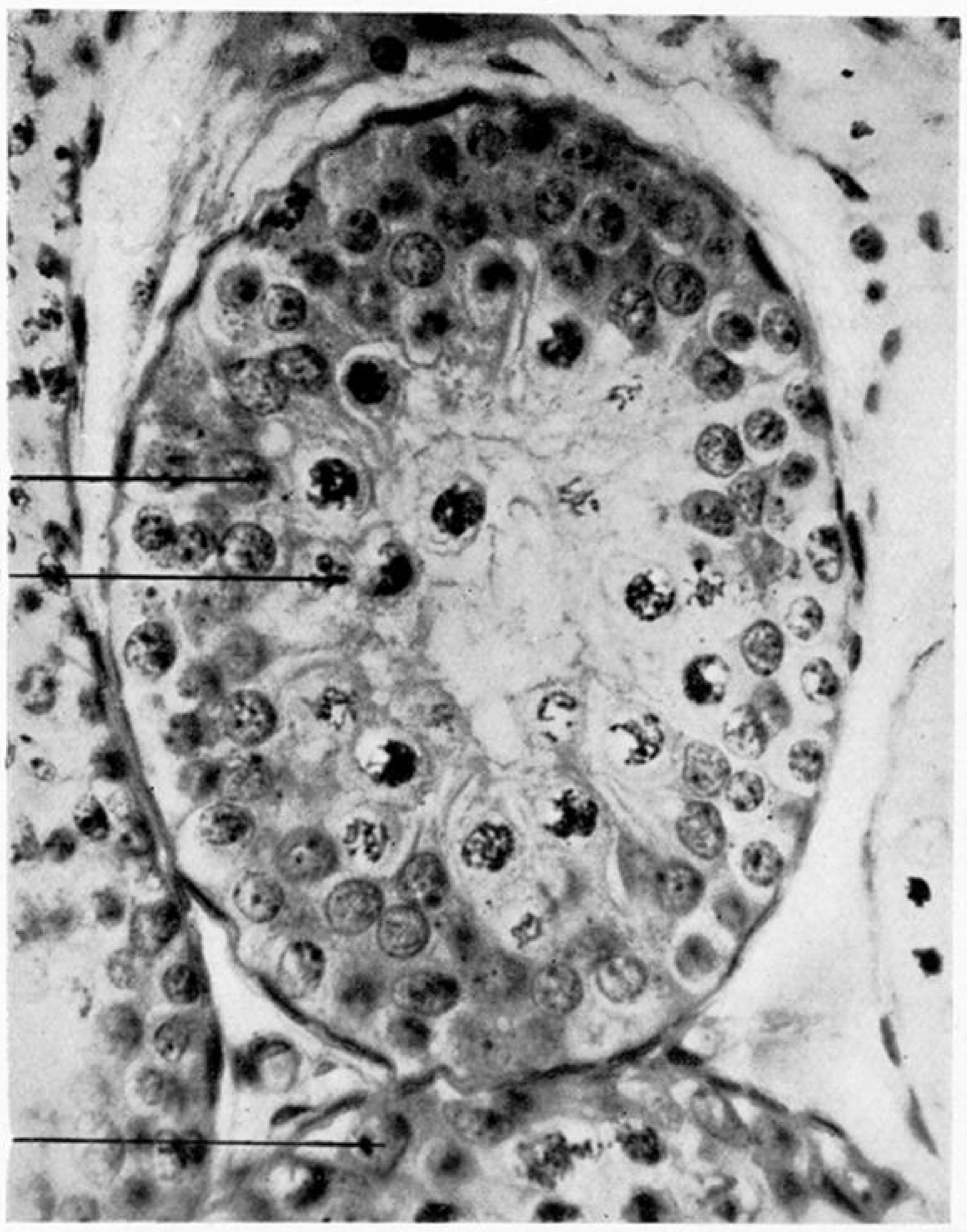

Fig. 20.

