PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

# The Reproductive Processes of Certain Mammals. Part IX. Growth and Reproduction in the Stoat (Mustela erminea)

Ruth Deanesly

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# XI—The Reproductive Processes of Certain Mammals

## Part IX—Growth and Reproduction in the Stoat (*Mustela erminea*)

*By* Ruth Deanesly, *M.A.*, *D.Sc.*,
*National Institute for Medical Research, London*

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[Plates 28 to 31]

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## I—Introduction

As the result of the investigations of Marshall (1904), Robinson (1918), Hammond and Marshall (1930), Allanson (1932) and others, we have an extensive knowledge of the reproductive cycle of the domestic ferret, but naturally, far less is known about the wild Mustelidae in Great Britain. Marshall and Jolly (1905), in reviewing the literature on the reproductive cycle in Carnivores, comment on the variability in this group and particularly on the frequent recurrence of oestrus in certain animals (such as the ferret, the domestic cat, and some of the larger Carnivora in Zoological Gardens), under conditions of captivity or domestication. A further example is found in the otter, which usually has one litter a year between October and February (Millais, 1905). Cocks (1881) states that the female otter in the absence of the male came on heat almost every month. When a male was put with this animal, mating took place on July 17 and August 12, and as the result of the second mating two young were born on October 12, gestation having lasted 61 days. It remains uncertain whether the recurrence of oestrus should be attributed to the conditions of captivity.

The Mustelidae in Great Britain most nearly related to the stoat are the polecat (of which the ferret is a domesticated variety), the pine-marten and the weasel. Most of our information about these animals is derived from Cocks's observations extending over many years. Cocks bred polecats in captivity and records that gestation lasts 40 days; in the wild the young are generally born in June. A hybrid ferret-polecat litter had a gestation of 42 days (Cocks, 1880, 1891). Cocks first bred the pine-marten in captivity in 1882; later, he established the length of gestation as 94–106 days (Cocks, 1900). Pairing took place in captivity in January, and two males were born in April; in July these were bigger than their mother and by the autumn they were full grown. An Irish marten sent to England in February had a litter on March 31 (Cocks, 1897). The stoat and weasel are much commoner than the polecat or pine-marten, but there seem to be no records of the length of gestation in these species, but only an assumption that it is six weeks, or as long as in the ferret. Simpson (1924) and Thompson (1931) state that the weasel may breed more than once a year, although Millais (1905) discredited the suggestion. Thompson says that the pairing season is from January to early March; the litter consists of 4–6 young. Simpson refers to "two, three or four litters from March to September." He describes the weasel as becoming pregnant again before the first litter is self-supporting, although the young can fend for themselves at six weeks old.

The stoat, on the other hand, is generally thought to breed once a year only, in the early spring. Millais (1905) mentions a litter in April, and comments on the variable number of stoats at a birth. A stoat-ferret hybrid had a gestation of 40 days. Simpson (1924) writes that stoats probably have one litter a year of five or six, born about April. Thompson (1931) says that stoats may pair as early as February and five or six young are born in April or May.

Since thousands of stoats are killed annually by game-keepers and others, no difficulty was experienced in getting a plentiful supply of material. Evidence was collected bearing on the limits of the breeding season and other features of the reproductive cycle, although the precise length of pregnancy could not be established in an investigation of this kind. Stoats are unsatisfactory animals to tame, and there seem to be no records of their breeding in captivity.

## II—Material and Methods

### (*a*) *Collection of Material and Records*

662 stoats were collected from different parts of England and Wales between November, 1930 and October, 1934. Sixty-six of these were sent in alive and killed in the laboratory; others were fixed in the field by gamekeepers, but most of the animals, owing to the expense and difficulty of procuring them alive and undamaged, were fixed in the laboratory, the interval after death varying from several hours to three days. Only about a quarter of the material was therefore suitable for detailed histological study, although in very few animals were the post-mortem changes such as to prevent a diagnosis of the condition of the reproductive organs. Against the disadvantages of post-mortem changes must be set the advantages of making notes on the condition of the intact animal, which is impossible when material is sent in fixed. Most of the Caernarvon stoats were dissected and fixed by Professor F. W. Rogers Brambell, in Bangor, and the majority were fresher than those sent to London from other districts.

Stoats were received from 30 different counties in England and Wales; the principal ones are listed below, but it is not suggested that the figures indicate the distribution of the stoat population in different parts of Great Britain. The collection included only one ermine and one partially ermine animal. The numbers were as follows :—

| | |
|---|---|
| Caernarvon . . . . . . . . | 306 |
| Nottinghamshire . . . . . | 52 |
| Hertfordshire . . . . . . . . | 52 |
| Huntingdonshire . . . . . | 40 |
| Yorkshire . . . . . . . . . | 37 |
| Sussex . . . . . . . . . . . | 26 |
| Merionethshire . . . . . . | 17 |
| 23 other counties . . . . . | 112 |
| Origin not recorded . . . . | 20 |
| Total . . . . | 662 |

Twenty-two stoats were discarded as useless for various reasons. In all, 392 males and 248 females were examined (Tables 1 and 2) ; it is doubtful if the excess of males in this collection is due to an abnormal sex-ratio, and not to the methods of trapping. In the adults it may be attributed to the females being less active during the months when they are pregnant and lactating.

As a check on the age of the animals, about 370 skulls were examined, and, unless damaged, preserved and cleaned, and 283 stoats were measured in length from the anterior end of the skull to the last caudal vertebra.

Owing to fixation in the field and other causes, the body weights were not recorded for 28 males and 14 females.

### (*b*) *Fixation, Weighing and Histological Work*

Fixation was in Bouin's aqueous or alcoholic fluid. The reproductive organs were weighed after transference to 70 per cent. alcohol ; for the male, the weights of the paired testes, epididymides and os penis were recorded, and for the female the weights of the decapsulated ovaries and uterus. (Throughout this paper, the terms testis weight, epididymis weight and ovary weight apply to the weight of the paired organs). The weights of the organs of six unilaterally cryptorchid males are omitted from the averages in Table 1.

The adult males during the breeding season, and the immature first year males showed so little variability in their reproductive organs that it was considered unnecessary to section material from all the animals. A selection was therefore made as follows : the testes were sectioned from 85 out of 163 adult stoats killed during March, April, and May ; all these, except five which dated from early March, contained spermatozoa. Since the testes examined included the smallest in these months, it was assumed that the remaining testes would be equally active, and they are listed accordingly in Table 1. The testes were sectioned from all adult stoats (those more than nine months old), killed during the rest of the year. Out of 181 immature (first year) stoats from May to December the testes were sectioned from only 72 animals, representative material being selected in each month according to the animal's freshness, body weight and testis size.

The epididymis was sectioned from 132 animals to ascertain growth and seasonal changes. The vas deferens was sectioned from 14 animals. The ovaries and uterus were examined histologically in all stoats, except 23 in July, which were so badly preserved that only the uteri were sectioned. In all others, complete serial sections were cut of at least one ovary, and several transverse sections were cut through the uterus. Both ovaries were sectioned from all pregnant stoats, and from a number of non-pregnant ones, but only one section in six was mounted from certain ovaries. The Fallopian tube was sectioned, in some cases serially, from 28 stoats, and the vagina from 75 stoats. Histological measurements were carried out with a micrometer eyepiece. The mammary gland was preserved from about 80 stoats and dissected and stained preparations were made according to the method described elsewhere (Deanesly, 1934).

## III—The General Morphology of the Reproductive Organs

### (*a*) *Male*

The stoat, like other Carnivora, has simple reproductive organs with only rudimentary accessory glands. The testes and epididymides descend into scrotal sacs at the onset of the breeding season, but lie inguinally in immature animals. There is an os penis which weighs 10–30 mg in most first year animals; it increases rapidly in weight at sexual maturity, and shows no definite regression during anoestrus so that it serves as a means of distinguishing adult males. The heaviest os penis in the present series weighed 89 mg, the average weight during the breeding season being 54 mg.

### (*b*) *Female*

The female reproductive organs resemble those of the ferret. The ovaries are flattened bodies enclosed in a capsule; their surface is smooth and neither follicles nor corpora lutea project conspicuously. The Fallopian tube is not coiled but lies in a ring round the ovary and opens into the uterus just below the extremity. The uterus is small and bicornuate, and the uterine canals run side by side for about 1·5 mm. and then fuse at the top of the cervix. The single cervical canal is lined by uterine endometrium almost up to the vaginal opening. The vagina is thin and terminates in a vulval swelling which enlarges to about 0·5 cm diameter just before oestrus; there are no vaginal glands. A minute knob of cartilage corresponding to the os penis may be found in the vulva.

The mammary glands are low on the abdomen. The nipples which are often asymmetrical in position, and sometimes in number, vary from 4–6 pairs and are inconspicuous in the non-parous animal.

## IV—Classification of Material

The breeding season of the stoat in England and Wales is comparatively restricted, the great majority of the young being born in March and early April. Under these circumstances it was expected that classification of material of unknown history brought in from the field would be a simple matter. In practice, however, certain difficulties arose in the months June to December, owing to the rapid growth of the young of both sexes (figs. 1–3), and to the scarcity of adult males after the end of June.

In order to ensure accurate diagnosis of the first year animals the skulls were examined in 370 stoats. This provided a ready means of identifying first year animals up till the end of the year in which they were born. In the final classification, male animals one year old or more could be distinguished by the size of the testes, except during the last four months of the year, and by the size of the os penis.

Female stoats, mostly pregnant and lactating in March and April, respectively, can readily be distinguished as second year parous animals from May to July by the nipples and mammary glands residue. Towards the end of the year it is necessary to rely upon the appearance of the skull or, when that is not available, upon the condition of the uterus. Parous uteri unfortunately are far less distinct from non-parous ones in the stoat than in species such as the squirrel and hedgehog, but they could generally be identified by the pigment in the gland tubules and stroma. Figs. 1 and 3 show that the first year female stoats cannot regularly be distinguished after May by their body weights, ovary weights or uterus weights.

The diagnosis of the condition of the reproductive organs of most of the males was easy since in the majority of animals caught the testes were either large—0·75–2·0 gm —and spermatic or obviously undeveloped and weighing only about 0·1 gm. Intermediate stages occurred in January, February, and early March, when the testes were increasing in size, and stages showing regression of the testes were found in 8 of the adult males taken between July and December.

In the females the determination of the stage of the sexual cycle was made by the usual methods; mammary glands and nipples were first examined when possible, and the appearance of the reproductive tract was noted. Oestrus females could be distinguished by their swollen Fallopian tube, cervix and vulva and by their enlarged uteri. Sections through the ovaries showed the presence or absence of follicles and corpora lutea, and sections through the accessory organs showed different conditions of the epithelium according to the stage of the ovarian cycle. Spermatozoa in the uterus provided evidence of recent mating. In the young female stoats, taken from May onwards, there was hardly any development of the nipples and mammary glands, but the ovaries and accessory organs revealed the same phases as those of the adults. Only a few of these animals were classified as not yet oestrus; most of them, when killed, contained corpora lutea in their ovaries.

Since no skulls were available for many of the January and February stoats, all animals have been listed as adults in these months, although most of the males are first year ones and some of the females are non-parous.

## V—Growth of the Stoat

Fig. 2 shows the growth of the young male stoat up to the end of the year in which it is born, and fig. 1 shows the body weights of adult stoats from January onwards. A comparison of these figures indicates that there are two main growth phases after the animal is weaned ; during the first of these, very rapid growth occurs so that in July, at three months old, the animal may weigh as much as 320 gm. From the end

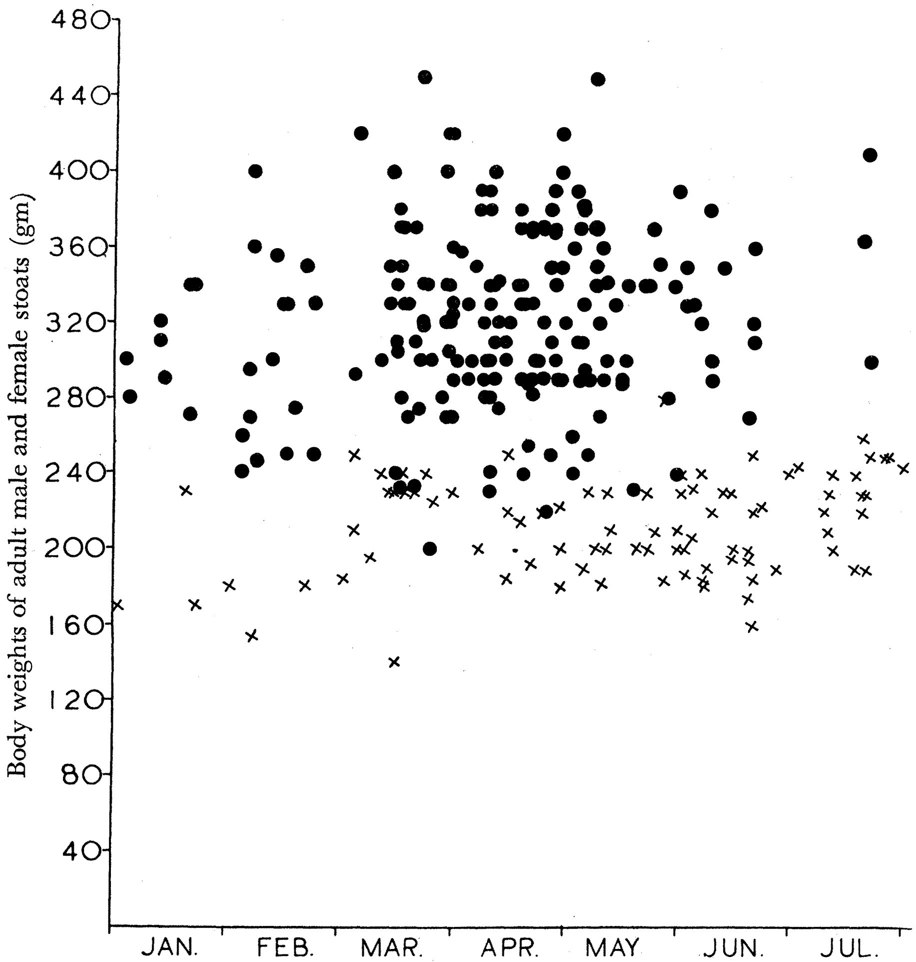


Fig. 1—Graph of the body weights of adult stoats from January to July, male ● x female. There is very little overlapping of the body weights of the two sexes.

of July till the end of December, however, there is only a slight rise in body weight, Table I. It is clear that although individual male stoats may reach the average breeding season body weight of adults by December of their first year, most of them fail to do so until the following March, when the average weight is about 60 gm higher.

Adult stoats seem to show a slight fall in body weight during the autumn and winter but there are not enough animals to establish this point clearly since some of those in January and February are in their first year.



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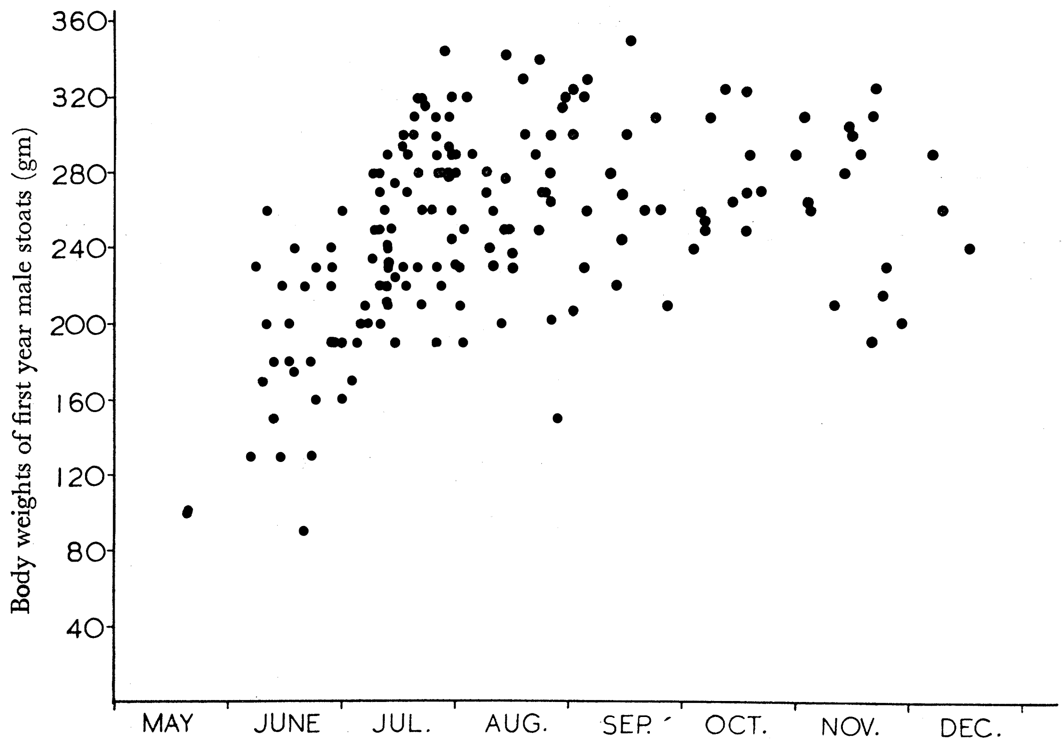


FIG. 2—Growth of the male stoat; graph of the body weights of first year males from May to December. Comparison with fig. 1 indicates that the full adult body weight is not reached until the stoat is about 10 months old, just before its first breeding season.

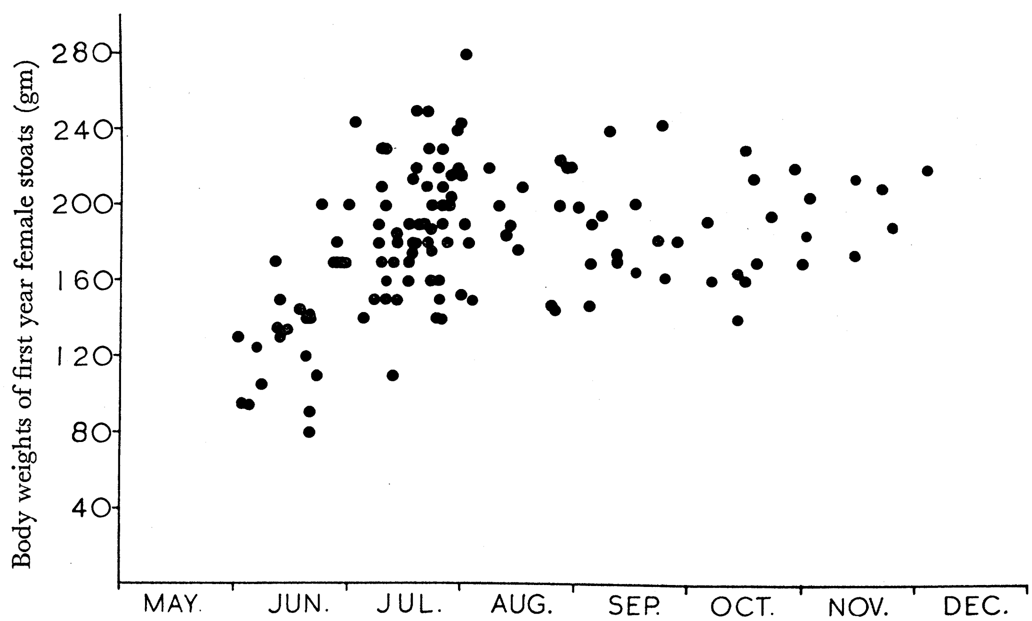


FIG. 3—Growth of the female stoat; graph of the body weights of first year females from June to December. Comparison with fig. 1 indicates that adult body weight is reached in July when the animal is only about 3 months old.