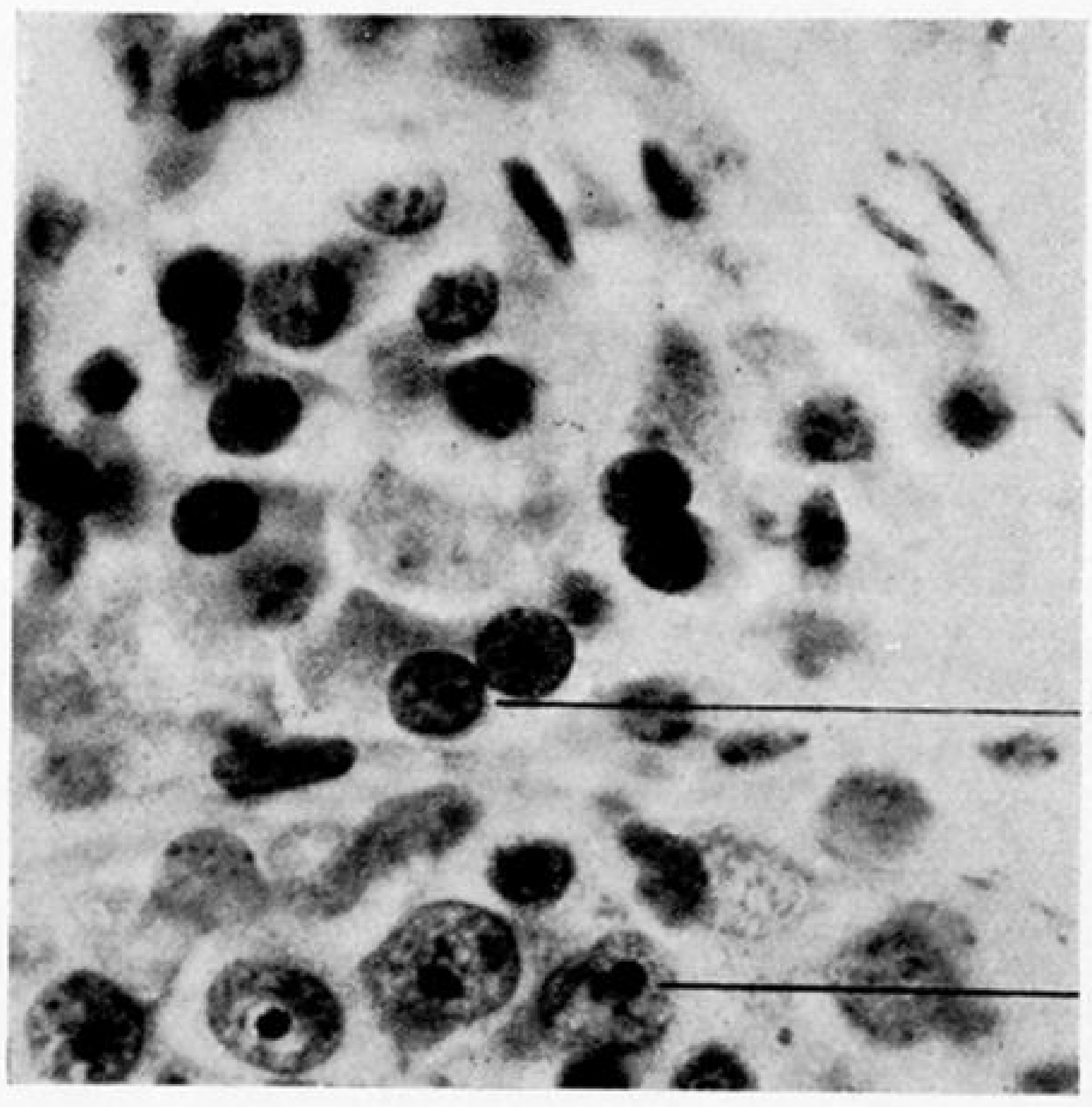

Fig. 21.