TABLE I—NUMBERS, DISTRIBUTION, BODY WEIGHTS AND WEIGHTS OF THE REPRODUCTIVE ORGANS OF MALE STOATS, AVERAGED FOR EACH MONTH OF THE YEAR.

| Month | Immature Stoats | | | | Adult Stoats | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | No | Body weight gm | Testis weight gm | Epididymis weight gm | No | Number in spermatogenesis | Body weight gm | Testis weight gm | Epididymis weight gm |
| January | — | — | — | — | 8 | 0 | 294 | 0·154 | 0·057 |
| February | — | — | — | — | 19 | 1 | 303 | 0·323 | 0·099 |
| March | — | — | — | — | 51 | 46 | 325 | 1·059 | 0·228 |
| April | — | — | — | — | 73 | 73 | 324 | 1·320 | 0·318 |
| May | 2 | 100 | 0·045 | 0·020 | 38 | 38 | 323 | 1·093 | 0·330 |
| June | 28 | 178 | 0·082 | 0·031 | 12 | 12 | 326 | 1·035 | 0·315 |
| July | 62 | 257 | 0·101 | 0·046 | 3 | 3 | 358 | 0·749 | 0·281 |
| August | 35 | 264 | 0·097 | 0·045 | 1 | 1 | 300 | 0·452 | 0·160 |
| September | 21 | 276 | 0·098 | 0·038 | — | — | — | — | — |
| October | 14 | 277 | 0·095 | 0·035 | 3 | 0 | 301 | 0·161 | 0·086 |
| November | 16 | 264 | 0·082 | 0·029 | 1 | 0 | 275 | 0·144 | 0·071 |
| December | 5 | 263 | 0·107 | 0·038 | — | — | — | — | — |
| Total | 183 | — | — | — | 209 | — | — | — | — |

Fig. 3 shows the growth of the young female stoat after weaning ; growth is rather less rapid than in the young male, the average weight reached in June being 140 gm as compared with 178 gm, Table II. The immature females, however, show a nearer approach to the adult body weight, 190—205 gm, fig. 1, than do the males. In July the average weight of the first year females, 196 gm, is only slightly below that of the parous stoats in the same month, 208 gm. In other words the female stoat at three months old has practically reached its full size. This early growth is associated with premature development of the reproductive organs.

Both male and female stoats attain adult length in July. This varies in the male from 35–41 cm, and in the female from 33–37 cm.

Like other Carnivora, the stoat shows very well-defined age changes in the skull during its first year of life. These were found useful in distinguishing well-grown first year from second year stoats. In addition to the closure of the sutures there are changes in the appearance of the skull due both to the gradual extension of the temporal muscles, and to increasing calcification. The most obvious sutures are the fronto-parietal and spheno-basilar which close and disappear fairly early in development, and the nasal sutures, which persist until later.

In June the permanent dentition is complete in most animals ; the skulls of the well-grown, three-months-old stoats are easily recognizable, however, by the open sutures and by the chalky appearance of the bone. The male skulls in June on the whole tend to be more undeveloped than the female ; the fronto-parietal and spheno-basilar sutures which are disappearing at this stage from the female skulls are more open. In both sexes the temporal muscles only extend part of the way up the parietals, and bone, which does not give origin to muscle is clearly distinguishable in the dry skull, fig. 8, Plate 28. In skulls of both sexes collected during July, the temporal ridges, beginning posteriorly at the external occipital protuberance, are

Table II.—Numbers, Distribution, Body Weights and Weights of the Reproductive Organs of Female Stoats Averaged for Each month in the Year

| Month | First year Stoats | | | | Adult Stoats | | | |
|---|---|---|---|---|---|---|---|---|
| | No | Body weight gm | Ovary weight gm | Uterus weight gm | No | Body weight gm | Ovary weight gm | Uterus weight gm |
| January | — | — | — | — | 5 | 190 | 0·034 | 0·070 |
| February | — | — | — | — | 4 | 190 | 0·043 | 0·075 |
| March | — | — | — | — | 16 | 224* | 0·053 | 0·060† |
| April | — | — | — | — | 13 | 208* | 0·054 | 0·282† |
| May | 2 | — | — | — | 16 | 210 | 0·064 | 0·151 |
| June | 25 | 140 | 0·041 | 0·073 | 26 | 208 | 0·065 | 0·105 |
| July | 55 | 189 | 0·049 | 0·075 | 19 | 228 | 0·061 | 0·124 |
| August | 19 | 197 | 0·048 | 0·071 | 2 | 257 | 0·087 | 0·112 |
| September | 16 | 197 | 0·045 | 0·069 | 2 | 221 | 0·028 | 0·119 |
| October | 13 | 185 | 0·040 | 0·073 | 1 | 150 | 0·031 | 0·076 |
| November | 7 | 197 | 0·038 | 0·068 | 2 | 198 | 0·034 | 0·065 |
| December | 1 | 220 | 0·042 | 0·079 | 4 | 211 | 0·023 | 0·073 |
| | 138 | | | | 110 | | | |

* Excluding late pregnancies.
† Excluding pregnant uteri.

fusing to form a sagittal crest; this leads to the formation of a deep V open anteriorly between the temporal crests, figs. 9 and 10, Plate 28. In some female skulls the sagittal crest does not develop very far, and the apex of the V may remain for some months, fig. 10, or even as late as the next breeding season, very close to the external occipital protuberance. In other females, and all males, the sagittal crest elongates until the V between the temporal crests is short and open as in fig. 11, Plate 28. Numerous transitional stages can be found, a typical one from a young male stoat in August being illustrated in fig. 9. Here the fronto-parietal suture has disappeared, the temporal ridges have partially fused, and there is the beginning of a sagittal crest. Characteristic of the young skull, however, are the open nasal sutures and the dull, rough surface of the bone.

By August the nasal sutures are disappearing, and the skulls are beginning to take on their adult appearance. The bone is becoming harder and has a more glossy surface, but the marks associated with the convolutions of the brain are less distinct than in the older stoat. Unfortunately, no skulls of second year animals were available for the months of September, November, and December. In October, the first year males were generally only distinguishable by the appearance of the bone, but most of the female skulls still showed signs of the recent fusion of the muscle ridges.

## VI—The Reproductive Cycle in the Male

### (a) *Breeding Season and Duration of Fertility*

Table I summarizes the data on seasonal changes in the male stoat. Spermatozoa are generally absent from the testes in February ; in the one recorded case of active testes, on February 7 in a second year animal, spermatozoa had not yet reached the epididymis. In March, however, almost all stoats are in spermatogenesis ; of the five exceptions in the series, three belonged to the first week in the month. Spermatozoa were found in all adult stoats caught in April, May, and June, of which the testes were examined and also in the only 4 adults taken in July and August.

As regards the fertility of the male stoat, the records of pregnancies, Table IV, seem to indicate that fertile matings only take place during a restricted period from the end of February until the beginning of April. There is ample evidence of matings in later months, Tables III and V, but apparently these, or certainly the great majority of them, prove infertile. The matter is further discussed in § VIII.

As in other mammals with periodic activity, the onset of spermatogenesis is marked by an increase in the size of the testes which descend into scrotal sacs. The testes of an anoestrus adult may weigh as little as 0·15 gm, but at their maximum in April the average weight is 1·32 gm—nearly 9 times as much.

Fig. 4 shows that most of this increase in size takes place in late February and early March, although during the first half of April the testes continue to enlarge. Between April 1 and 15, 31 stoats had an average testis weight of 1·35 gm, and 39 stoats in the second half of the month had an average testis weight of 1·30 gm. The difference is slight, but taken with the further fall to an average testis weight of 1·09 gm, which occurs in May, it seems probable that the peak of testis activity is passed by about the middle of April, although spermatozoa are abundant for some time afterwards. Maximum testis size therefore is not reached until shortly after most of the fertile matings have taken place. Table IV shows the fall in testis weight from July onwards. From October till December or January the testis remains at a very low level of activity ; in this and other respects the stoat closely resembles the related ferret (Allanson, 1932).

The epididymis shows size changes comparable to those of the testis, the anoestrus weight being 70–80 mg, and the breeding season weight up to 400 mg, but there is a slight lag both when the weight is rising and falling as compared with the testis, Table I.

The os penis undergoes rapid growth in March in animals having their first breeding season ; before the breeding season it weighs 20–30 mg, but a month later it has approximately doubled.

### (b) *Condition of First Year Stoats*

Table I and fig. 4 show that the testes reach a weight of about 100 mg in the four-months-old stoat in July, and that no further growth takes place until the following year, the testes remaining very undeveloped. Since testes of this type are common up till January, but absent during March and April, it may be assumed that all male stoats become spermatogenic for the first time at about 10 or 11 months old, that is, they are ready to breed in the season following the one in which they were born.

## VII—Histological Changes in the Male Reproductive Organs

### (*a*) *Seminiferous Tubules and Interstitial Cells of the Testis*

The immature testes up till about the end of August show little variation in appearance. The tubules in section generally have a diameter of about 60–70 μ, and are

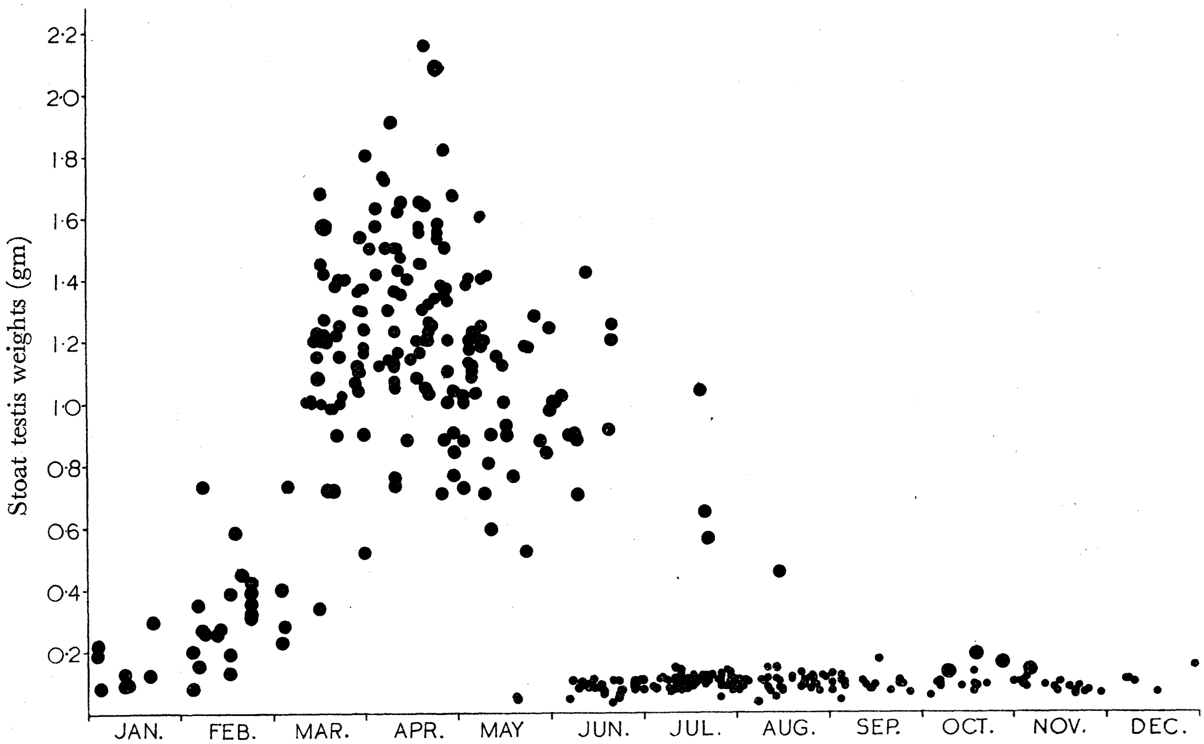


Fig. 4—Testis weights of immature and adult stoats showing the seasonal changes in the latter. The weights of the adult anoestrus testes overlap those of the immatures in October and November. Adult ●, immature •.

filled with syncytium and lined by a single row of spermatogonia with nuclei 4-5 μ in diameter and Sertoli cells. Occasional spermatogonia, larger than the others, can be seen lying free in the syncytium; these are the so-called winter spermatogonia resembling those described in the bat by Van Beneden and Courrier (Courrier, 1927), fig. 22, Plate 29. It is clear that in the stoat, some of the spermatogonia at the edge of the tubule enlarge and migrate inwards to form the "winter" spermatogonia, whose nuclei may be as much as 16 μ or 20 μ in diameter. These nuclei appear to divide by mitosis, but occasionally cell division is incomplete and cells with two nuclei or with an irregular nucleus can be found.

The polygonal interstitial cells in these immature testes occupy nearly half the area of the section; they have nuclei 5 μ in diameter, and an area of about 50 sq μ. Larger interstitial cells are often found next to the tunica. In these testes there is no regular formation of primary spermatocytes and mitoses are comparatively rare.

From September till the end of the year, although the immature testes show no increase in average size, proliferation takes place and the tubules become lined with a double row of spermatogonia. In stoat 609, taken on September 16, where the testes weighing 0·18 gm are larger than in any other immature animal before January, the tubules are still small—about 84 μ diameter—and solid, but spermatogonia are in mitosis. Smaller testes in September, however, are in the resting condition. Large "winter" spermatogonia are still present in the autumn months, and there is some indication that their numbers increase just before the first proliferation phase and thereafter diminish. Since there is no evidence of extensive pycnosis it is probable that these cells eventually give rise to primary spermatocytes. Mitoses tend to become more numerous towards the end of the year, but even as late as December 16 very undeveloped testes can be found. The interstitial cells show no appreciable changes.

In January, excluding those of two obviously second year stoats, the testes vary from 0·085–0·188 gm in weight. In the largest of this group the tubules have a diameter of 100–120 μ, and the spermatogonia nuclei are now slightly larger than those of the interstitial cells. About half of the tubules in a section contain primary spermatocytes in mitosis, but no lumen has yet appeared. The interstitial cells show an infiltration of capillaries and lymphatics.

Two second year stoats in January (identifiable as such by the os penis) have testes weighing 0·22 and 0·30 gm; these show further proliferation and tubule enlargement up to 170 μ.

In February there is great spermatogenic activity while the testis is increasing rapidly in size, fig. 4. All stages of spermatogenesis can be found, although actual spermatozoa only occur in one animal during this month, No. 656, February 7, and then they are very rare and absent from the epididymis. Only one other stoat in February showed spermatids, No. 248, February 16. This, like No. 656, was an obvious second year animal. Most of the testes in February show at least the beginnings of a lumen in the tubules, but only in the largest is it fully formed. In these testes the tubule diameter is about 170 μ no greater than in the largest January testes.

In March all testes over 0·73 gm and some of those under that weight are spermatic, the smallest of the latter weighing 0·28 gm. Testis enlargement and spermatogenesis evidently proceed rapidly at the end of February and the beginning of March, Table I and fig. 4. In the fully developed active testis the tubules have a diameter of about 200–210 μ. In March the interstitial cells reach their maximum size which is a little greater than in the immature or anoestrus testis; the nuclei are 7–8 μ in diameter, and the cell area in section is about 100–150 sq μ, but both are variable.

The tubules seem to reach their maximum diameter at a testis weight of 0·9 gm or less, and thereafter they show little increase, so that it must be assumed that, as in other species, increase in the length of the tubule takes place, as the testis grows. (Rowlands and Brambell, 1933; Allanson, 1933, 1934.)

During April and May all adult animals have spermatozoa, and the testes do not differ appreciably in section from the functional ones found in March. There is no obvious decrease in tubule diameter or in interstitial cell size. Even in June, more than two months after the last recorded pregnancy, there are only slight signs of the onset of anoestrus; some of the testes show a disappearance of the later stages of spermatogenesis from a few of the tubules, but spermatozoa and mitotic figures are still abundant. Table I shows that the average weight of the testes remains almost stationary in May and June, but falls sharply in July to judge from the only three adult males caught during that month. One of these still had large testes, 1·04 gm, but all show a slight but definite fall in tubule diameter to about 190 μ. The interstitial cells seem to show nuclear and cytoplasmic shrinkage. The lumen of the tubules is becoming obliterated. In all July testes, however, spermatogenesis seems to be still proceeding.

Only one adult stoat with testes weighing 0·45 gm was taken in August; regressive changes in the seminiferous tubules are very marked, though a few spermatozoa can still be found. The average tubule diameter is about 140 μ. A few of the tubules contain only Sertoli cells, spermatogonia, and primary spermatocytes, but most of them show later stages of spermatogenesis; the cells, however, are not regularly arranged and often are clumped together and appear to be degenerating. The interstitial cells have regressed to the same size as those in the immature testis.

The testes of the remaining adult stoats, three killed in October and one in November, can be described together. They are comparable to those of the late autumn ferret (Allanson, 1932), and show the usual characteristics of anoestrus testes. They are so small as to be superficially similar to the immature testes at the same season of the year, fig. 4; the tubule diameter is approximately the same, about 80 μ, and the tubules which are filled with syncytium contain only Sertoli cells, primary spermatogonia, and winter spermatogonia, with few mitotic figures. The adult anoestrus testes, however, can be distinguished by the following characteristics: (1) the conspicuous thickening of the tunica caused by the contraction of the testis to one-ninth of its full size; (2) the similar thickening of the basement membrane round each tubule which results in a slight separation between the spermatogonia nuclei and those of the membrane; and (3) the infiltration of leucocytes and endothelial cells among the interstitial tissue. The second of these features is more prominent in October, when the testes have recently shrunk, than in November.

In the anoestrus testis the interstitial tissue, having regressed proportionately less than the seminiferous tubules, is more prominent than in the fully developed organ, although the actual cells are smaller, figs. 23, 24, Plate 29.

### (*b*) *Epididymis*

In first year stoats the epididymis, like the testis, remains small and no active growth takes place after August until just before the next breeding season, Table I.

Up till July or August, however, the epididymis appears to grow steadily, but from then onwards it seems to shrink, indicating perhaps a seasonal variation comparable to that found in the adult animals. The highest epididymis weight for an immature animal before the end of December is 105 mg in August.

Table I shows the increase in the weight of the epididymis before and during the breeding season. Unlike the testis, which arrives at its maximum average weight in April, the epididymis does not attain its maximum weight until June so far as can be determined from the present material. It therefore illustrates the usual lag in the development of the accessory organs as compared with the testis (Allanson, 1934), but it is surprising that it should reach its maximum as in the bat (Courrier, 1927) after the time of fertile mating is past. From July onwards, the epididymis of adult stoats shows a steady fall in weight until in October it is no larger than in the most developed of the immature animals.

Histologically, the epididymis shows seasonal changes of the usual type, but anoestrus regression is not conspicuous until August. It is uncertain whether or not spermatozoa persist until September, but by October they had disappeared and they were not found in the epididymis again until March. In the females, uterine spermatozoa were found in all months of the year except November and December.

Correlated with the changes in weight of the organ are changes in the diameter of the epididymal tube. Early in the breeding season, in the smallest epididymis containing spermatozoa, the diameter, including the surrounding muscle layers, is only 96 μ, but it may reach 190 μ in the fully developed organ. From July onwards there is a steady decrease; typical measurements are July 143 μ, August 110 μ, October 92 μ and 73 μ, and November, 72 μ. The diameter of the epididymis tube in the immature stoat measures about 60 μ before January, when growth begins. A few immature animals, however, have slightly enlarged epididymides, 65–105 mg, in which the diameter of the tube reaches 90-100 μ in August. These epididymides are less muscular than those of anoestrus adults.

During the breeding season the epithelium has a height of 24-30 μ, but it falls to 8–10 μ at the lowest point of anoestrus.

### (*c*) *Vas Deferens*

This shows the normal seasonal changes. From March to May the diameter, excluding the muscle layers is about 200 μ, and in a November adult about 130 μ so far as can be determined. Similarly, the epithelium has a height of about 30–35 μ in the breeding season, and 10-15 μ in anoestrus. In immature males in the autumn the vas deferens has a diameter of about 90 μ, and the height of the epithelium is 10–20 μ. The vas deferens shows an increase in diameter, and in the height of the epithelium in January, as soon as the testis begins to develop.

Spermatozoa were found in the vas deferens from March till August 14 in the present series.

## VIII—The Reproductive Cycle in the Female.

### (a) *Limits of the Breeding Season.*

The present material indicates that almost all stoats become pregnant in March or early April, Table III. Only 3 out of 16 stoats in March were non-pregnant, and these were killed on the 1st, 8th, and 15th, the last being an exceptionally small ermine animal. The first stoat pregnancy of the year, an early one, was recorded on

Table III—Adult Female Stoats Classified according to the Condition of their Reproductive Organs

| Month | Number of animals | Pregnant | Lactating | Non-pregnant: recently parous after April — Number without corpora lutea | Number with large follicles | Number with corpora lutea | Number with uterine sperm |
|---|---|---|---|---|---|---|---|
| January | 5 | — | — | — | — | 5 | 1 |
| February | 4 | — | — | — | — | 4 | 3 |
| March | 16 | 13 | — | — | — | 3 | 3 |
| April | 13 | 3 | 9† | — | — | 1 | 1 |
| May | 16 | — | 9† | — | — | 7 | 4 |
| June | 26 | — | — | 1 | 1 | 25 | 7 |
| July | 19 | — | — | — | — | 8+11* | 8 |
| August | 2 | — | — | — | — | 2 | 2 |
| September | 2 | — | — | 1 | 1 | 1 | — |
| October | 1 | — | — | — | — | 1 | 1 |
| November | 2 | — | — | — | — | 2 | — |
| December | 4 | — | — | 1 | — | 3 | — |

* The ovaries of 11 badly preserved July stoats, whose uteri were in the luteal phase, were not sectioned.

† See Table V.