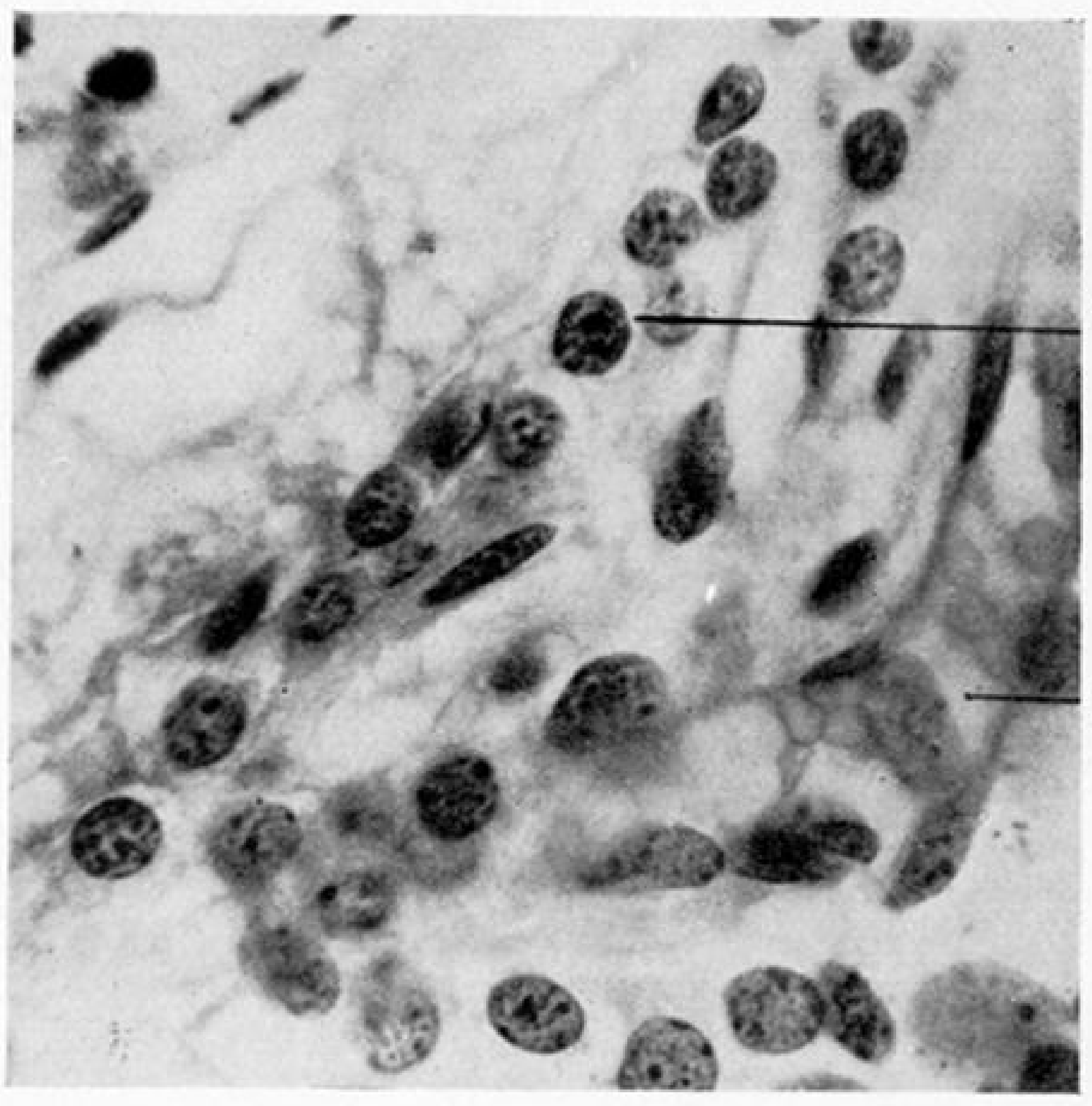

Fig. 22.

Plate 35.

Fig. 18.—Testis of No. 237, killed 11 November. Tubules in anœstrous condition with no stages later than primary spermatocytes. Interstitial cells small. × 100.

Fig. 19.—Testis of No. 80, killed 7 May. Tubules in full activity, interstitial cells large. × 100.

Fig. 20.—Seminiferous tubule of No. 237, killed 11 November, showing large numbers of spermatogonia and primary spermatocytes. × 430.

Fig. 21.—Interstitial tissue of No. 237, killed 11 November. Nuclei crowded, cytoplasm scanty. × 650.

Fig. 22.—Interstitial tissue of No. 80, killed 7 May. Cells larger, cytoplasm intensely eosinophil. × 650.

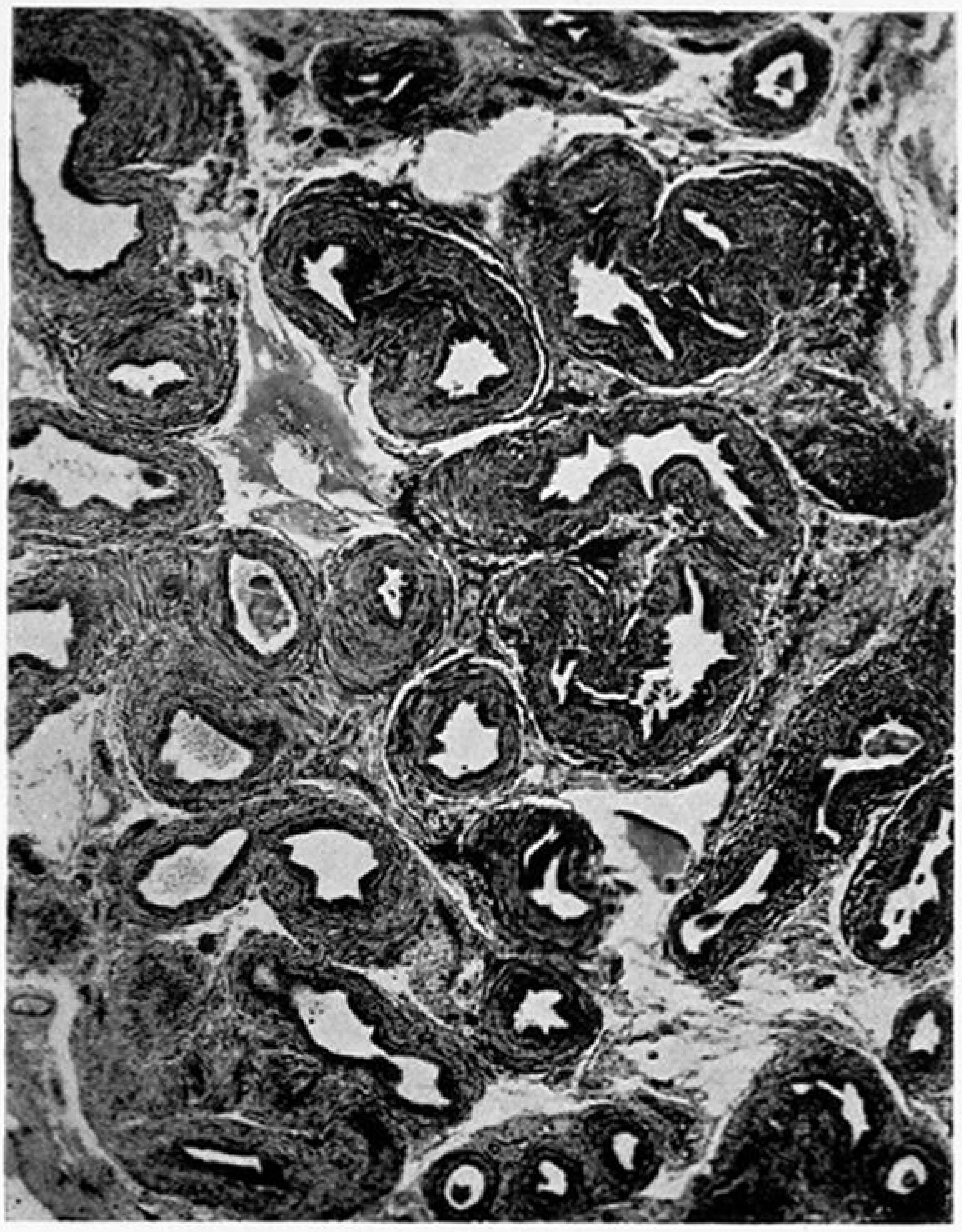

Fig. 23.