March 11 and the latest, which was almost full term, on April 10. A fairly early pregnancy (No. 305) was found as late as April 7, but probably most young are born by the end of this month. Of the 13 female stoats (adults) taken in April, 3 were pregnant, 9 were lactating, and the last, a second year animal, with vestigial nipples and mammary gland, showed no signs of recent pregnancy. This stoat, killed on April 29, had ovulated and mated, but had apparently missed the normal breeding season.

The earliest post-partum stoats were killed shortly after parturition on April 11 and 15, exactly a month after the earliest pregnancies, and the latest stoat in full lactation was killed on May 22. Since the male is generally not in spermatogenesis until the beginning of March, pregnancy can hardly be longer than 6 weeks, as in the ferret, and is more probably about 30 days in length.

### (*b*) *Pregnancy, Litter Size and Lactation*

Table IV gives the records of 16 pregnant stoats, of which 12 showed definite uterine swellings, and the remainder were distinguishable by the corpora lutea and mammary glands, as well as by the weight and appearance of the uterus. The number of foetuses varied from 6 to 13 with an average of 9. They were fairly equally distributed (50 and 58) between the two horns of the uterus. From the total number of corpora lutea it appears that 108 out of 135 ova have become implanted. The proportion would be higher (97 out of 112) if No. 298, in which a very large ovulation has taken place, is excluded. Only 5 swellings in the series showed signs of foetal reabsorption. The spacing of the ova seems to be facilitated by their internal migration across the top of the cervix, as in the shrew (Brambell, 1935) and possibly in the hedgehog (Deanesly, 1934). In 3 out of 12 stoats (Nos. 659, 269 and 287) the corpora lutea in one ovary are fewer than the number of embryos in either uterine horn and consequently migration must have taken place. The average number of corpora lutea of pregnancy is 10·7 or, without No. 298, just under 10. In the latest pregnancy, judged by the absence of amniotic fluid to be nearly full-term, the average weight of the foetuses was 3·3 gm after fixation.

Lactation seems to last about 5 weeks ; stoats with fully developed mammary glands, Table V, were taken only in April and May. The first young animals—a litter of six—were obtained on May 19 ; two males weighed 98 and 101 gm, but unfortunately no weight records were kept of the others which were similar and included two females. Out of 16 adult female stoats in May, 9 with their mammary glands fully developed were classified as lactating, and 7 as post-lactation since the glands had regressed to a fraction of the full size. Glands of this type were found from May 11–June 14. Only 6 stoats in June still had appreciable mammary glands, all of which were regressing ; the largest residue was from an animal killed on June 1st. It is probable that intermittent suckling occurs during this month, since some of the nipples on regressed glands are generally enlarged, but in most stoats lactation is over and 20 out of 26 parous females in June showed only traces of mammary glands, although the nipples were readily distinguishable.

### (*c*) *Ovulation and Mating in Lactating and Post-lactation Stoats*

No immediate post-partum ovulation was found. The corpora lutea of pregnancy disappear soon after parturition and were only distinguished in 4 out of 9 lactating animals in April, Table V. In the same month, 2 lactating stoats had no corpora lutea whatever in their ovaries. As in other species, however, anoestrus does not persist during the whole of lactation ; in some lactating stoats there were ripe follicles and in 4 others a fresh ovulation had taken place. In May, 2 lactating stoats killed on May 6 and 8 were oestrus, and all other females, 7 lactating and 7 with regressing mammary glands, showed recent corpora lutea.

There is no persistent oestrus ; ovulation appears to be spontaneous (*see* § VIII*d*). Oestrus and ovulation are accompanied by the usual changes in the accessory organs.

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TABLE IV—DETAILS OF STOAT PREGNANCIES

| Date | | Number of animal | Uterus weight | Embryo weight | Distribution and number of swellings | Embryos reabsorbing | Distribution and number of corpora lutea | Diameter of corpus luteum | Mammary gland : largest nipple area | Notes |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | gm | gm | | | | mm | | |
| March | 13 | 259 | 0·18 | — | — | — | 6+3 | 0·99 | 0·3×0·3 cm . . | Early implantation |
| | 4 | 347 | 0·21 | — | — | — | 4+4 | — | 0·3×0·3 cm . . | Early implantation |
| | 4 | 346 | 0·25 | — | — | — | 2+7 | 1·05 | 0·5×0·4 cm . . | Early implantation |
| | 11 | 257 | 0·33 | — | 4L+4R | — | 6+5 | 1·05 | 0·5×0·3 cm . . | Uterine swellings very small |
| | 23 | 283 | 0·34 | — | — | — | 7L+3R | 1·01 | 1·0×0·9 cm . . | Uterine swellings indefinite |
| | 14 | 262 | 0·58 | — | 5L+5R | — | 5+7 | 1·05 | Gland thin and continuous | — |
| | 30 | 659 | 1·06 | — | 4L+4R | — | 6L+2R | 1·30 | Nipple area, 1×0·7 cm thickening | Migration of ova |
| | 17 | 269 | 1·94 | — | 6L+7R | 1 | 5+8 | 1·11 | Gland diffuse and continuous | Migration of ova |
| | 25 | 286 | 2·00 | — | 2L+6R | 1 | 2+6 | 1·15 | Gland not preserved . | — |
| | 17 | 270 | 2·45 | — | 3L+5R | — | 4L+5R | 0·95 | Nipple area, 0·7×0·7 cm | Ovaries not well fixed |
| April | 7 | 305 | 3·20 | — | 5L+5R | — | 7+5 | 1·07 | Nipple area, 1·1×0·9 cm | — |
| March | 31 | 298 | — | 0·16 | 5L+6R | 1 | 8+15 | 1·08 | Nipple areas just joining : 1·1×0·9 cm | — |
| | 26 | 287 | — | 0·45 | 5L+4R | — | 6L+3R | 0·88 | Nipple areas joined . | Migration of ova |
| | 30 | 294 | — | 0·90 | 4L+5R | — | 4L+7R | 0·92 | Nipple areas joined : maximum width 1·6 cm | — |
| April | 6 | 304 | — | 1·55 | 4L+4R | 2 | 4+5 | 0·78 | Nipple areas joined . | Ovaries not well fixed |
| | 10 | 352 | — | 3·30 | 3L+3R | — | 5+5 | 0·91 | Nipple areas joined . | Nearly full term pregnancy |

The corpora lutea in the non-pregnant animal (corpora lutea of ovulation or pseudo-pregnancy) are all of the same type, but are smaller than those of pregnancy; the uterine epithelium undergoes a proliferation characteristic of the luteal phase (p. 486)

TABLE V—LACTATING STOATS CLASSIFIED ACCORDING TO THE CONDITION OF THEIR REPRODUCTIVE ORGANS

| Month. | Number of animals | Number with corpora lutea of pregnancy | Number without corpora lutea | Number with large follicles | Number with corpora lutea of pseudo-pregnancy | Number with uterine sperm |
|---|---|---|---|---|---|---|
| April . . . . . . . . . . . . | 9 | 4 | 2 | 2 | 3 | 4 |
| May . . . . . . . . . . . . | 9 | 1 | 1 | 2 | 7 | 5 |

and similar to that of the early stages of pregnancy, but the regressing mammary gland does not react perceptibly The average number of corpora lutea in an ovary, 4·75, is approximately the same as during the breeding season.

Tables III–V show the remarkable fact that 93 out of 99 adult female stoats distributed throughout the year (whose ovaries were sectioned), had one set of corpora lutea and the exceptions were lactating, oestrus or pro-oestrus animals. In the whole series, however, only one non-pregnant stoat killed on March 8 had corpora lutea transitional to those of pregnancy; in the remainder the corpora lutea were quite distinct. Since those of one cycle tend to disappear before the follicles have ripened for the next oestrus, it is impossible to determine accurately the number or length of the post-pregnancy cycles in the stoat. A consideration of the available material indicates, however, that several ovulations normally occur between one breeding season and the next. All adult stoats show corpora lutea of ovulation or pseudo-pregnancy after June 1, so that ripe follicles, recent corpora lutea and enlarged uteri, fig. 6, occurring later in the year must be regarded as evidence of further oestrus periods. In June, July, and August the poor preservation of much of the material made it often impossible to diagnose the age of the corpora lutea from their histological appearance, but well-vascularized bodies could be found in adult stoats whose uteri showed an early post-oestrus endometrium (p. 486). Such animals were taken in all months between July and September; an oestrus parous animal was killed on September 16. Other stoats in November and December seemed to show cyclic activity.

Since at least two stoats in January had recent corpora lutea it is likely that there is no period of complete anoestrus in the female. The uterus shows a normal involution after pregnancy, but its weight does not fall below that found at the beginning of the breeding season, fig. 6, nor does it show any obvious endometrial regression other than that occurring at the end of any luteal phase.

The presence of spermatozoa in the stoat uteri, Tables III and V, makes it clear that mating takes place outside the breeding season proper, both during and after lactation. In April, spermatozoa were found in one lactating stoat with oestrus follicles, and in 3 stoats which had ovulated. In May, spermatozoa were found in the uteri of 9 out of 16 female stoats, of which one was oestrus and 8 had ovulated. In June and July adult stoats with uterine spermatozoa were fairly common, and they were also seen in the only adult female taken in October.

It is impossible from the present material to say whether or not the luteal phase is prolonged by sterile mating. It is reasonable to assume that there are unmated post-ovulation stoats in the present series, but their reproductive organs are histologically indistinguishable from those of animals which show evidence of sterile mating. Since in all cases the uterine endometrium undergoes the development characteristic of the luteal phase, the term pseudo-pregnant will be applied to all non-pregnant animals after ovulation.

### (*d*) *Ovulation and Mating in Young First Year Stoats*

In § V it was shown that the young female stoat, unlike the male, reached adult body weight in June or July. The ovaries and uterus also grow very rapidly, and their weights overlap those of the adult animals from June onwards, figs. 5 and 6, The reproductive organs become active even before adult body weight is acquired, and stoats weighing 80, 85, 90 and 94 gm were all found to have ovulated, as well as other larger animals. Out of 25 first year stoats in June, 23 had ovulated and the other 2, dating from June 1 and June 6, had large follicles. The accessory organs showed the characteristic cyclic changes, but the corpora lutea were small like those of parous stoats at the same season. It seems to be quite common for these growing first year stoats to mate ; spermatozoa can be found in their uteri from the beginning of June till October, Table VI. Since the males have quite undeveloped reproductive organs up to the end of the year in which they are born, the young females must mate with the adults.

Table VI—First Year Female Stoats Classified according to the Condition of their Reproductive Organs

| Month | Number of animals | Number without corpora lutea having large follicles | Number with corpora lutea of ovulation | Number with uterine sperm |
|---|---|---|---|---|
| June | 35 | 2 | 23 | 8 |
| July | 55 | — | 43+12* | 21 |
| August | 19 | — | 19 | 9 |
| September | 16 | — | 16 | 8 |
| October | 13 | 1 | 12 | 6 |
| November | 7 | — | 7 | — |
| December | 1 | — | 1 | — |

* The ovaries of 12 badly preserved July stoats whose uteri were in the luteal phase were not sectioned,

Ovulation is spontaneous : a first year female stoat taken in May and kept in the laboratory was found to have a corpus luteum in the ovary.

As far as can be determined, all first year female stoats ovulate in June or earlier, and apparently further ovulations and pseudo-pregnancy cycles take place. Enlarged uteri, well-vascularized corpora lutea and in one animal (No. 637 in October) oestrus follicles were found later in the year. Fig. 6 shows that immature stoats with uteri weighing about 0·1 gm namely, of nearly oestrus size, were taken at the end of July and in August, September, and November.

There seems to be no difference in cyclic activity after June between the first year and adult females.

(*e*) *Discussion.*

It was thought that the oestrus cycle of the stoat would be very similar to that of the closely related ferret, but actually the females of the two species show some striking differences. The ferret has one six months breeding season a year in which it may have two litters ; it ovulates only after mating, and sterile mating is followed by a well-developed pseudo-pregnancy (Marshall, 1904 ; Hammond and Marshall, 1930). Young ferrets do not come into oestrus in the year in which they are born.

The stoat, as described above, has a single breeding season, but is polyoestrus ; it ovulates spontaneously, and has one litter followed by a series of sterile cycles in which pseudo-pregnant changes are slight. The young ovulate freely in the year in which they are born, but rarely, if ever, get pregnant.

The weasel, which belongs to the same family, is believed to breed more than once a year (Simpson, 1924), and probably shows other differences in its reproductive cycle. It is clear that, as regards their mode of breeding, anatomically closely related animals may vary considerably, some of the differences being ascribable to differences in body weight and growth rate, but others apparently due to specialization of the endocrine and reproductive system along different lines.

Adult male stoats are known to have spermatozoa in the testes at least from March until August, and as early as February 7 active testes may be found. Moreover, females killed in January, September, and October, in addition to the months mentioned above, show spermatozoa in the uteri so that it may be assumed that active males occur over eight and a half months of the year from the middle of January to the beginning of October, although they are not very common before March, and anoestrus regression begins in July. This period corresponds roughly with the period of fertility in the male ferret (Allanson, 1932).

Female stoats, however, only become pregnant in March and early April although ovulations and cyclic activity take place throughout the year. Not long after parturition oestrus reappears, and the question naturally arises why these adult oestrus females do not get pregnant a second time. In some of them the first ovulation occurs before the mammary gland has regressed when the animal may be assumed to be still suckling, or to have not long ceased to do so, but in others, such as No. 439 in May which had hollow corpora lutea and a regressed mammary gland, the continuance of lactation can hardly be said to have inhibited a fresh pregnancy. It can be argued that the deficiency is on the male side, since by the beginning of May the testis has begun to lose weight although it is still large and contains spermatozoa ; by analogy with the ferret at the onset of anoestrus, such animals may be less fertile. In view of the condition of the testes and the frequency of matings, however, it is extremely doubtful if this explanation is valid. The numbers of animals in which uterine spermatozoa were found are obviously only a very rough guide to the proportion of mated females in the present collection, and it is reasonable to believe that stoats commonly mate at oestrus as long as the males are active. Unless the males are uniformly infertile therefore, which seems improbable, the absence of pregnancies must be attributed to the females. When parous adults and fully developed first year animals mate, ovulate and remain sterile during a great part of the year, the cause is probably a fundamental one. It is significant that, as far as we can tell, no corpora lutea resembling those of pregnancy are formed before the last week of February, or after the end of March (*see* p. 468). Female stoats in February, killed before February 21, had all mated, presumably with fertile males, but were non-pregnant and only had small corpora lutea in their ovaries.

It may be suggested as a provisional hypothesis, that corpora lutea can only become fully luteinized, as in pregnancy, during a restricted time of the year, when the secretion of the anterior lobe of the pituitary is at its maximum ; at other times, cyclic activity of the reproductive organs continues, but, in the absence of the maximum luteal stimulation, the uterus is not sensitized and implantation of fertilized ova cannot take place. If the infertility of the stoat, except during a short period of the year, is due to a cycle in the pituitary, then the female may be said to have a clearly defined anoestrus lasting longer than that of the ferret, but compatible with a higher level of activity, since ovulation and mating can still take place although pregnancy is impossible.

One first year stoat only, a large animal weighing 244 gm killed on July 31, showed any traces of pregnancy ; the uterus was not large, 0·06 gm, but the uterine mucosa was very similar to that of a post-partum animal, in which the endometrial glands were only just reforming after the repair of the epithelium and the disappearance of the debris of pregnancy. From the slight development of the uterine muscle, however, and the absence of pigment, this animal might have recovered and ovulated following an abortive pregnancy rather than a full term one. No mammary gland development was observed. In view of the numbers of animals examined it is doubtful if this anomalous specimen has any significance.

To summarize, the stoat reproductive cycle shows at least two interesting features, the first being the fact that whereas the male has a complete anoestrus, the female can apparently ovulate at all times of the year, and the second being the frequent occurrence in both mated and unmated animals of infertile reproductive cycles. Such apparent inefficiency in breeding seems to be commoner in wild species than would be expected. Hedgehogs show infertile reproductive cycles in both mated and unmated animals (Deanesly, 1934), and there is also clear evidence of infertile cycles in *Evotomys*, the bank vole (Brambell : unpublished information). On the other hand, in the grey squirrel (Deanesly and Parkes, 1933), and in the shrew (Brambell, 1935) ovulation seems to be followed almost invariably by pregnancy, and this is probably also true of the mole, which breeds only once a year (Altmann, 1927).

## IX—The Ovary

### (*a*) *General*

The stoat ovary, figs. 12-21, Plates 28 and 29, is very similar histologically to that of the ferret, since much of it consists of glandular interstitial cells and atretic follicles ; there is no accumulation of corpora lutea from successive ovulations. Pigment is sometimes abundant in the ovaries of pregnant and parous animals.

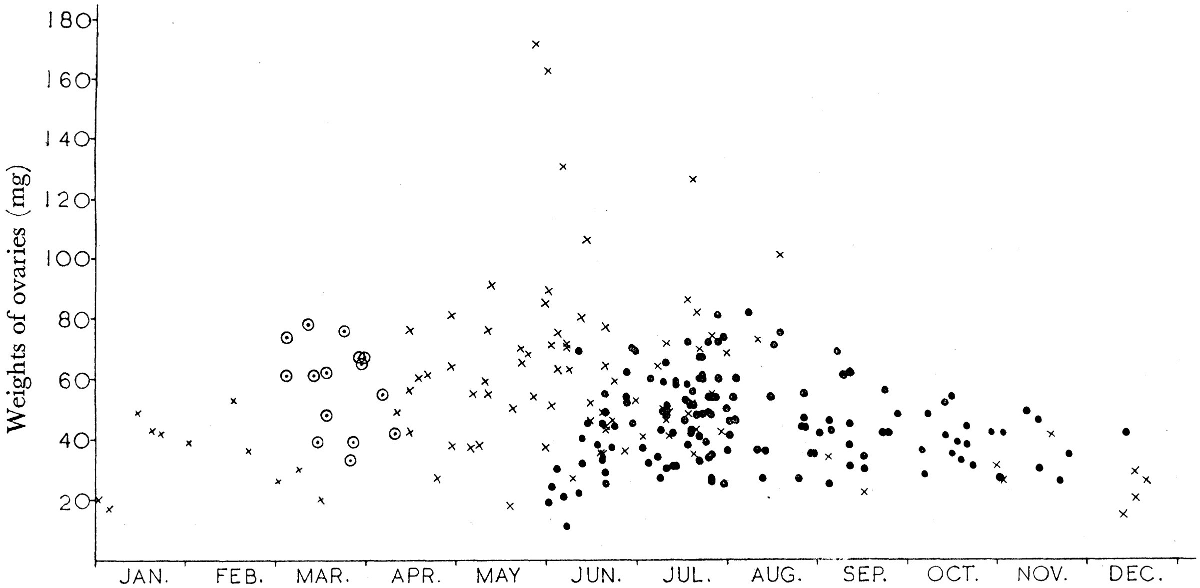


Fig. 5—Ovary weights of adult (×), pregnant (⊙) and first year (●) stoats. From June onwards the ovaries of first year stoats are indistinguishable by their weights from those of adults.

Table II and fig. 5 show the variations in the weight of the ovary in the first year, pregnant and parous stoats. In first year animals the average weight of the ovaries varies comparatively little between June and December, but it seems possible to distinguish a phase of rapid growth up till July, followed by a slight shrinkage from about the middle of September. During pregnancy the ovary weights show a slight increase, as might be expected, but a greater enlargement takes place after the breeding season is over, in the months May to August, although the ovaries are then very variable. This enlargement is caused by a temporary increase in the atretic follicles, and interstitial cells, which apparently regress during the winter months. In the mole there is an even more striking ovarian enlargement, after the breeding season is over, also due to an increase in the interstitial cells, which diminish again before the onset of the next breeding season (Altmann, 1927).

### (*b*) *The Follicles : Growth and Maturation.*

The early stages of follicular growth show no unusual features ; an antrum forms when the diameter of the follicle is about 250 μ and that of the ovum is 75–80 μ. The ovum does not reach its full size, 90-95 μ, until the follicle diameter is about 360 μ ; this is at a later stage than in most of the small mammals already examined (BRAMBELL, 1928, PARKES, 1931). The follicular epithelium also continues to grow for some time, and the nuclei are not full size until the follicle diameter is more than 420 μ.

Normal follicles over 250 μ in diameter were not very common in the material examined, firstly because, as in the ferret, there is a tendency for theca luteinization to take place at this stage, and secondly, because post-mortem changes affect the larger follicles sooner than other parts of the ovary, and it so happened that most of the oestrus and pro-oestrus stoats were not fixed until some time after death. Such animals, including one which had mated shortly before death, showed follicles 520-590 μ in diameter. Although the ultimate, pre-ovulation, size of the ripe follicle could not be determined, it must be small for the size of the animal (PARKES, 1931) since the above follicles already showed pre-ovulation congestion of the theca, fig. 12, Plate 28. Other oestrus stoats, mated or unmated, had follicles with diameters up to 660 μ as far as they could be measured. In the ripe follicle the nuclei of the follicular epithelium have a diameter of 5–6 μ; there is very little surrounding cytoplasm. The theca interna is well developed and contains numerous capillaries and large epithelioid connective tissue cells.