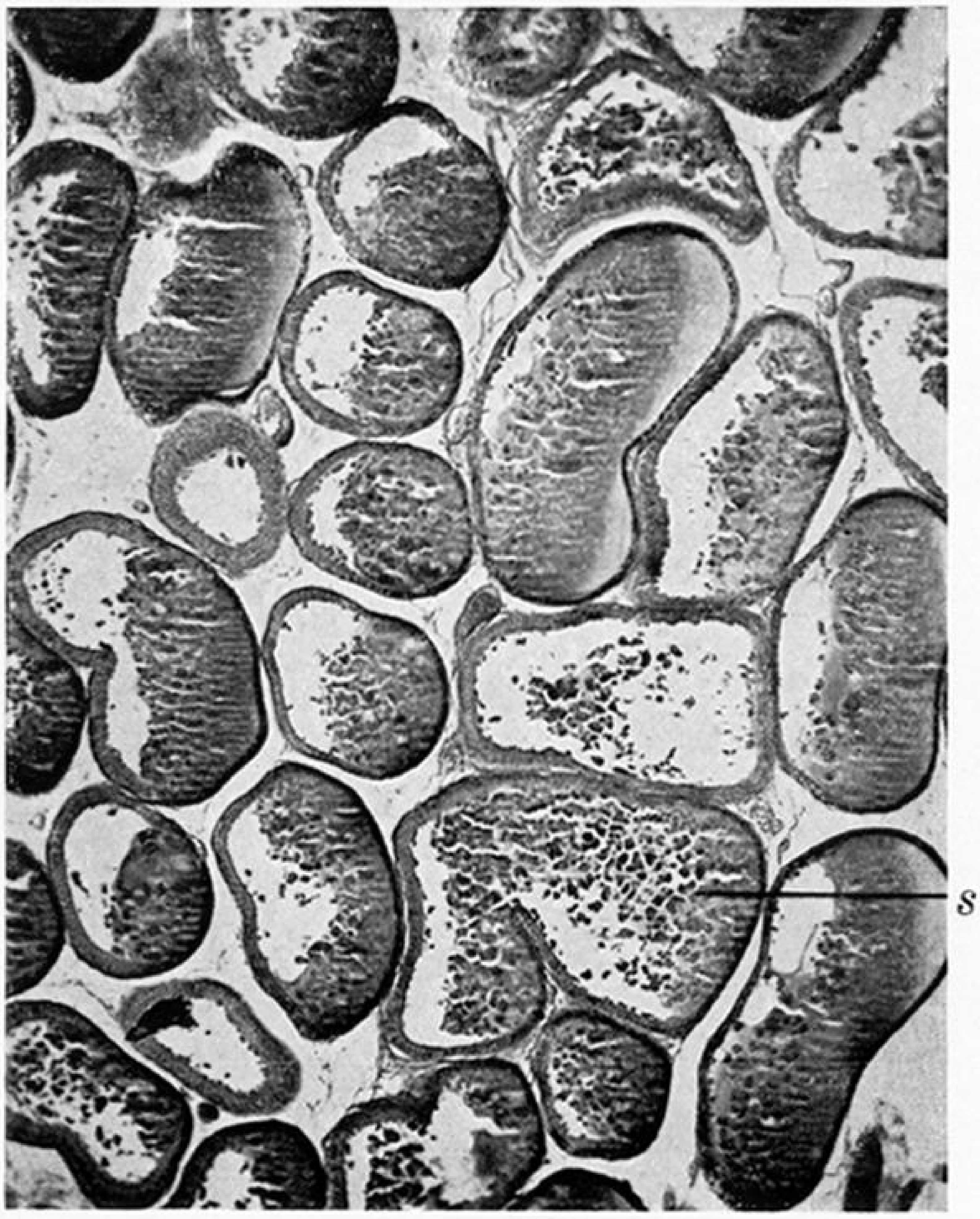

Fig. 24.

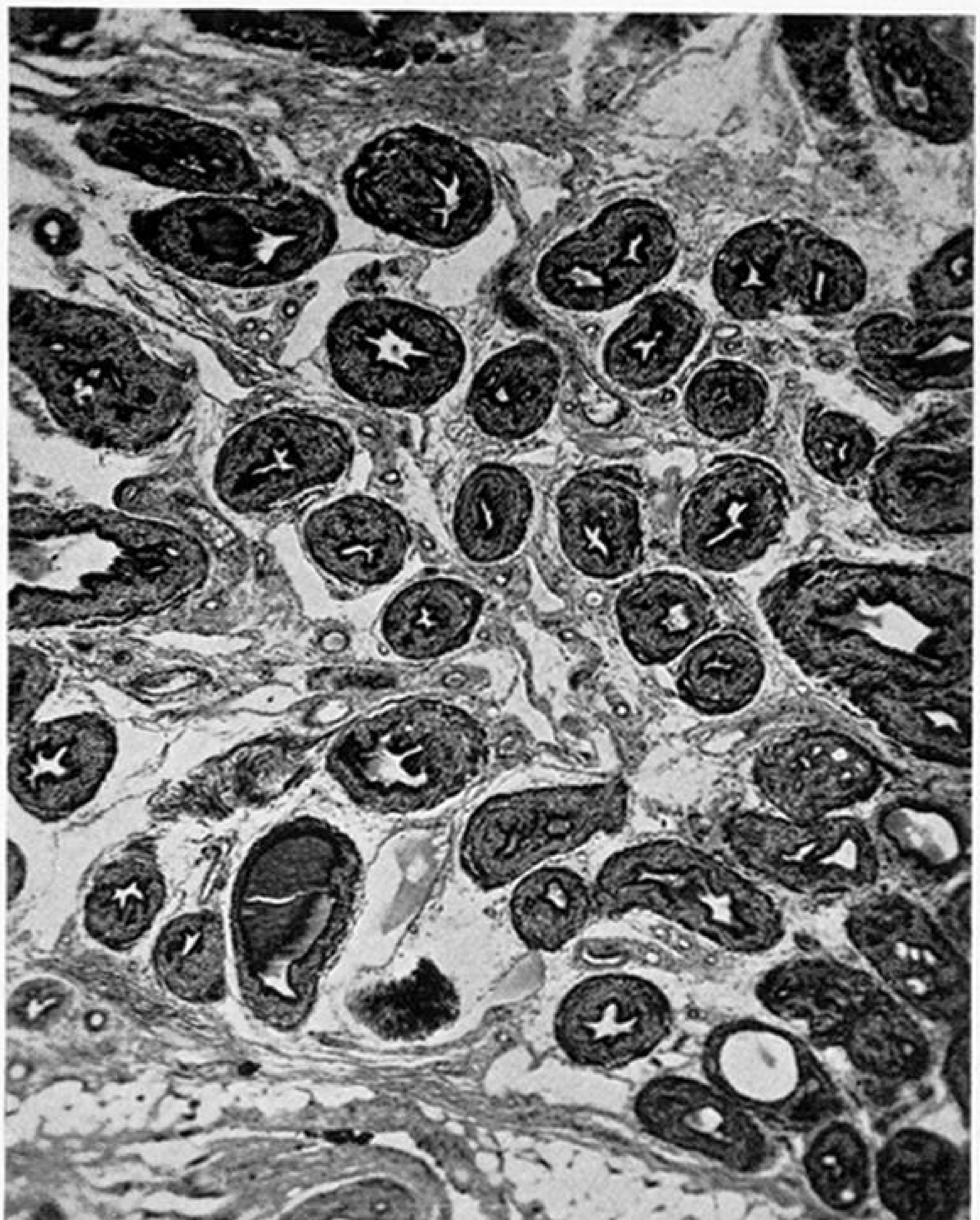

Fig. 25.