### (*c*) *Corpora Lutea of Ovulation and Pseudo-pregnancy*

Only three stoats in the series show hollow corpora lutea, so that the transition from the ruptured follicle to the corpus luteum of ovulation is probably very rapid, as would be expected from the small size of the antrum in the ripe follicle. A lactating stoat had corpora lutea with a central blood clot surrounded by a layer of lutein cells about twelve or fifteen cells deep. The boundaries of these cells could not be distinguished, but their area was about 80–100 sq μ. The nuclei were slightly larger than in the ripe follicle. In fully formed corpora lutea of ovulation the cells were very similar, with 5–6 μ nuclei, and an area of 80–120 sq μ. These corpora lutea of ovulation are well vascularized, but the lutein cells remain small, fig. 16, Plate 29. The fully developed corpus luteum has a mean diameter of 0·70–0·75 mm. Only one non-pregnant animal has a corpus luteum with a mean diameter of as much as 0·84 mm, and this is a mated female, killed on March 8 at the beginning of the breeding season. The lutein cells and nuclei in this stoat, fig. 17, Plate 29, are intermediate between those of ordinary corpora lutea of ovulation and developing corpora lutea of pregnancy, such as those of No. 259 the earliest implantation stage recorded. The occurrence of such corpora lutea in a non-pregnant stoat in March is significant, since it shows that a luteinizing stimulus may be operative at the beginning of the breeding season even after infertile mating. Neither of the other two mated, non-pregnant females killed in March possessed similar corpora lutea, but this may be accounted for by the fact that one female weighed only 140 gm, and its development was perhaps retarded, while the other, killed on March 1, had old corpora lutea, the products of an ovulation some time in February.

The corpus luteum of ovulation or pseudo-pregnancy shrinks to about 0·55 mm in diameter before the next oestrus, and disappears by the time the follicles have ripened. All corpora lutea in an ovary therefore belong to the same cycle; the number varies from 1–10. Fig. 6 shows the frequency distribution of corpora lutea in 64 parous and 112 immature stoats outside the breeding season; it is strikingly similar in the old and young females, as are the respective averages of 4·75 and 4·8 corpora lutea per ovary in the two groups. There was no monthly variation in the number of follicles

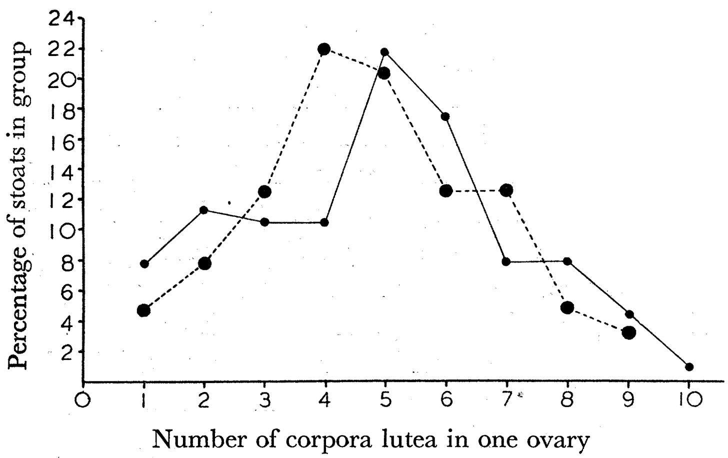


FIG. 6—Frequency polygon for the numbers of corpora lutea in 64 adult and 115 immature stoats. The figures on the base line are the numbers of corpora lutea in one ovary, and the vertical column gives the percentage of animals in each group with 1–10 corpora lutea respectively. The dotted line shows corpora lutea distribution in parous stoats, and the continuous line in non-parous stoats. The frequency distribution is similar in the two types.

ovulating. In pregnant stoats (excluding stoat 298) there was a similar average of 4·9 corpora lutea per ovary, so that it may be assumed that a total of 9–10 corpora lutea in each cycle is a constant average for the species.

### (*d*) *Corpora Lutea of Pregnancy*

The earliest implantation stage, in which the total weight of the uterus was only 0·19 gm, was associated with corpora lutea much larger than those of ovulation, although not yet fully developed. The mean corpus luteum diameter was 0·99 mm, and the lutein cell nuclei had a diameter of about 8 μ, while the area of the cells was about 250 sq μ. Table IV shows that all the other corpora lutea of pregnancy had reached or passed their full size, ranging from 1·1–1·3 mm mean diameter; one or more corpora lutea were measured at each stage unless the preservation of the ovaries was very bad. In the fully formed corpus luteum the polygonal lutein cells have an area of 300–400 sq μ, and each cell is surrounded by capillaries ; the nuclear diameter is about 9μ. In stoat 298 the lutein cells are all of the same size, but some of the numerous corpora lutea have mean diameters as low as 0·6 mm, suggesting that follicles smaller than usual had ovulated.

The latest four pregnancies in the series have regressing corpora lutea, fig. 15, Plate 29, which show shrinkage of the lutein cells and nuclei. In the first of these the embryos only weighed 0·45 gm, so that the corpora lutea presumably begin to degenerate soon after mid-pregnancy. As already stated they disappear during lactation.

### (*e*) *Interstitial Cells and Atretic Follicles*

The interstitial tissue of the stoat ovary is extremely variable, and difficult to define. Since all the ovaries of first year animals examined histologically contained ripe follicles or corpora lutea, there are no stages showing the first appearance of the interstitial cells. In an 85 gm first year stoat killed on June 2, which had ovulated, there are groups of regular cuboid interstitial cells in the ovary, of the type found in the rabbit ovary. These cells have an area of about 300 sq μ, and nuclei 5–6 μ in diameter ; a number of degenerating ova is scattered among them, but it is impossible to say whether all these cells originally formed part of atretic follicles. Follicular atresia is, of course, very common in the stoat ; usually it is the theca cells which enlarge and multiply, while the granulosa cells degenerate. The theca cells take on the appearance of lutein cells and eventually surround the degenerating ovum. Similar luteinized bodies have been described in various species, both in normal baboon ovaries (Zuckerman and Parkes, 1932), and after pituitary injections in the ferret (Hill and Parkes, 1930), and rat (Engle and Smith, 1929).

In the stoat there is no doubt that a large proportion of the interstitial tissue is derived thus from atretic follicles, so that there is great variability in the size and appearance of cells in a single ovary, figs. 19, 20. If the term luteinization be used for the change from the small cell with little cytoplasm to the glandular type, then it may be said that not all interstitial cells become fully " luteinized " and those that reach the maximum size regress subsequently and later degenerate and disappear.

A study of the seasonal changes in the stoat ovary indicates that the interstitial tissue reaches its maximum in post-lactation stoats from May to August. During these months the largest cells have an area of about 450 sq μ, and nuclei 5–6 μ in diameter, fig. 20, Plate 29. Later in the year most of the interstitial tissue consists of smaller cells about 60 sq μ, in area and the ovaries show a corresponding decrease in size, fig. 19, Plate 29. In first year stoats the interstitial tissue is also at a maximum in July and August, fig. 21, but the cells generally do not reach so large a size as those in the ovaries of parous stoats.

Just before the breeding season and during pregnancy the interstitial cells seem to shrink and degenerate in large numbers, and their disappearance sometimes leaves spaces in the middle of the ovary occupied only by connective tissue and blood vessels, fig. 15, Plate 28. During this phase pigment accumulation is very marked in the degenerating cells. During lactation the interstitial cells are variable ; in some animals they are small but in others " luteinization " has again become active, fig. 12, Plate 28.

## X—The Uterus

### (*a*) *General*

The stoat uterus shows comparatively slight variations in weight, except during pregnancy and after parturition ; the post-partum uterus undergoes rapid involution and recovery. Table II and fig. 7 show the variations in the weights of parous and

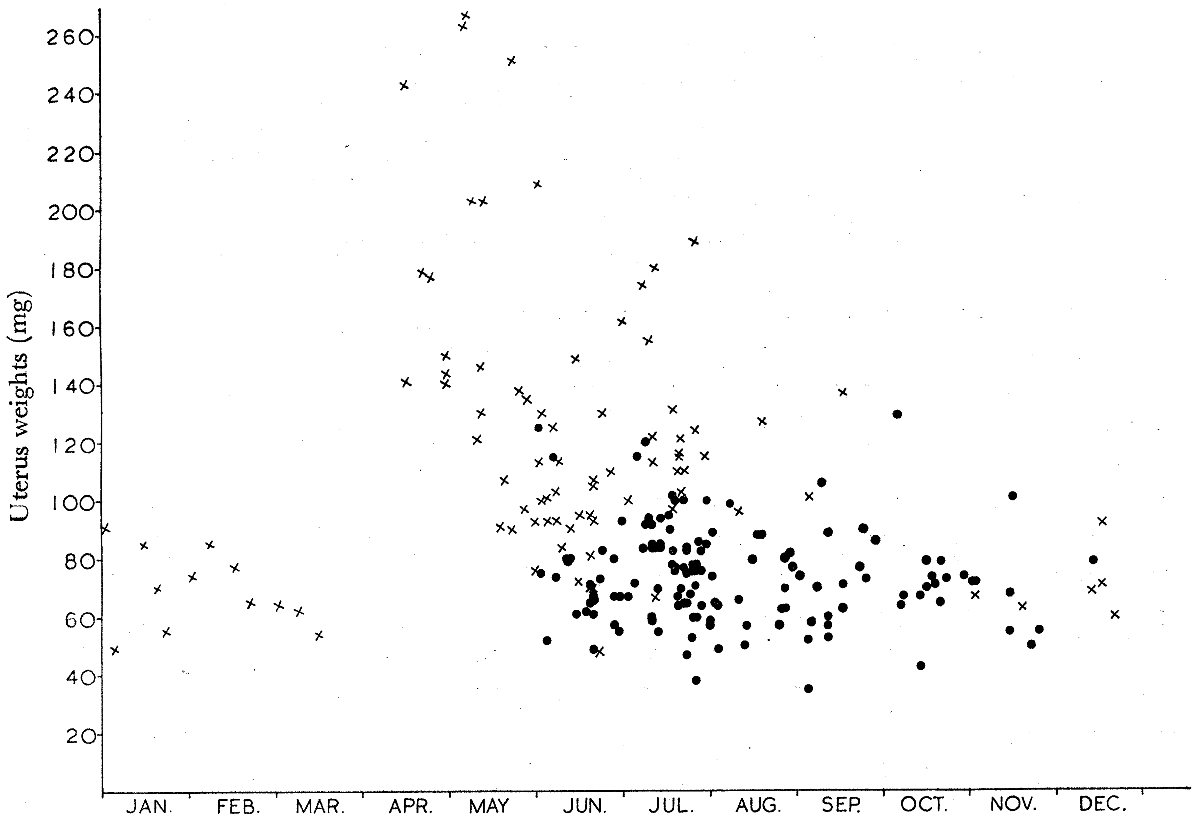


Fig. 7—Uterus weights of adult, mainly parous, × and first year ● stoats. Pregnant and early post-partum uteri are excluded. The parous uteri show a gradual decrease in weight after parturition, but only to the level found at the beginning of the breeding season. The larger uteri of first year animals are those which are pro-oestrus or oestrus.

non-parous uteri through the year. From September until about February parous uteri weigh 0·05–0·14 gm, enlarging to the latter weight at oestrus and regressing in the luteal phase. Between April and August the range of variation is much greater, the largest uteri, next to the early post-partum ones, being those which have recovered rapidly during or after lactation and again become oestrus. Exceptionally large uteri of this type with a thick muscular wall and a well developed oedematous mucosa are found in April and May. Later in the year the enlargement due to the previous pregnancy tends to disappear.

From June onwards the weights of the uteri of first year animals overlap those of the parous ones, although their average weight is much lower, Table II and fig. 7. Near oestrus the non-parous uterus weighs 100–125 mg, and during the luteal phase it falls to about 55 mg.

The uterine mucosa contains numerous gland tubules which at first grow out radially from the epithelium, figs. 25, 31, Plates 30 and 31, and subsequently become convoluted and run parallel to the length of the uterus, so that they are cut across in transverse sections.

### (*b*) *The Uterus in First Year Stoats.*

The stoat uterus has its adult characteristics rather before the animal is three months old, and when its body weight is 80–100 gm. Table III shows that only two stoats in the series had not yet passed their first oestrus ; these two had the largest non-parous uteri in June, one of which is shown in section in fig. 25, Plate 30, to illustrate the oestrus condition. The endometrium has epithelium 10–12 $\mu$ high, consisting of closely packed, rather irregular cells and the stroma is oedematous and contains numerous leucocytes.

The luteal phase in non-parous uteri, found in association with recent corpora lutea of ovulation, is illustrated in figs. 26, 29, Plate 30. In these sections the oedema of the stroma has subsided and the lining epithelium has increased in height to 30–40 $\mu$ and now consists of elongated cells with rod-shaped nuclei about 10–11 $\mu$ in length fig. 32, Plate 31. The epithelium later tends to invade the underlying mucosa, so that an irregular lighter-staining border of tissue gradually forms round the lumen. This development of the luteal phase is shown in figs. 27, 33, Plates 30 and 31 ; the epithelial nuclei have now changed their shape and are oval rather than rod-like ; they measure about 8–9 $\mu \times 3$–$3 \cdot 5\ \mu$. The full luteal proliferation develops quite slowly, and intermediate stages showing the gradual growth of the epithelium are common. Occasional glandular cysts develop in the mucosa, not associated with any particular phase of the cycle, fig. 32, Plate 31.

There seems to be no distinct breakdown of the epithelium at the end of the luteal phase ; the fresh epithelial proliferation of glandular tissue merges with the rest of the mucosa. The epithelium round the lumen either loses the cytoplasmic border by secretion, or perhaps is merely stretched by the pro-oestrus oedema, and becomes low again at the time of the next ovulation.

Spermatozoa are frequently found in the uterine glands of first year stoats ; Table III, fig. 37, Plate 31, shows them in the gland tubules of a non-parous uterus from a stoat killed in October. Since few if any males are fertile during that month, it is probable that uterine spermatozoa remain distinguishable histologically for fairly long periods.

### (*c*) *The uterus in pregnant stoats*

In early pregnancy, even after definite uterine swellings can be seen, the glandular development of the mucosa is essentially similar to that found in the non-pregnant stoat uterus after ovulation, although there is growth, oedema, and increased vascularization. Figs. 30, 34, Plates 30 and 31, show a section through the uterus of a very early pregnancy ; the epithelium is 25–30 μ high, and a few glands are opening into the lumen, but little proliferation has taken place, although the corpora lutea have reached their full size. In the first six stoats in Table IV the uterine mucosa between the blastocysts is of the type shown in fig. 30. In stoat 262 the epithelium round the implantation sites has begun to proliferate further, and is growing into irregular tufts of cells, while the endometrial glands are dwindling and no longer open into the lumen. Stoat 659, the next in the series, has uterine swellings four times as large as those of stoat 262, and there is a corresponding advance in the progestational proliferation between the embryos. The epithelium has grown into a series of rounded projections or villi, and the more superficial of the original endometrial glands are atrophying, only the deeper ones persisting unchanged. Fig. 35 (stoat 269) shows a slightly later stage of this process in which the villi are beginning to branch and interlace. In stoats 286, 270, and 305 the villi are more finely sub-divided and consist of syncytial epithelium enclosing connective tissue and blood vessels. In stoat 298 the syncytial nuclei are much enlarged and irregular, and the proliferation is transitional to that in stoat 287, fig. 36, Plate 31, where the nuclei are much further enlarged. It is noticeable that the full uterine proliferation is not developed until late in pregnancy, near the time when the corpora lutea regress. The uterine changes appear to be very similar to those described in the ferret, where the ultimate syncytial proliferation is reached in the fifth week of pregnancy and breaks down shortly afterwards (Hammond and Marshall, 1930).

Owing to the disappearance of the original endometrial glands, spermatozoa do not remain for long in the pregnant uterus ; a few were still present in stoat 262, but none was found in later stages. Spermatozoa in recently parous stoats must therefore indicate fresh matings since parturition.

### (*d*) *The Uterus in Post-partum and Parous stoats*

Two stoats killed on April 11 and 15 had early post-partum uteri weighing 0·65 gm and 0·71, respectively ; these still contained syncytial debris in the lumen. The mucosa was reduced to an irregular layer of epithelium and a few gland tubules. In the next stage examined, from a stoat killed a few days later, the uterus weighed only 0·28 gm, and regeneration of the mucosa had begun ; the lumen was lined by a regular epithelium from which fresh gland tubules were growing radially into the stroma. All the other post-partum uteri in April and May showed complete endometrial regeneration ; with one exception they were either oestrus or post-oestrus.

Sections through oestrus uteri from lactating stoats are reproduced in figs. 28 and 31, Plates 30 and 31 ; the epithelium is low and the stroma oedematous and infiltrated by leucocytes. The stroma capillaries are congested. In fig. 31 many of the glands appear radial in section owing to their recent out-growth.

The luteal development of the endometrium resembles that already described in the immature stoat. Spermatozoa are fairly common in the gland tubules, Table V. The muscular layers and blood vessels derived from pregnancy continue to diminish during the summer, causing a gradual reduction in the average weight of the uterus, although there are no histological signs of anoestrus regression. It is possible to distinguish parous uteri both during and after involution by the presence of pigment granules in the epithelium of the deeper-lying glands and in the stroma.

## XI—The Fallopian Tube

In the stoat the Fallopian tube shows cyclic variations such as have been described in other mammals. These changes seem to be trifling in animals with a short recurrent cycle such as the small rodents, the shrew (Brambell, 1935), and the hedgehog (Deanesly, 1934), but well marked when there is a longer interval between ovulations as in the pig (Snyder, 1923), and the squirrel (Deanesly and Parkes, 1933.) If this generalization holds, then the extent of change in the Fallopian tube of the stoat indicates a moderately long cycle. Sections through the Fallopian tube were examined from 28 stoats. At oestrus the whole tube is swollen to at least double its former size ; the increase can readily be distinguished in the fresh animal. The stroma becomes oedematous and the epithelium proliferates and increases in complexity ; the cells grow from 5–8 μ to 20–30 μ in height. After ovulation the oedema subsides, and the tube rapidly returns to a resting condition in which the stroma is dense, and the epithelial cells are low and have no distinct cytoplasmic border. A search was made for tubal ova where the corpora lutea were recent, but none were found. Intermediate stages showing pro-oestrus growth of the Fallopian tube could be distinguished in post-partum and other stoats.

## XII—The Vagina and Vulva

Sections through the vagina and vulva of 75 stoats were examined, including some collected in every month of the year. There are no vaginal glands. The vaginal epithelium undergoes a well-defined cycle of the usual type, with growth, stratification and cornification before oestrus and subsequent sloughing. The epithelium remains low, in some regions only two-layered, during the luteal phase and fresh growth does not begin until shortly before the next oestrus. The epithelium varies in thickness from the cervix to the vulva ; near the latter it is 8-10 μ at its lowest, and 60–70 μ at its maximum. In the upper vagina the thickness of the epithelium is 20–30 μ during the luteal phase and 80–130 μ at oestrus.

In early pregnancy, the vaginal epithelium consists of an unstratified dense layer of small cells, 12–20 μ thick. During later pregnancy this layer becomes thicker and infiltrated by leucocytes in the upper part of the vagina ; there is a tendency for the cells to elongate at right angles to the lumen and a border of small columnar cells gradually forms in which the nuclei are larger than those in the basal layers. In a later pregnancy, a section through the enlarged, lower part of the vagina shows a further stage of the process ; there is now a single regular row of columnar cells 20–30 μ high in which the nuclei lie basally, leaving a deep cytoplasmic border next to the lumen.

The vulva is essentially similar to that of the ferret (HAMMOND and MARSHALL, 1930), although not equally conspicuous ; it swells at the approach of oestrus and gradually subsides afterwards. Sections through it show partially cornified epithelium arranged in projections or villi containing large cores of lymphoid tissue. The epithelium increases near oestrus and is shed after ovulation.

## XIII—THE MAMMARY GLANDS

The mammary glands and nipples were examined in nearly all female stoats dissected in the laboratory and about 80 glands were fixed and preserved. In the fresh first year animal neither mammary glands nor nipples could be readily seen ; the gland development even after ovulation and infertile mating is negligible. If the skin is fixed, very tiny rudiments, 2–3 mm in diameter, can sometimes be distinguished, for example, in a 180 gm first year pseudo-pregnant stoat in June. No larger gland areas were observed in stoat 256 (killed on March 8) which had corpora lutea intermediate between those of ovulation and pregnancy (p. 482).