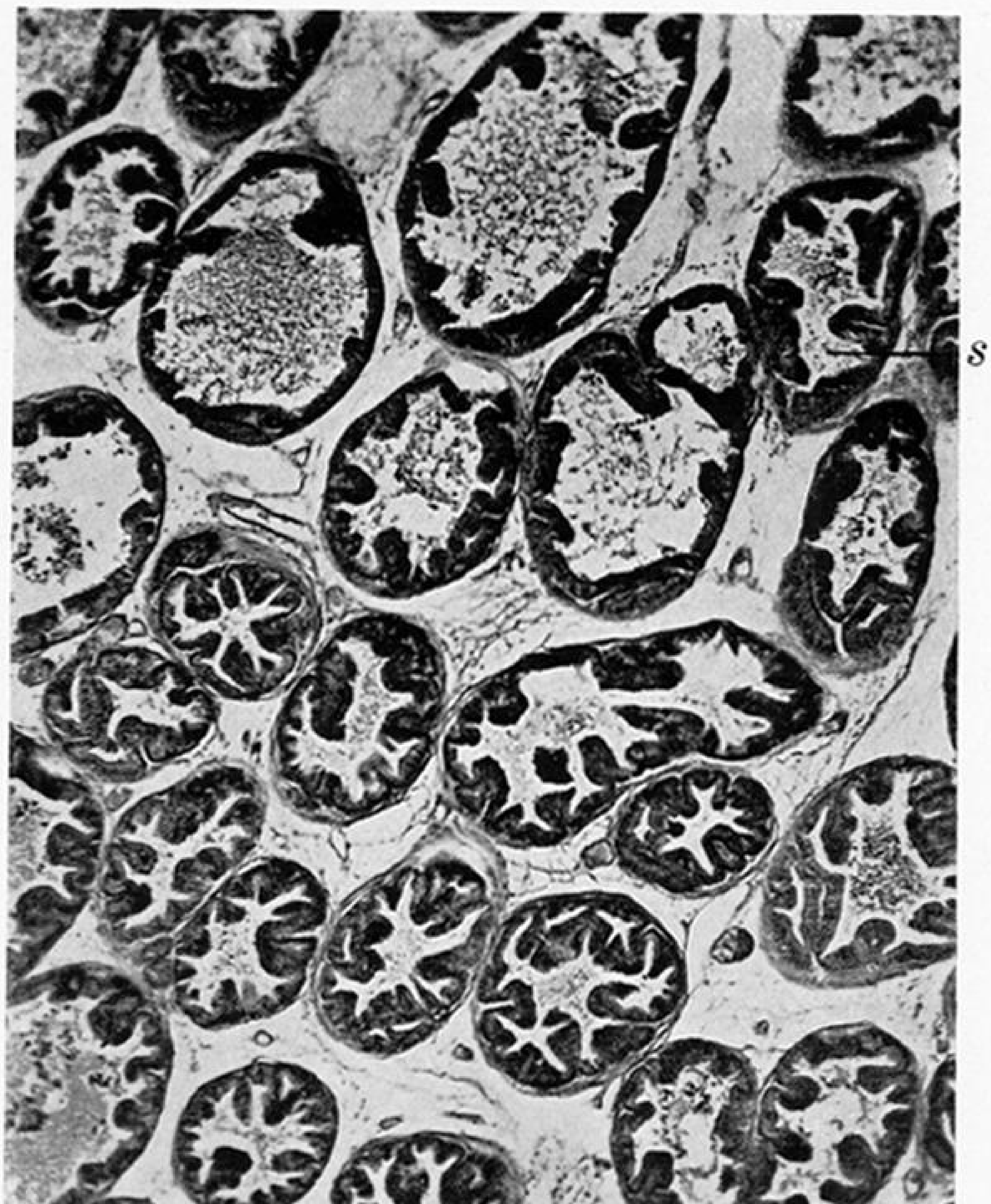

Fig. 26.

Plate 36.

Fig. 23.—Seminal vesicle of No. 9, killed 18 November. Tubules shrunken, little secretion. × 40.

Fig. 24.—Seminal vesicle of No. 252, killed 18 April. Tubules filled with secretion. × 40.

Fig. 25.—Prostate of No. 25, killed 13 February. × 40.

Fig. 26.—Prostate of No. 252, killed 18 April. × 40.

Fig. 27.

Fig. 28.