Table IV summarizes the mammary gland development during pregnancy ; even in the earliest stages examined there was definite growth beyond anything seen in non-pregnant stoats. The nipple areas, starting from tiny patches in first pregnancies gradually enlarge and become confluent when the embryos weigh about 0·16 gm. Thereafter the gland thickens and broadens until at the end of pregnancy the two sides meet in the middle posteriorly. In two stoats a slightly different type of growth was seen ; there was a continuous, thin gland in early pregnancy, in which the separate nipple areas, rather square in shape, could still just be distinguished. By analogy with the mammary glands of other species such as the squirrel (DEANESLY and PARKES, 1933, fig. 32) it may be concluded that this type of growth is found in animals which have been pregnant before, where full mammary gland development has already taken place.

After parturition, a thick compact gland forms each side, measuring 6–7 cm long and 2–2·5 cm at its widest. The two glands meet in the middle line for the last 4 cm. The 18 fully developed mammary glands examined vary slightly in size and shape, but are essentially similar. It is not uncommon to find anteriorly two or more regressing nipple areas which are thin and transparent, although the rest of the gland is thick ; this is presumably due to a surplus of nipples and gland areas some of which are unused and have atrophied.

The nipples, enlarged by lactation, persist after the gland has completely atrophied. Regressing mammary glands are found in May and June, but the gland vestiges are almost invisible from July onwards. Generally, however, some of the nipples are much bigger than the others in the same animal and remain longer distinguishable. Nearly all parous stoats in July were readily identifiable by their nipples, but these become inconspicuous later in the year.

The initial expenses of this work were defrayed by a grant from the Royal Society to Dr. A. S. Parkes, F.R.S., who began to collect stoats in 1930. I am indebted to him both for his continued assistance with the collection of animals, and for his criticism and interest in the work.

My most cordial thanks are also due to Professor F. W. Rogers Brambell, of University College, Bangor, for weighing, recording and dissecting no less than 270 stoats. His unstinted co-operation was most valuable in the work of collecting a complete histological series.

I wish to thank further Dr. S. Zuckerman, of the Department of Human Anatomy, Oxford, for help in describing the changes in the skulls.

## XIV—Summary

During 1930–34, 662 stoats were collected from thirty counties in England and Wales for studying the growth and reproductive cycle of the species.

There is a restricted breeding season; the young are all born in the early spring, generally in April.

The males reach their adult weight of about 325 gm, and become sexually mature in the season following their birth. In first year males the testes remain very small (about 0·1 gm) until January or February and then enlarge; the average weight of all testes in March is 1·06 gm, and in April 1·32 gm. From July onwards the testes in adults regress rapidly until, in October and November, they are aspermatic and hardly larger than those of immature first year animals. Although most male stoats do not come into spermatogenesis until March, and show regressive changes in July, there is evidence of occasional fertile males in January and February, and also in August and September, so that they probably occur over a total period of eight and a half months.

Female stoats reach their adult weight of about 190 gm in July, when they are four months old. They first come on oestrus and ovulate spontaneously in May or June, before they are fully grown, and further ovulations take place at intervals of not less than a month before the next spring, when these animals become pregnant for the first time. Many first year females mate at oestrus, but mating proves sterile outside the limited breeding season.

Pregnant stoats were only found in March and April; the number of foetuses varied from 6–13 with an average of 9. Lactation lasts about five weeks and ends during May, after which all parous stoats have regressing mammary glands.

When still lactating, stoats come into oestrus and ovulate; mating takes place at these times, but no second pregnancies were found. Further ovulations and infertile cycles, accompanied by matings while the males are active, take place in later months of the year.

The average number of follicles rupturing together is 4–5 in one ovary. The corpora lutea in non-pregnant stoats, whether first year or adult animals, are uniformly small; their development is not affected by infertile mating, and they differ markedly from the larger corpora lutea of pregnancy.

The reproductive cycle of the stoat, therefore, is of a type not hitherto described, in which the effective breeding season is short, although the female apparently ovulates all the year round, and fertile males occur during two-thirds of the year. As in other mammals, the limitation of the breeding season may be attributed to a seasonal change in the pituitary. In the male, judged by the shrinkage of the testes, there is a sharp fall in pituitary activity in the late summer, whereas in the female a lesser decline in activity occurs earlier in the year. This does not inhibit cyclic changes in the ovaries and accessory organs, but it apparently renders impossible the full luteinization of the corpora lutea and the sensitization of the uterus for implantation of ova, so that there are no further pregnancies until the following spring.

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## XVI—Description of Plates

* Indicates material showing post-mortem degeneration.

### Plate 28.

All skulls shown in dorsal view X $1\frac{1}{4}$. Ovaries X 32.

Fig. 8—No. 458 : 1st year ♀, June 27th, 170 gm. This skull has well-defined nasal sutures. The parietals are not yet fully calcified and have a rough surface. The temporal muscle ridges have not fused ; there is still a broad median tract between them.

Fig. 9—No. 568 : 1st year ♂, August 3rd. 320 gm. In this skull the muscle ridges have fused posteriorly, and there is the beginning of a sagittal crest. The temporal crests form a deep V.

Fig. 10—No. 633 : 1st year ♀, October 18th. 170 gm. This skull illustrates the later coalescence of the muscle ridges in the skull of the female as compared with the male. The nasal sutures are now almost obliterated.

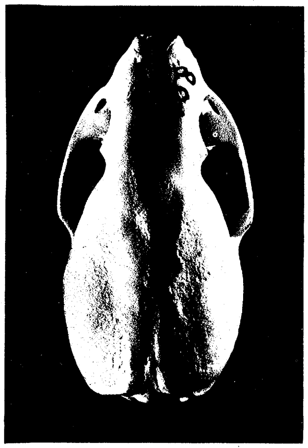
Fig. 11—No. 534 : 2nd year ♀, July 2nd. 250 gm. This shows the shape of the skull in the adult female. Anteriorly the temporal crests now form a short open V, and the skull seems laterally compressed in that region. The skull is fully calcified.

Fig. 12*—No. 402 : May 6th. Part of an ovary of a lactating stoat with ripe follicles; the interstitial tissue is very well developed.

Fig. 13—No. 137 : March 1st. Part of an ovary showing seven corpora lutea which have developed after infertile mating just before the breeding season. There are also numerous luteinized follicles containing degenerate ova.

Fig. 14—No. 269 : March 17th. Part of an ovary showing a median section through a fully developed corpus luteum of pregnancy.

Fig. 15—No. 287 : March 26th. Part of an ovary in late pregnancy showing approximately median sections through three corpora lutea which have shrunk considerably. The medulla of the ovary consists mainly of fibrous tissue and blood vessels, apparently owing to degeneration of the interstitial tissue. Contrast fig. 12.



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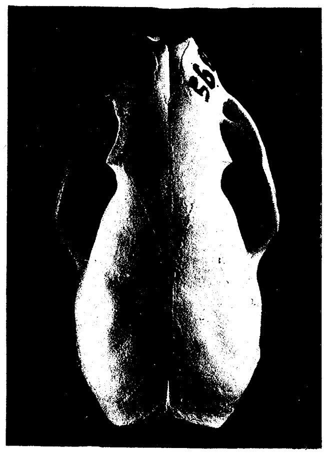

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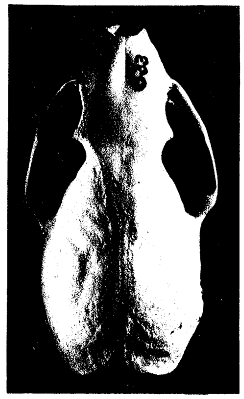

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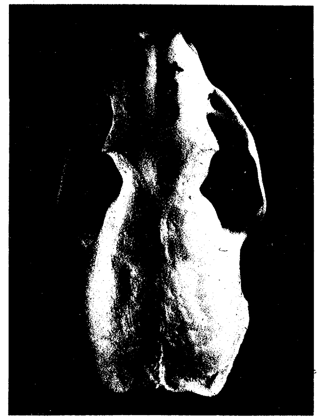

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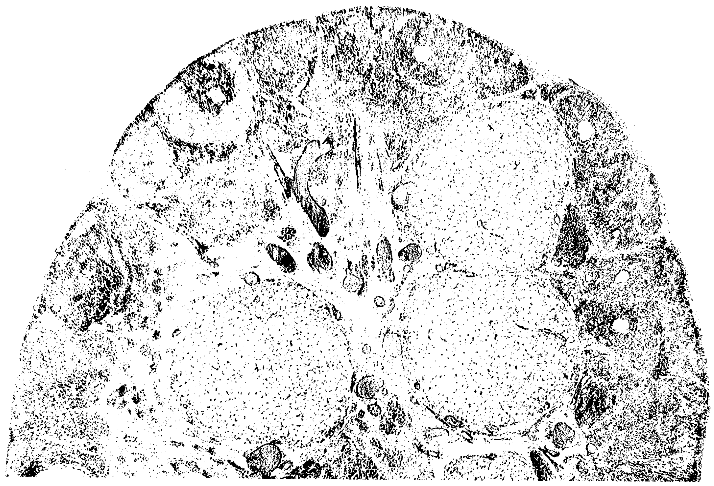

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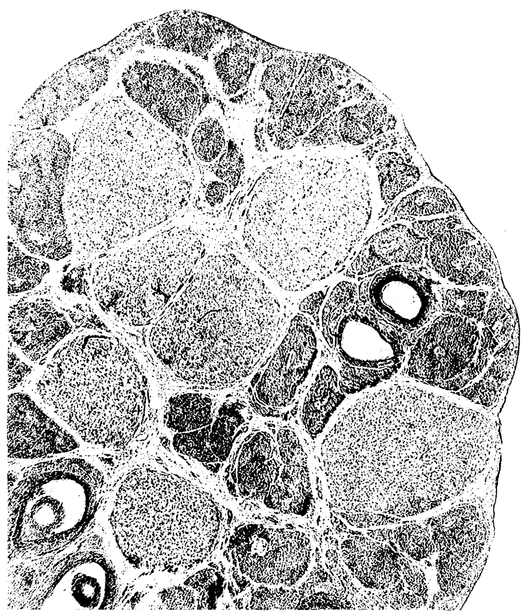

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## Plate 29.

Fig. 16—No. 469 : June 29th. Well-vascularized corpus luteum and part of a second one in a first year stoat. The interstitial cells are shown at a higher magnification in fig. 21. X 90.

Fig. 17*—No. 256 : March 8th. A corpus luteum in a non-pregnant stoat at the beginning of the breeding season. The luteal cells, though apparently regressing, are larger than in any other non-pregnant stoat (p. 24). X 90.

Fig. 18—No. 269 : March 17th. Higher magnification of part of the fully developed corpus luteum of pregnancy shown in fig. 14. X 90.

Fig. 19—No. 244 : January 19th. Cells from a luteinized follicle with degenerate ovum and, above, other ovarian interstitial cells containing pigment. X 370.

Fig. 20—No. 20 : June 15th. Typical interstitial cells, large and small, from the ovary of a post-lactation stoat. X 370.

Fig. 21—No. 469 : June 29th. Interstitial cells in the ovary of a first year stoat. Compare fig. 16 from the same ovary. X 370.

Fig. 22—No. 110 : July 7th. Part of the testis of a 200 gm first year stoat. The tubules are small and undeveloped, but contain occasional large winter spermatogonia. There is much intertubular tissue, including glandular interstitial cells. X 188.

Fig. 23—No. 381 : May 9th. The testis of this stoat weighed 1·2 gm and showed no regressive changes. Compare the tubule and interstitial cell size with those of figs. 22 and 24. X 188.

Fig. 24—No. 635 : October 26th. The testes of this adult, second year stoat weighed only 0·16 gm. The section shows the small seminiferous tubules with a thickened basement membrane. Large winter spermatogonia can be seen. The interstitial cells are smaller than in the active or the immature testis, and the intertubular tissue contains many leucocytes. X 188.

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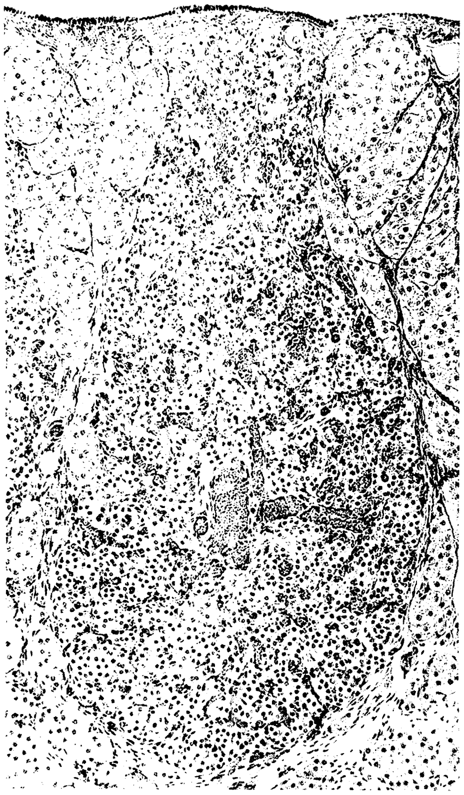

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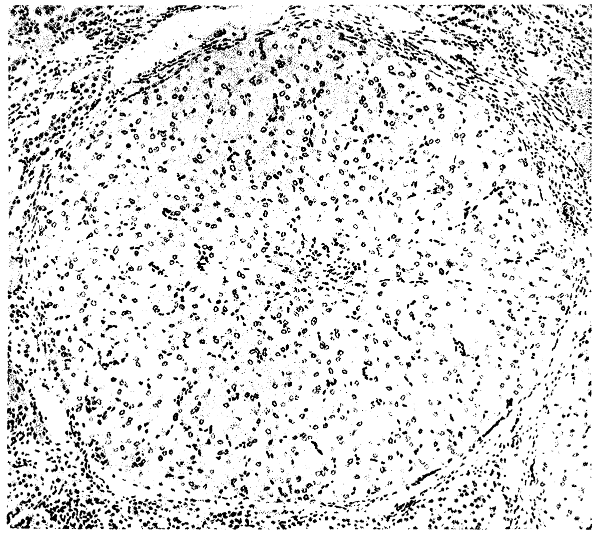

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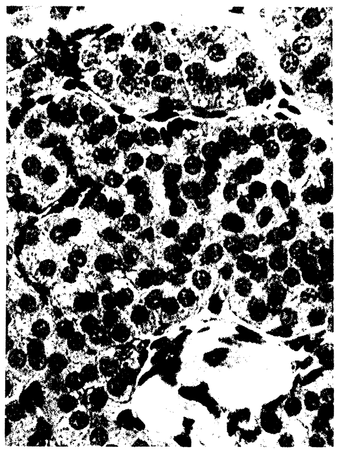

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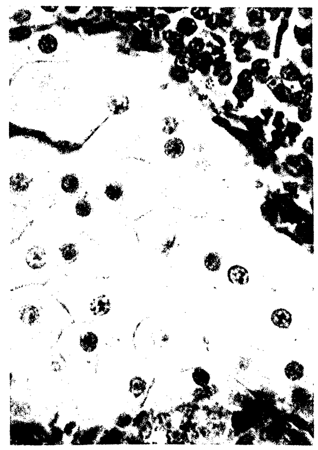

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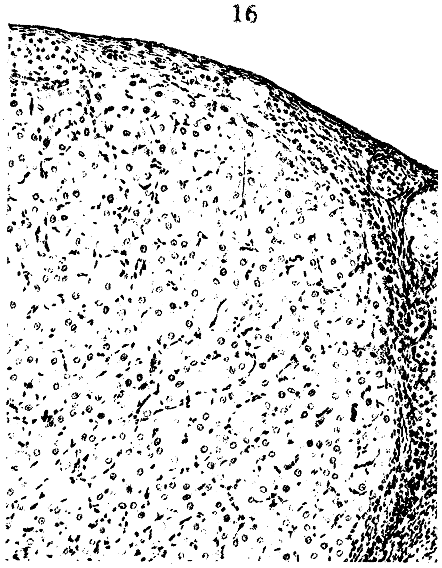

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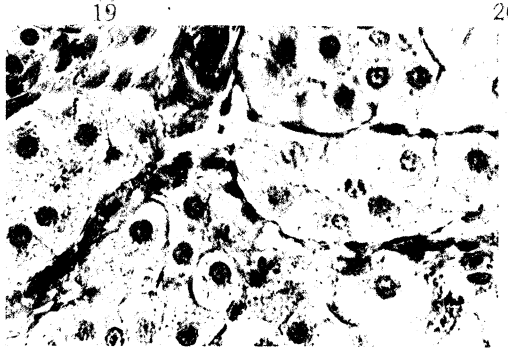

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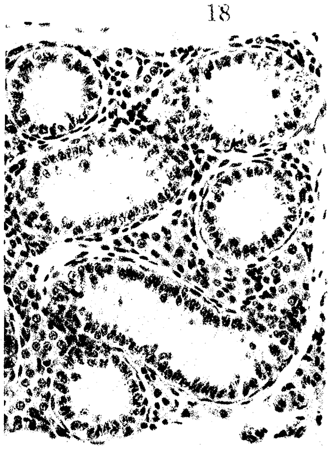

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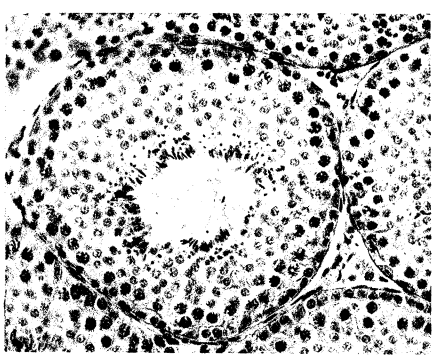

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PLATE 30.

Transverse sections through stoat uteri. X 47, except fig. 30, X 37.

FIG. 25—No. 419 : June 1st. Oestrus uterus in a first year stoat. The epithelium is low and the mucosa oedematous.

FIG. 26—No. 443 : June 20th. Pseudo-pregnant uterus from a mated first year stoat ; the mucosa is much denser than in fig. 25, and the epithelium has proliferated.

FIG. 27—No. 141 : October 6th. Uterus of a mated first year stoat showing a later stage of the same proliferation as in fig. 26.

FIG. 28—No. 18 : April 21st. Oestrus uterus in a lactating stoat which has just mated.

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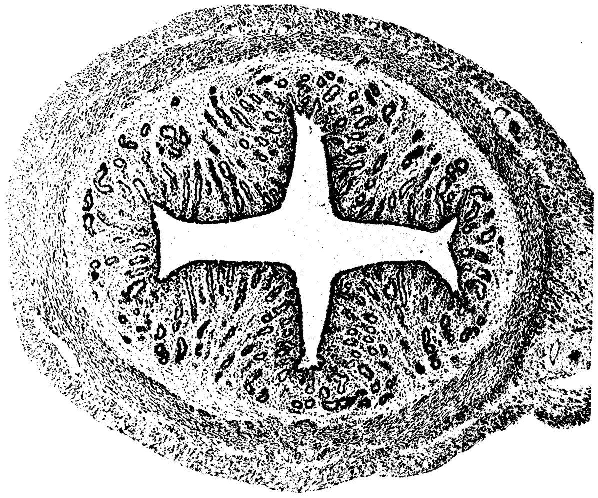
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



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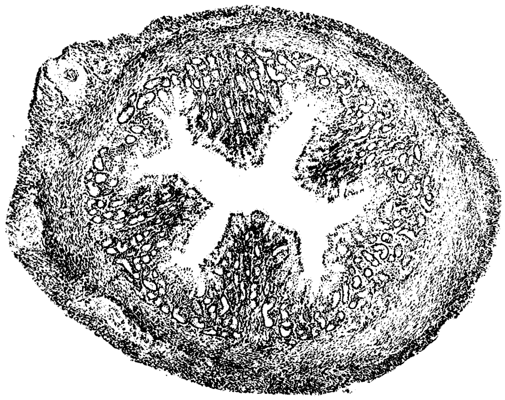

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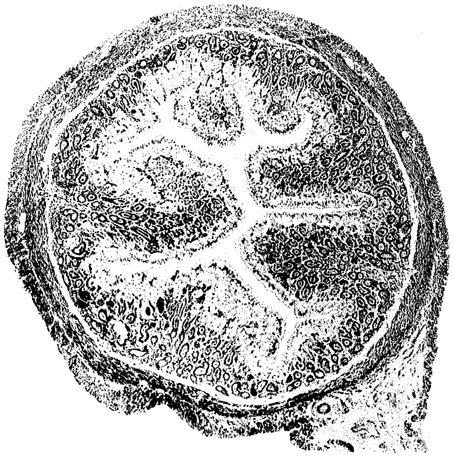

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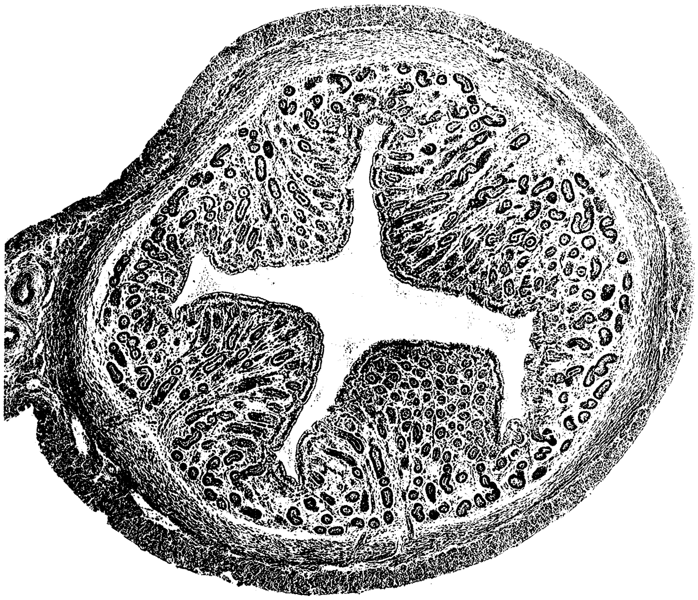

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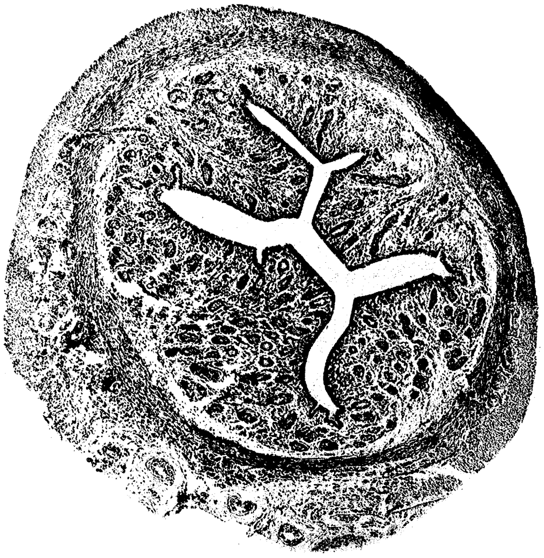

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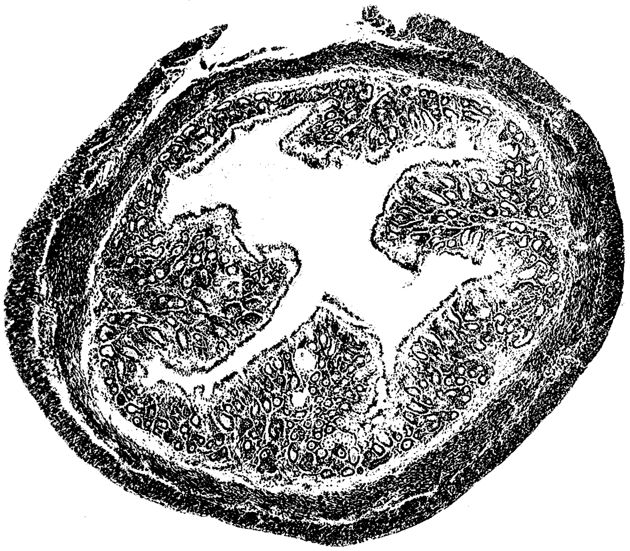

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PLATE 31.

FIG. 31—No. 402 : May 6th. Part of an oestrus uterus in a lactating stoat which has just mated. Note the low epithelium, the oedematous stroma infiltrated by leucocytes, and the newly grown radial gland tubules. X 150.

FIG. 32—No. 469 : June 29th. Early luteal proliferation as in fig. 26 showing the high epithelial cells and rod-shaped nuclei. There is a glandular cyst in the mucosa. X 150.

FIG. 33—No. 141 : October 6th. Later stage of luteal proliferation as in fig. 27. X 150.

FIG. 34—No. 347 : March 4th. Epithelial proliferation in early pregnancy as in fig. 42. The openings of the gland tubules are becoming obliterated. X 150.

FIG. 35—No. 269 : March 17th. Uterine mucosa in mid-pregnancy between the embryos. The epithelium is becoming syncytial. X 60.

FIG. 36—No. 287 : March 26th. Syncytial proliferation of the uterine mucosa, between the embryos, in late pregnancy. X 60.

FIG. 37—No. 141 : October 6th. Spermatozoa in the uterine gland tubules. X 920.


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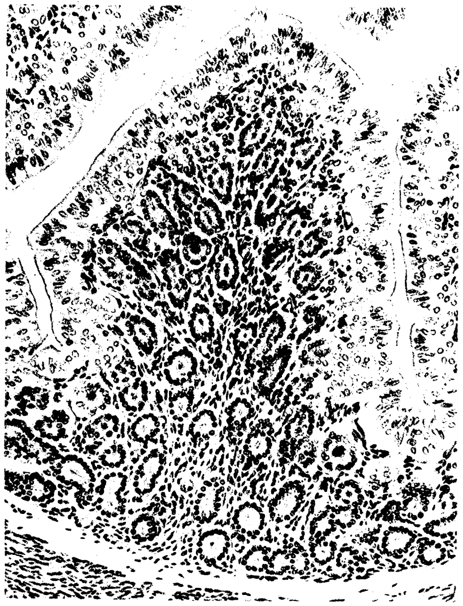
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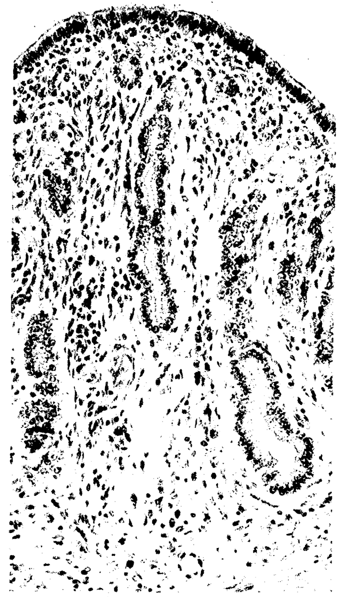
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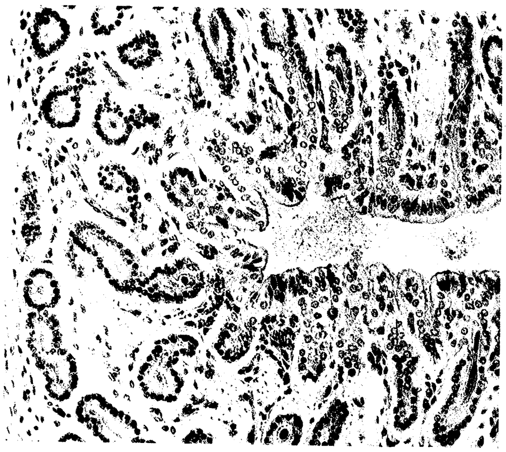
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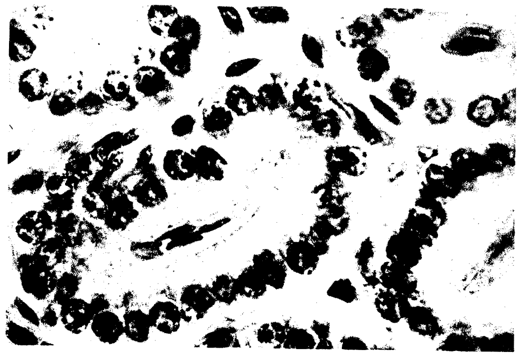
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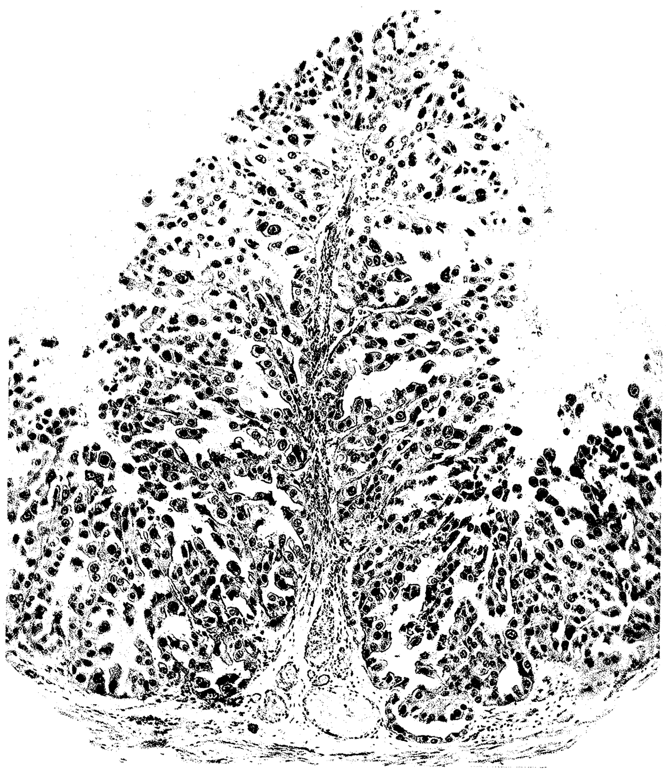
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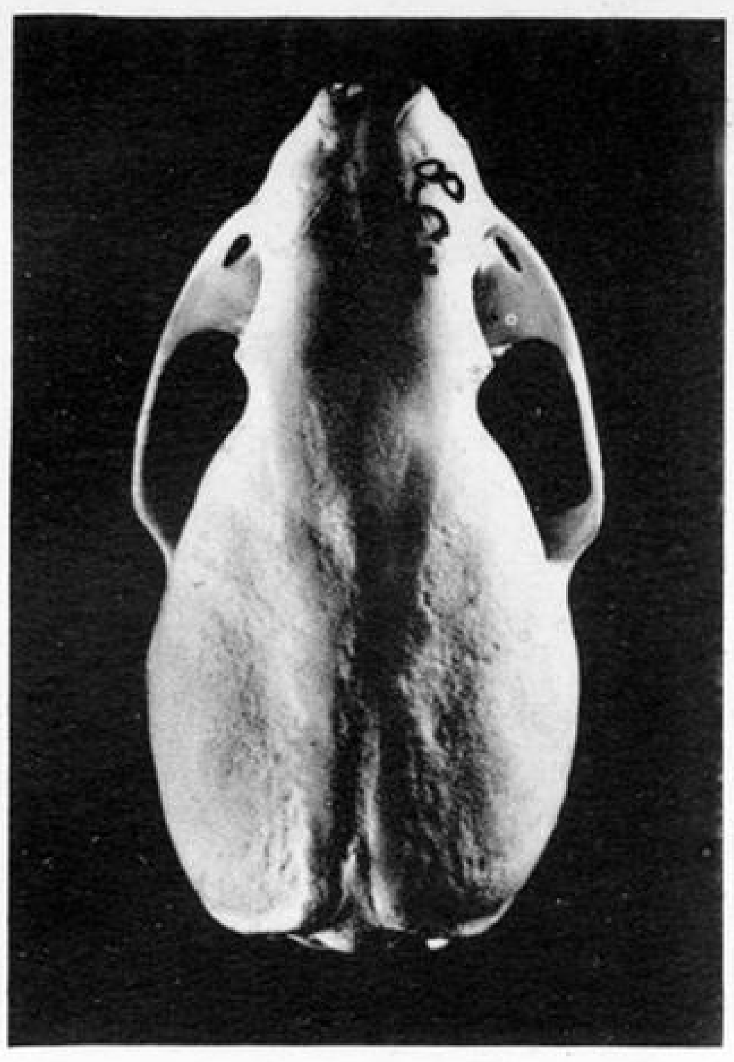

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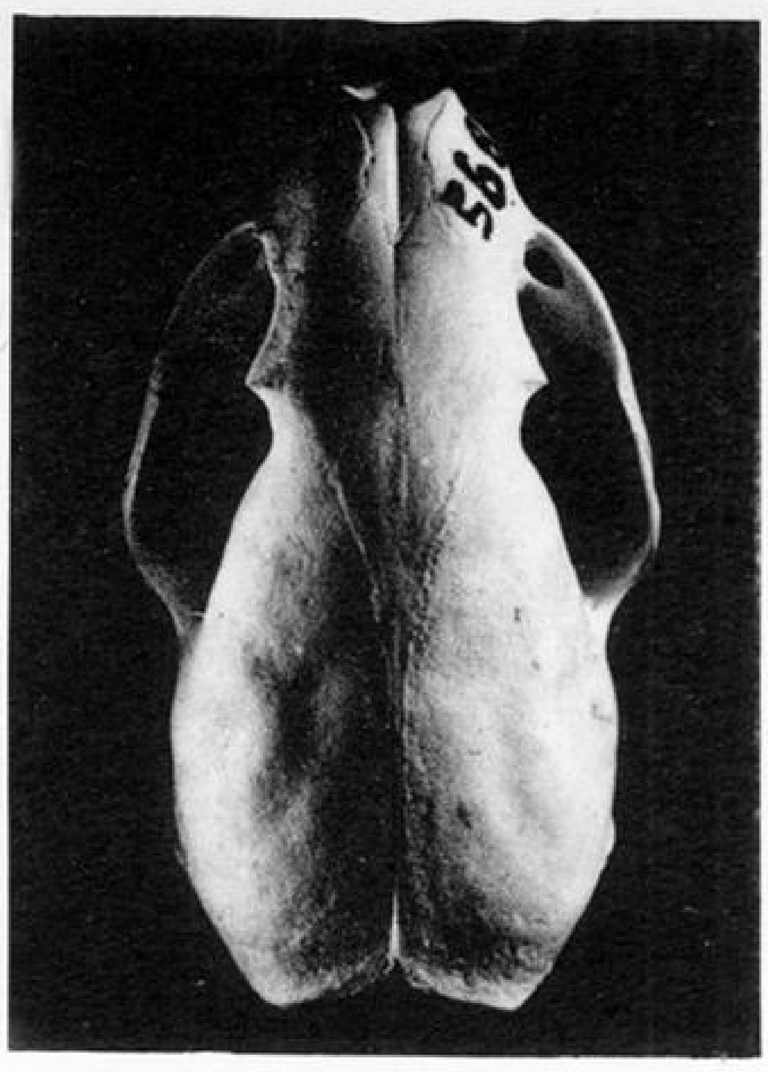

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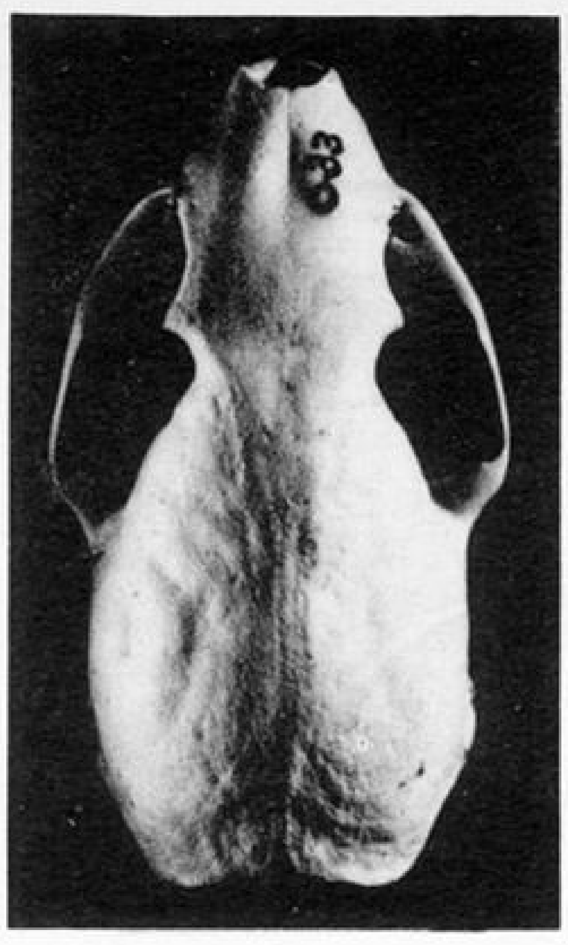

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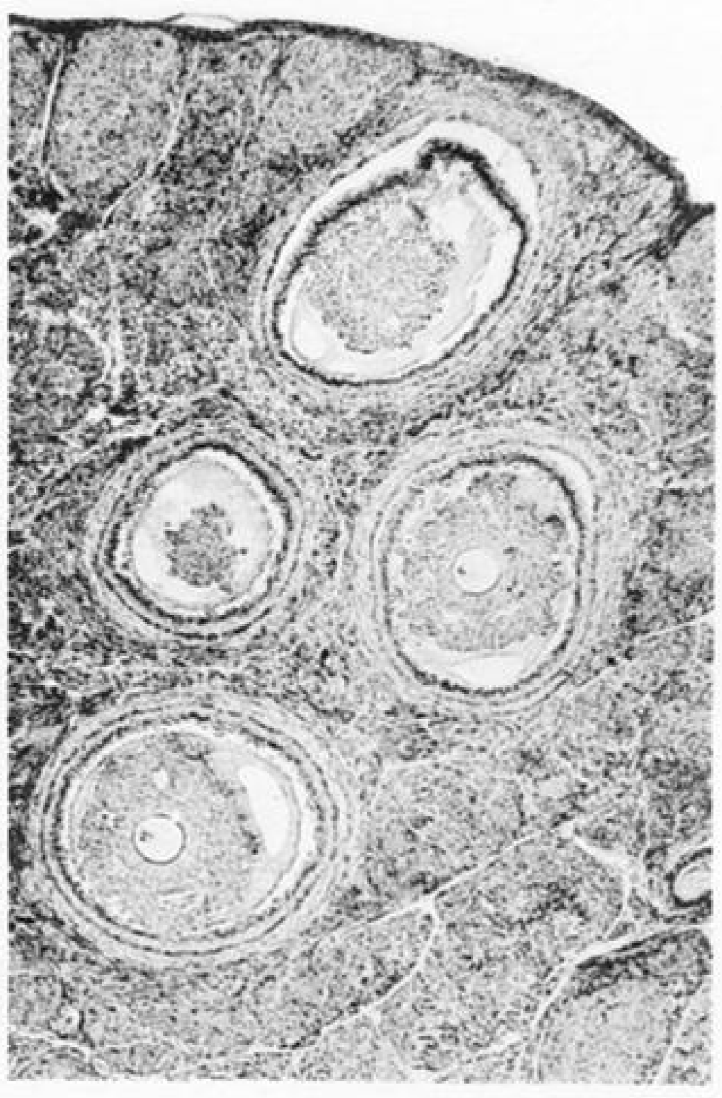

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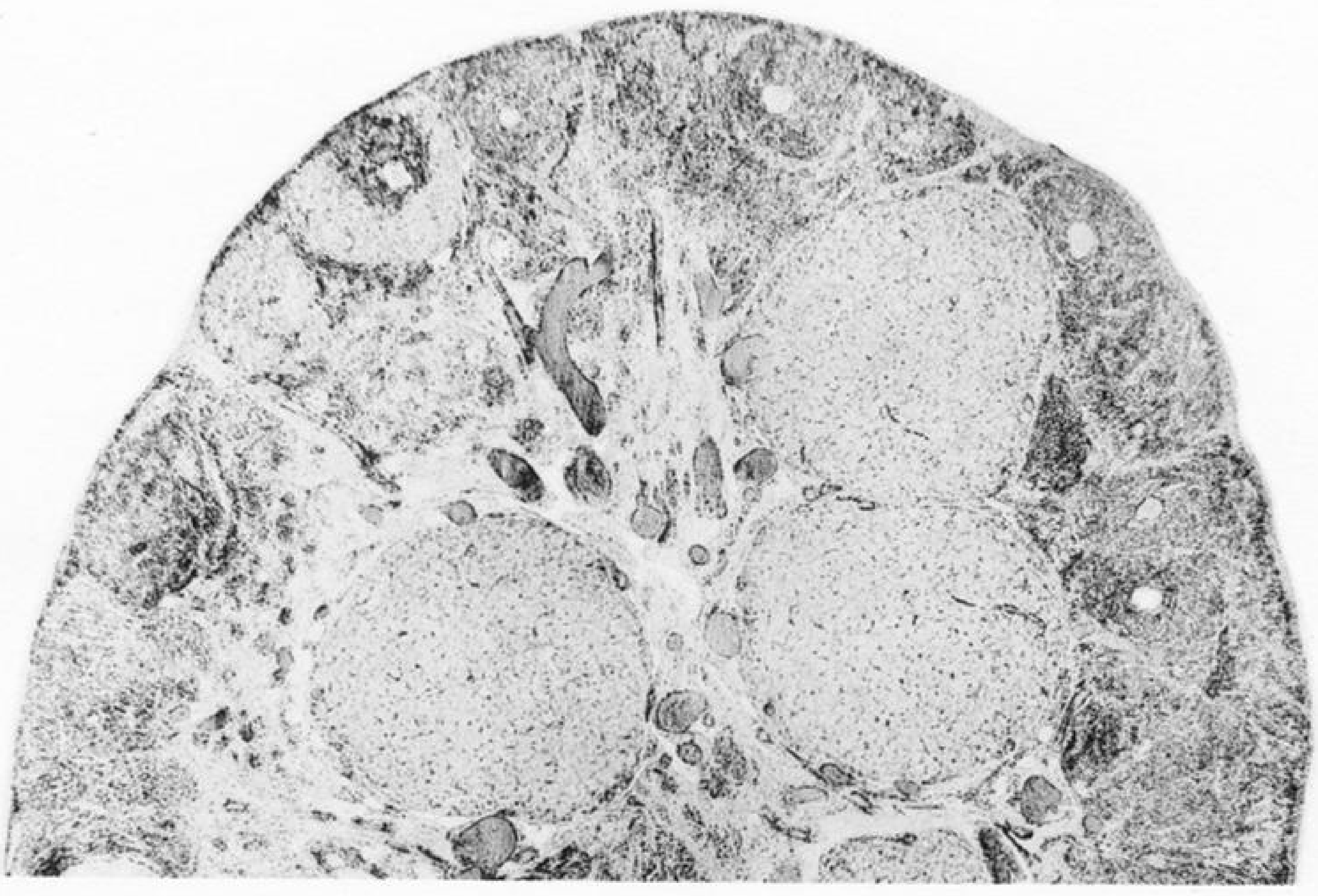