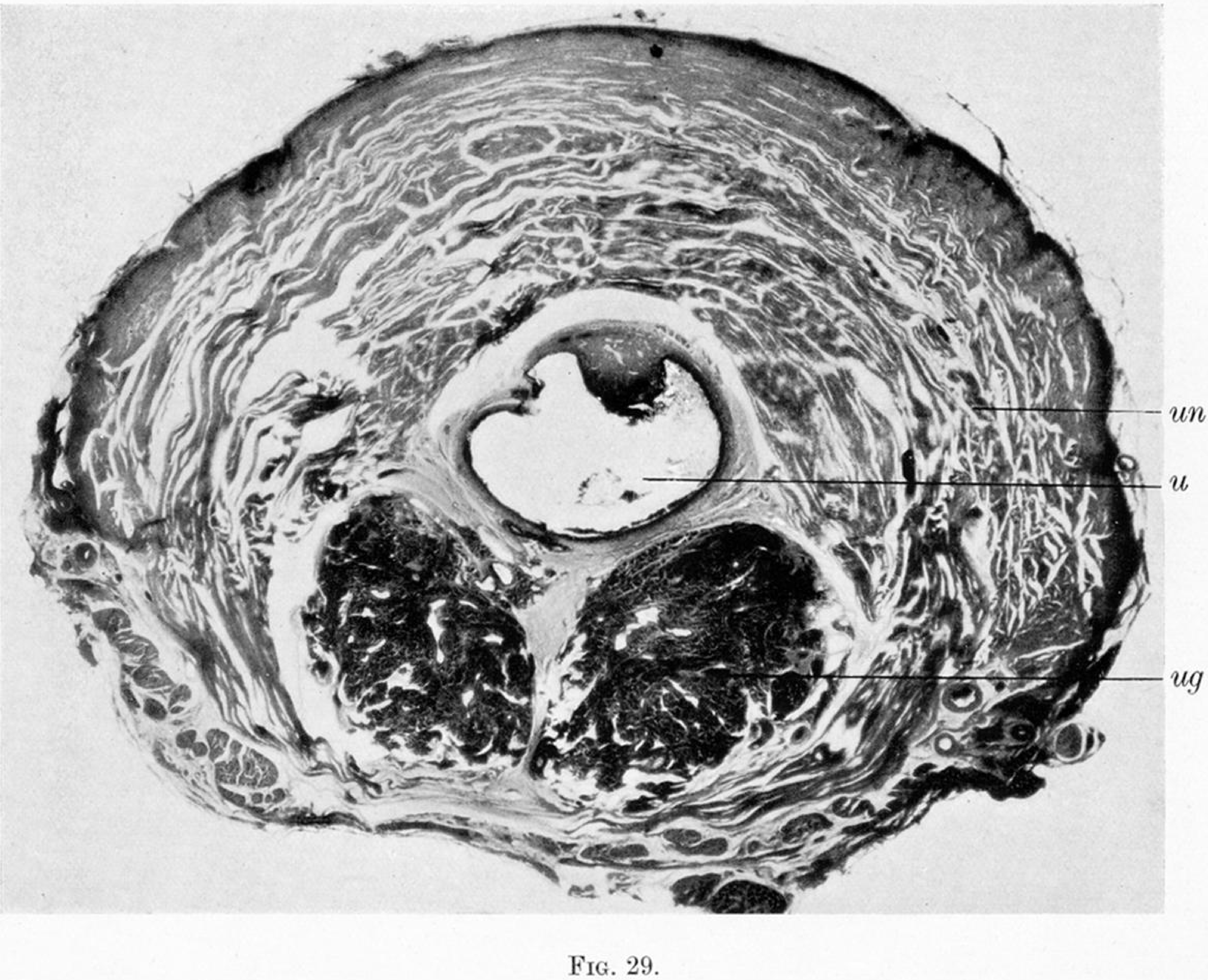

Fig. 29.

Plate 37.

Fig. 27.—Cowper's gland of No. 240, killed 28 January. × 40.

Fig. 28.—Cowper's gland of No. 88, killed 6 May. × 40.

Fig. 29.—Urethra from animal killed in July, showing the two masses of glandular tissue ventral to the urogenital tract.