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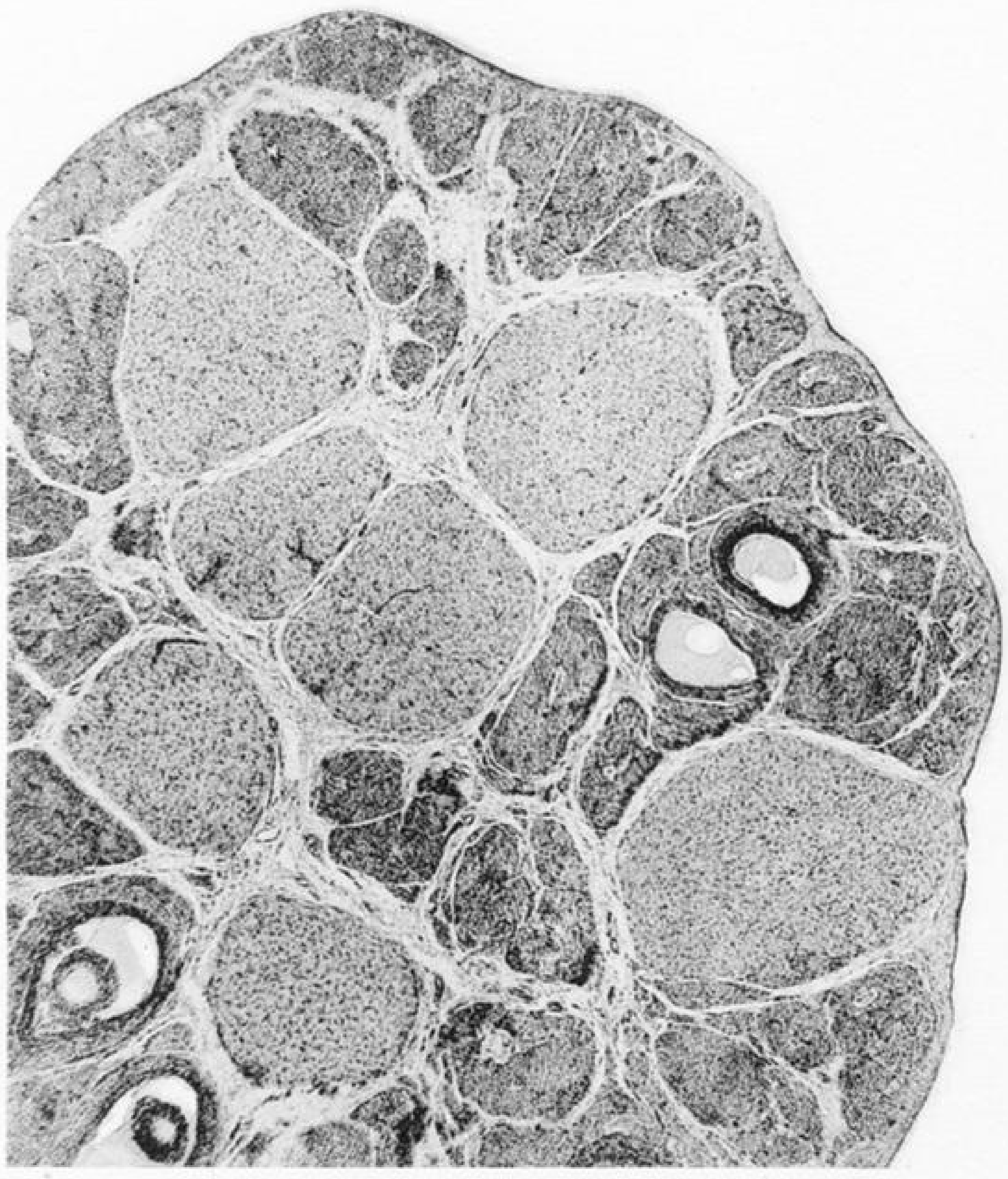

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Plate 28.



All skulls shown in dorsal view X $1\frac{1}{4}$. Ovaries X 32.

Fig. 8—No. 458 : 1st year ♀, June 27th, 170 gm. This skull has well-defined nasal sutures. The parietals are not yet fully calcified and have a rough surface. The temporal muscle ridges have not fused ; there is still a broad median tract between them.

Fig. 9—No. 568 : 1st year ♂, August 3rd. 320 gm. In this skull the muscle ridges have fused posteriorly, and there is the beginning of a sagittal crest. The temporal crests form a deep V.

Fig. 10—No. 633 : 1st year ♀, October 18th. 170 gm. This skull illustrates the later coalescence of the muscle ridges in the skull of the female as compared with the male. The nasal sutures are now almost obliterated.

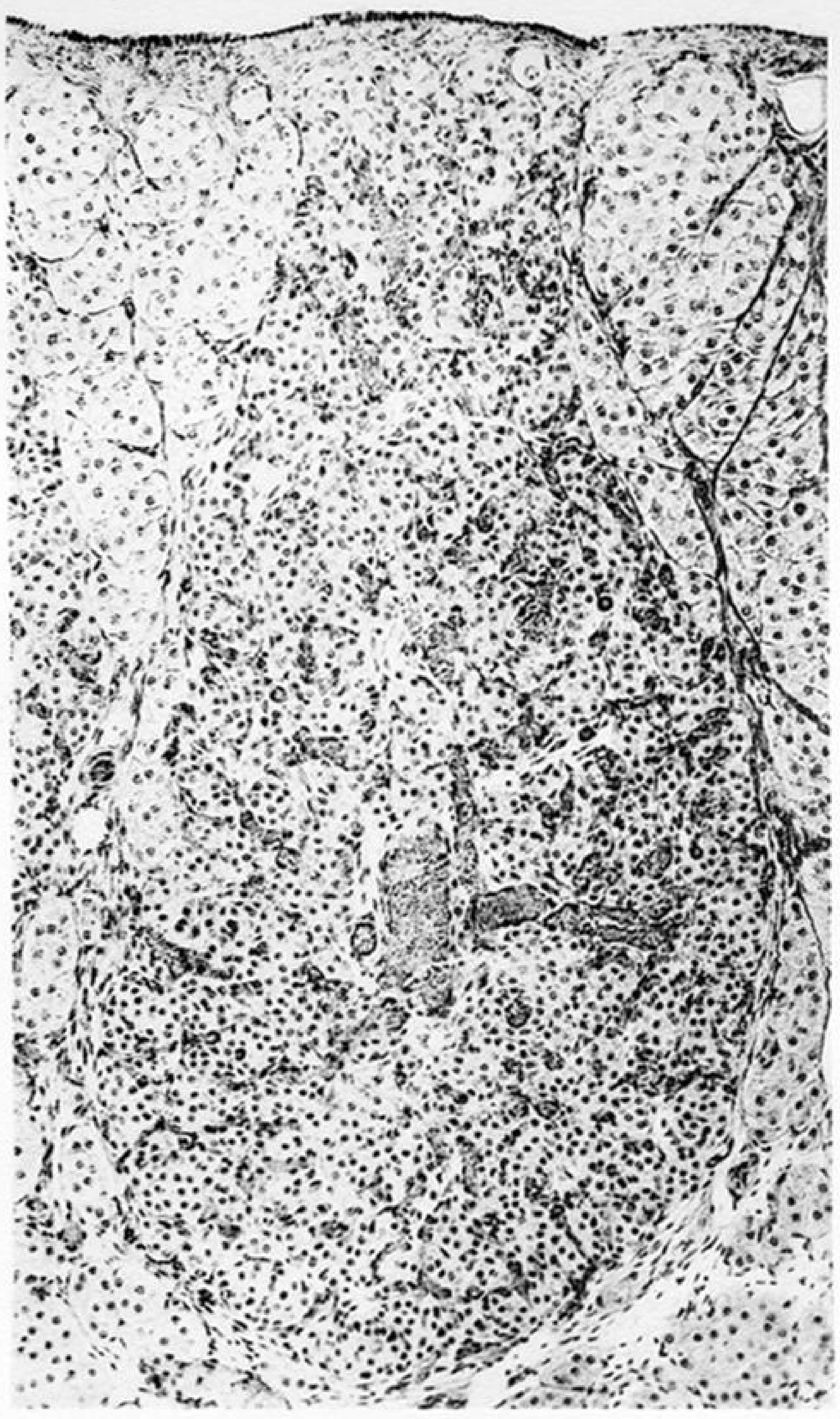
Fig. 11—No. 534 : 2nd year ♀, July 2nd. 250 gm. This shows the shape of the skull in the adult female. Anteriorly the temporal crests now form a short open V, and the skull seems laterally compressed in that region. The skull is fully calcified.

Fig. 12*—No. 402 : May 6th. Part of an ovary of a lactating stoat with ripe follicles; the interstitial tissue is very well developed.

Fig. 13—No. 137 : March 1st. Part of an ovary showing seven corpora lutea which have developed after infertile mating just before the breeding season. There are also numerous luteinized follicles containing degenerate ova.

Fig. 14—No. 269 : March 17th. Part of an ovary showing a median section through a fully developed corpus luteum of pregnancy.

Fig. 15—No. 287 : March 26th. Part of an ovary in late pregnancy showing approximately median sections through three corpora lutea which have shrunk considerably. The medulla of the ovary consists mainly of fibrous tissue and blood vessels, apparently owing to degeneration of the interstitial tissue. Contrast fig. 12.



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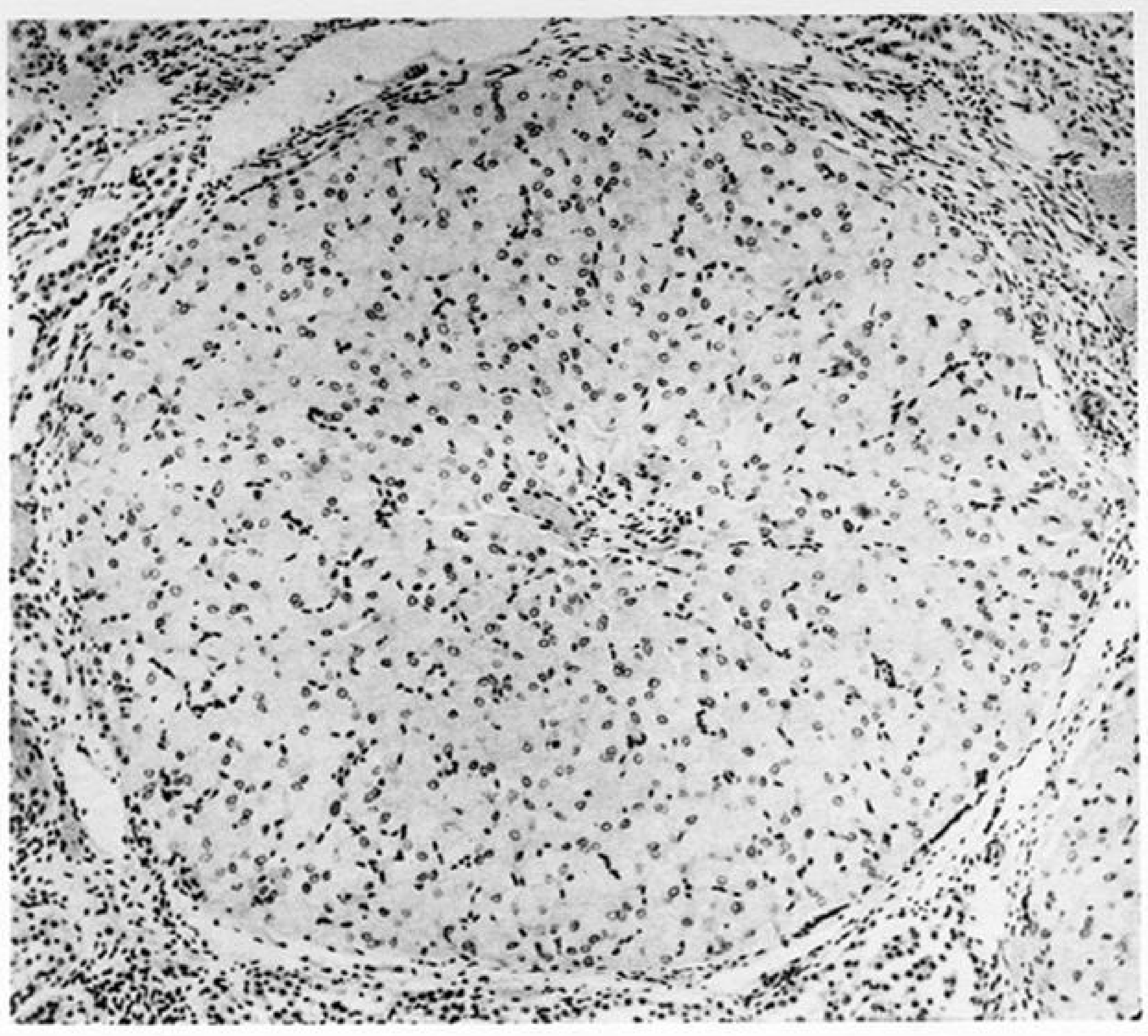

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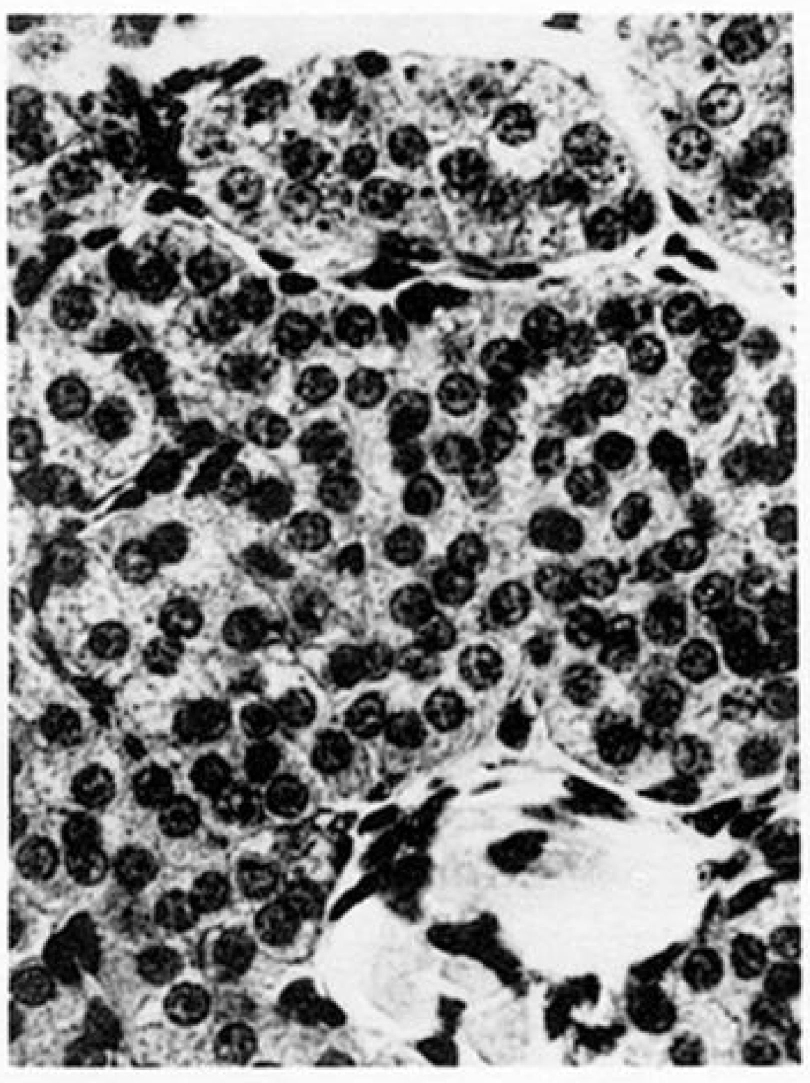

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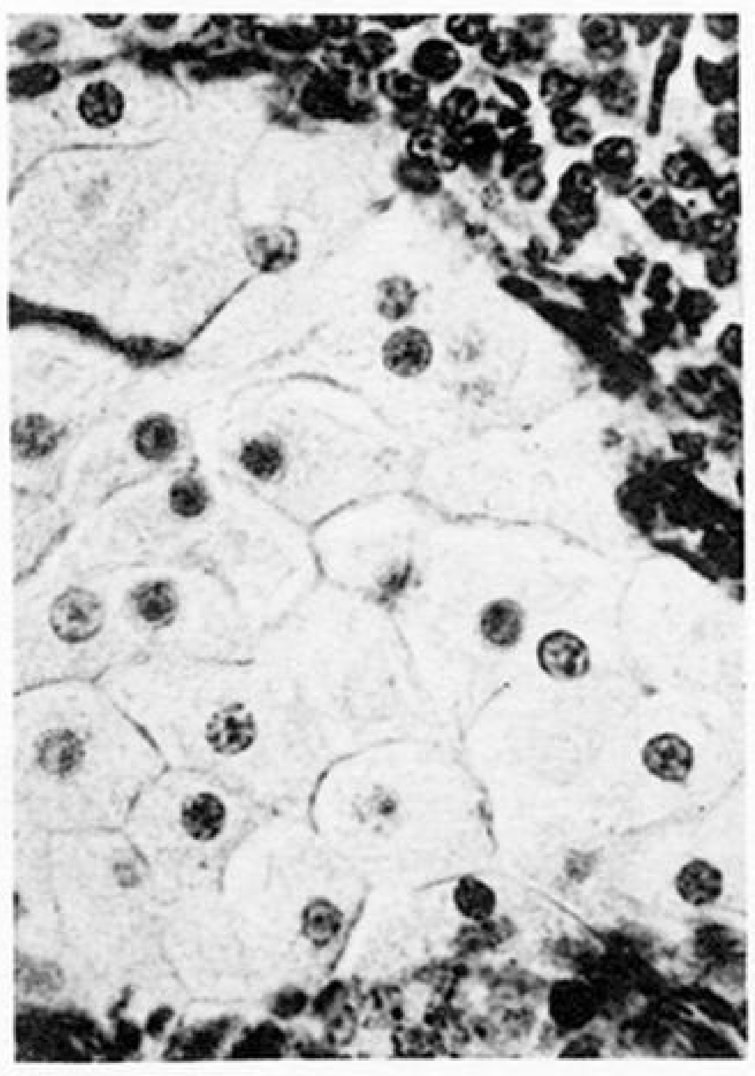

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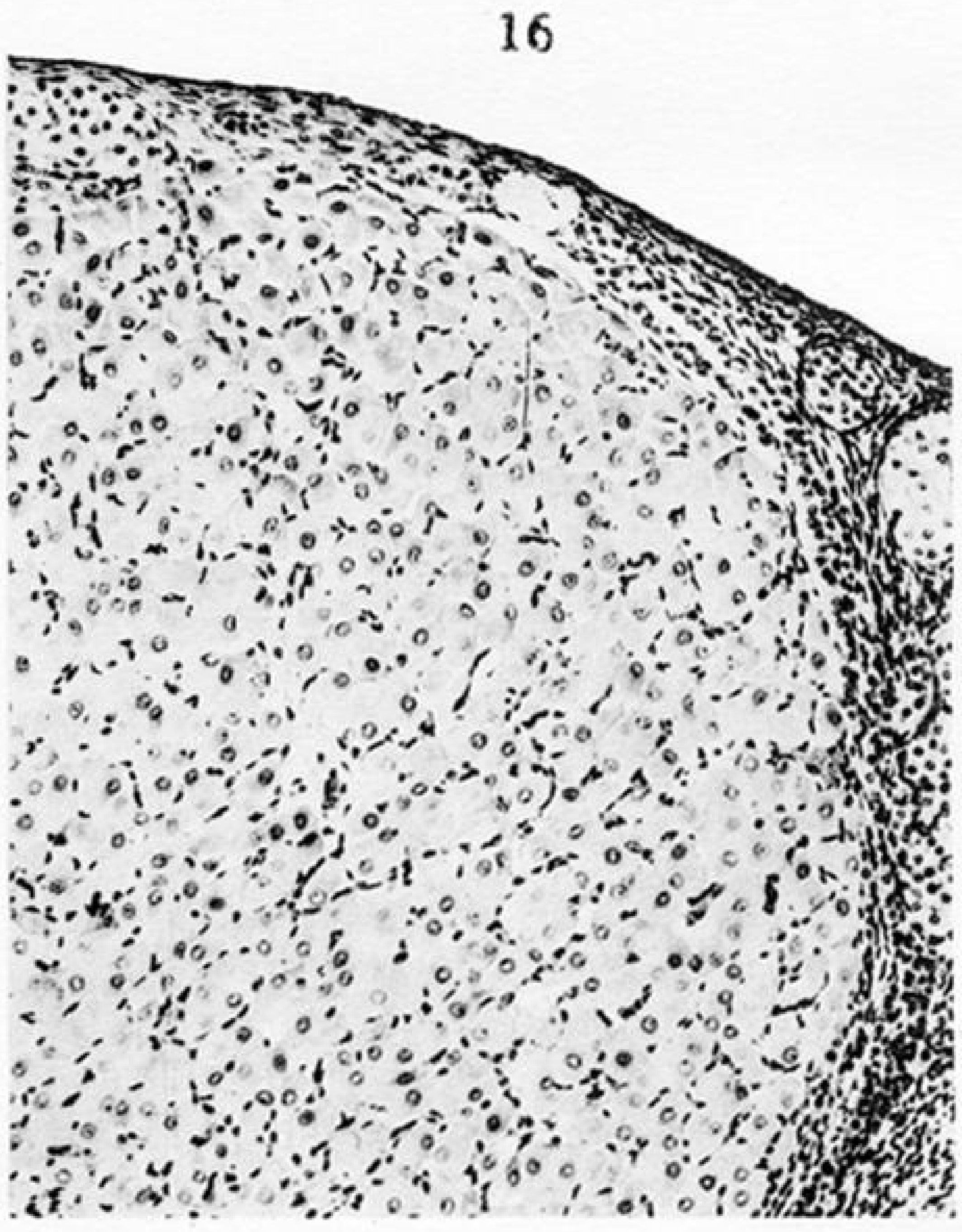

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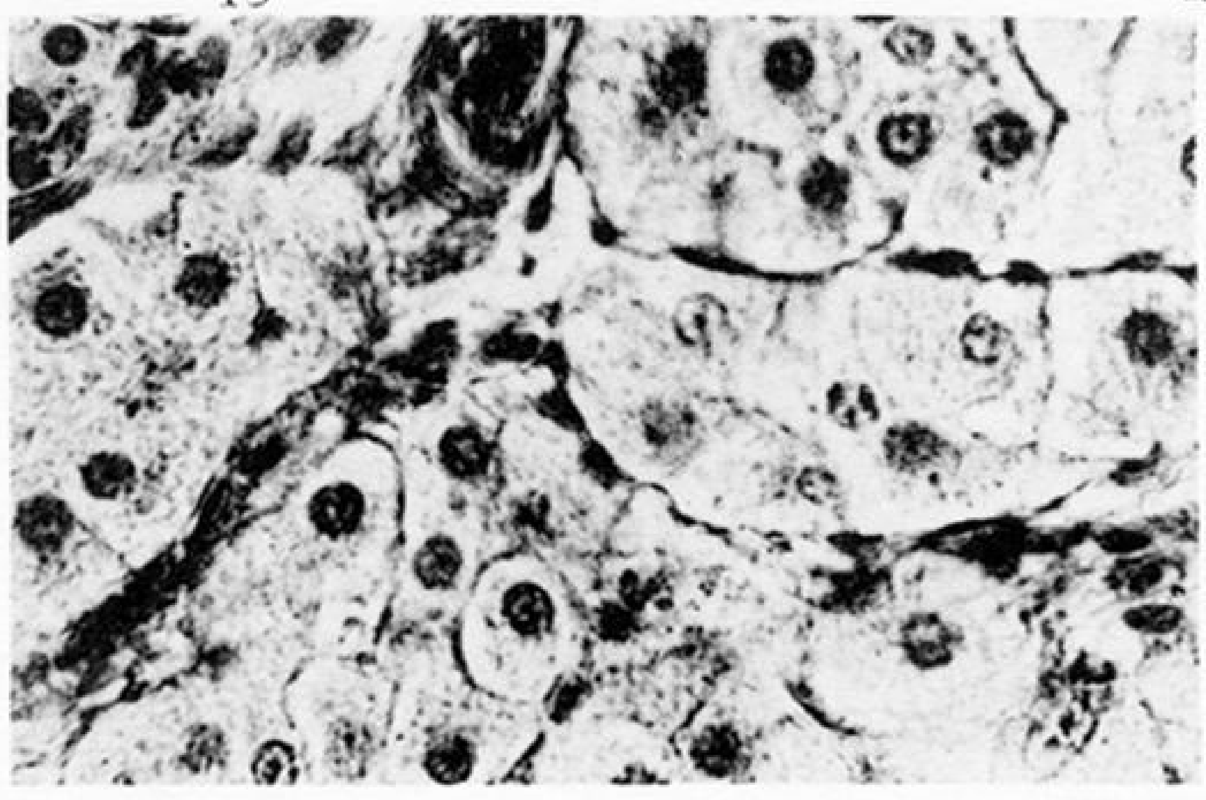

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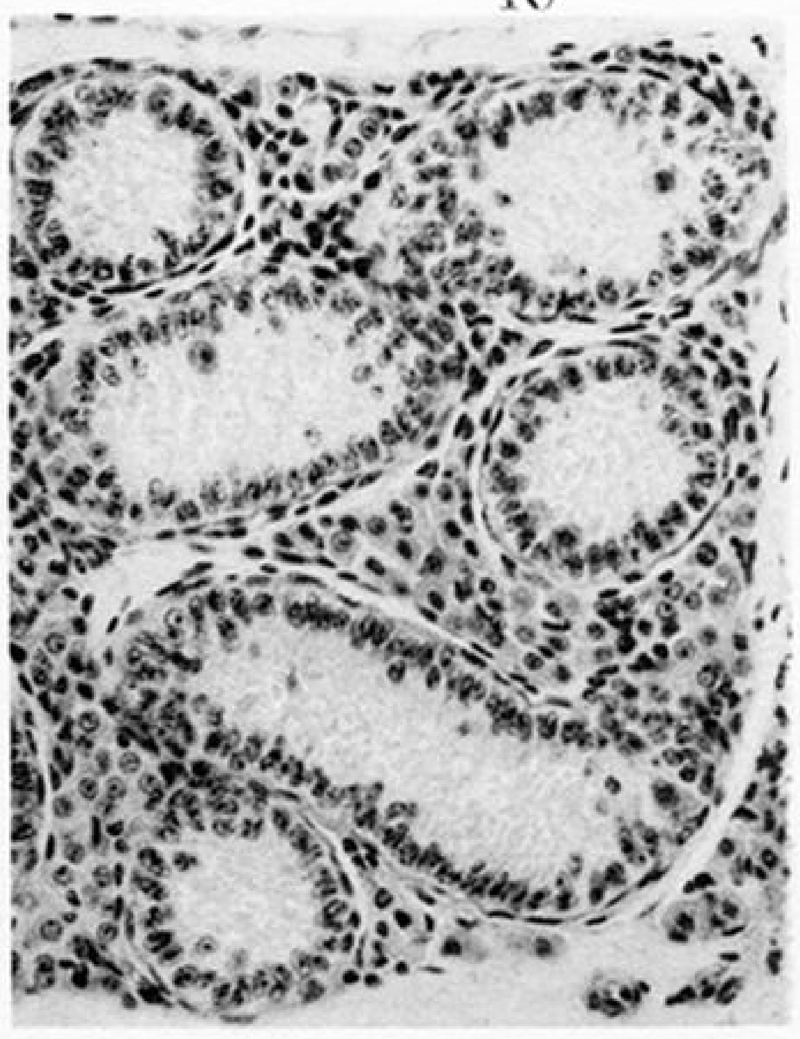

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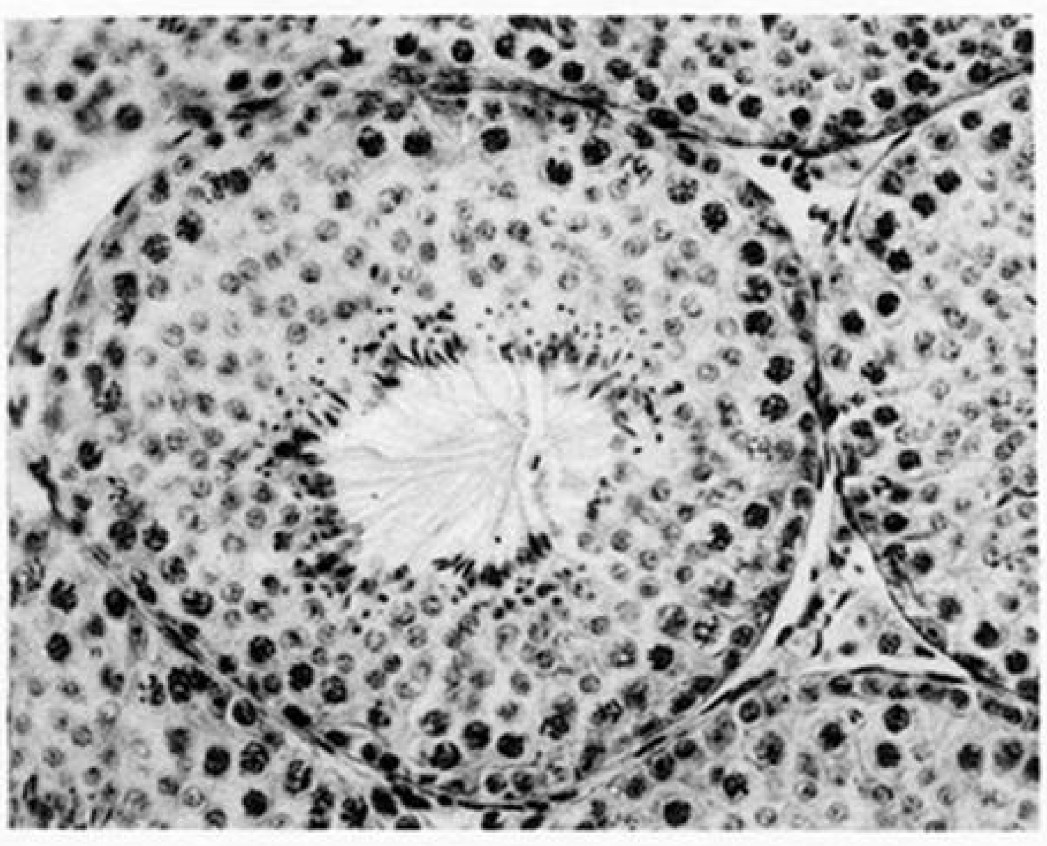

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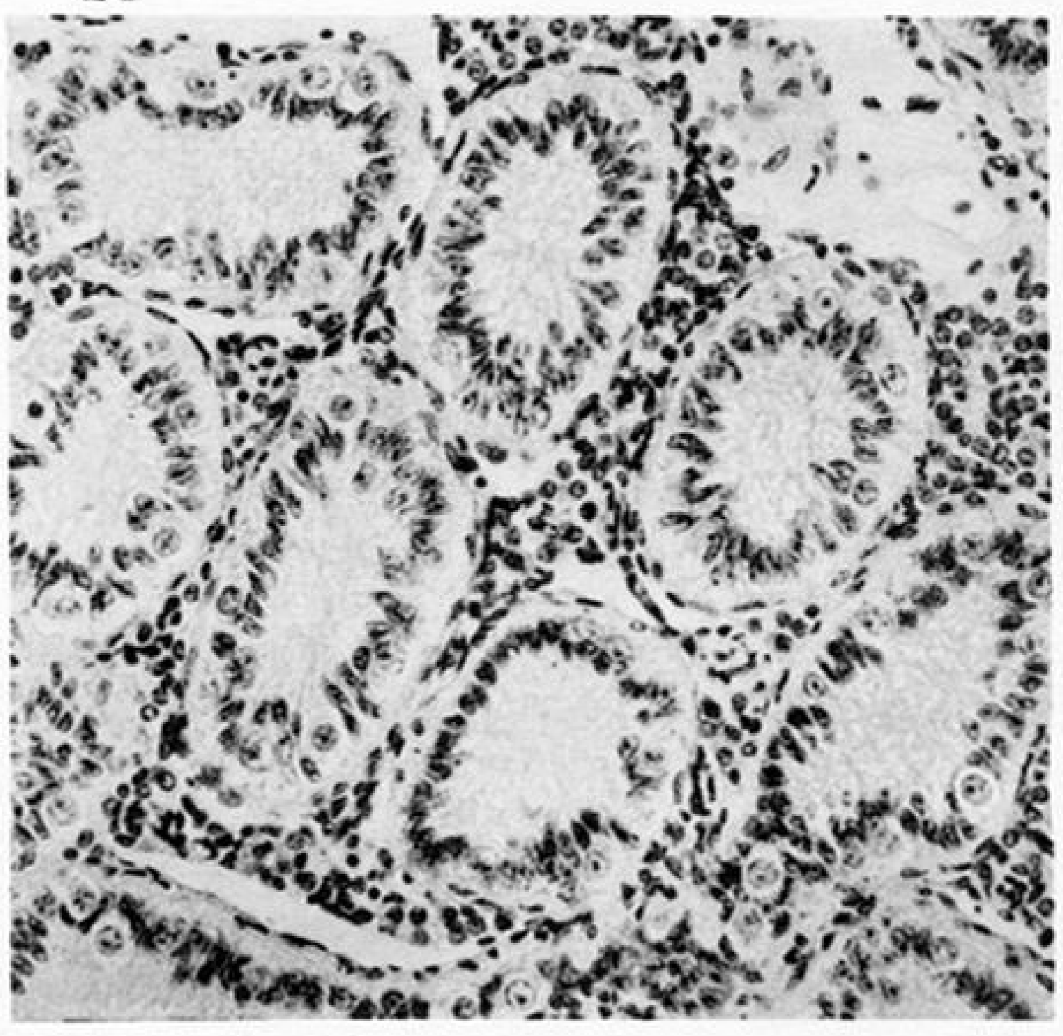

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PLATE 29.

FIG. 16—No. 469 : June 29th. Well-vascularized corpus luteum and part of a second one in a first year stoat. The interstitial cells are shown at a higher magnification in fig. 21. X 90.

FIG. 17*—No. 256 : March 8th. A corpus luteum in a non-pregnant stoat at the beginning of the breeding season. The luteal cells, though apparently regressing, are larger than in any other non-pregnant stoat (p. 24). X 90.

FIG. 18—No. 269 : March 17th. Higher magnification of part of the fully developed corpus luteum of pregnancy shown in fig. 14. X 90.

FIG. 19—No. 244 : January 19th. Cells from a luteinized follicle with degenerate ovum and, above, other ovarian interstitial cells containing pigment. X 370.

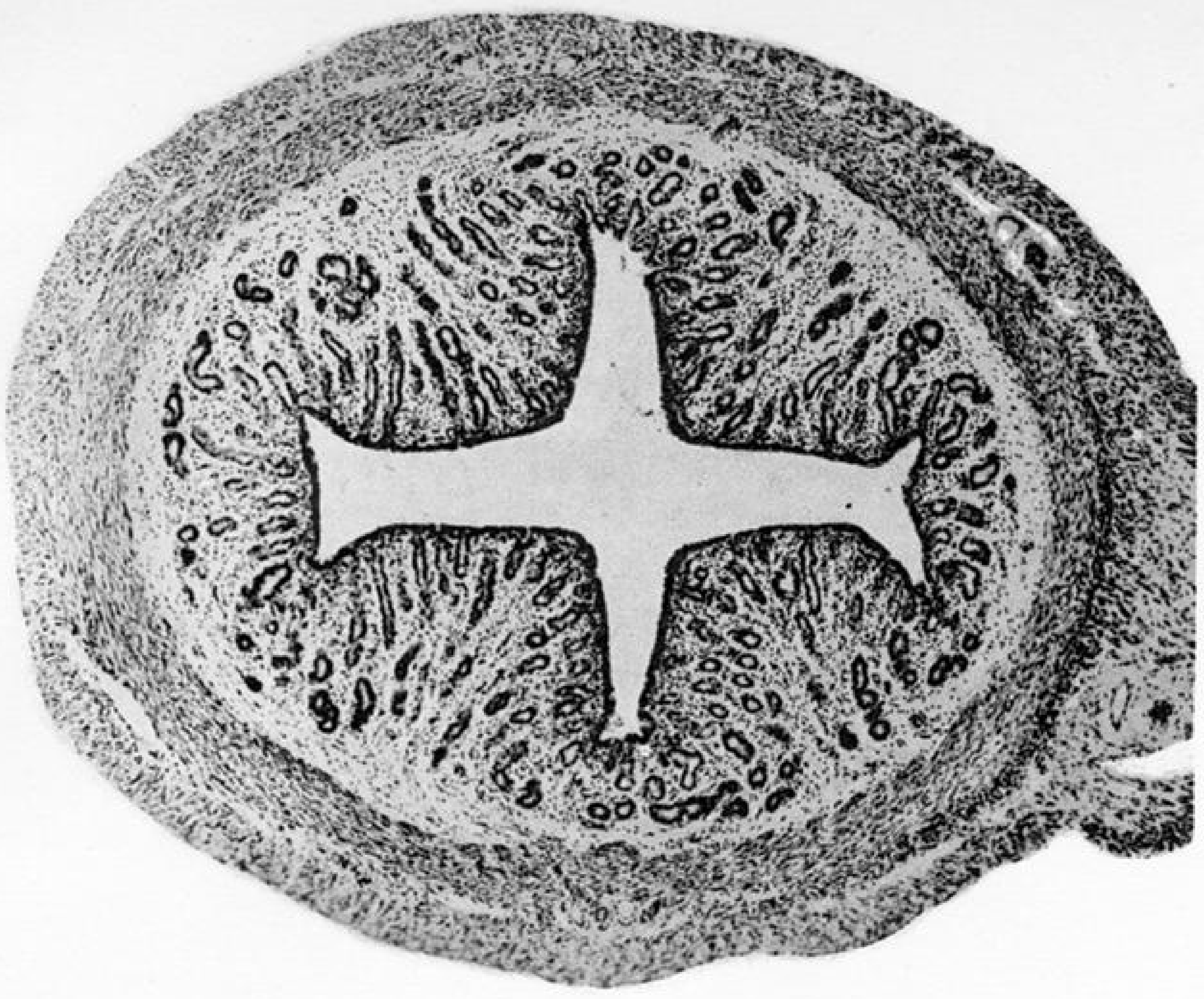
FIG. 20—No. 20 : June 15th. Typical interstitial cells, large and small, from the ovary of a post-lactation stoat. X 370.

FIG. 21—No. 469 : June 29th. Interstitial cells in the ovary of a first year stoat. Compare fig. 16 from the same ovary. X 370.

FIG. 22—No. 110 : July 7th. Part of the testis of a 200 gm first year stoat. The tubules are small and undeveloped, but contain occasional large winter spermatogonia. There is much intertubular tissue, including glandular interstitial cells. X 188.

FIG. 23—No. 381 : May 9th. The testis of this stoat weighed 1·2 gm and showed no regressive changes. Compare the tubule and interstitial cell size with those of figs. 22 and 24. X 188.

FIG. 24—No. 635 : October 26th. The testes of this adult, second year stoat weighed only 0·16 gm. The section shows the small seminiferous tubules with a thickened basement membrane. Large winter spermatogonia can be seen. The interstitial cells are smaller than in the active or the immature testis, and the intertubular tissue contains many leucocytes. X 188.



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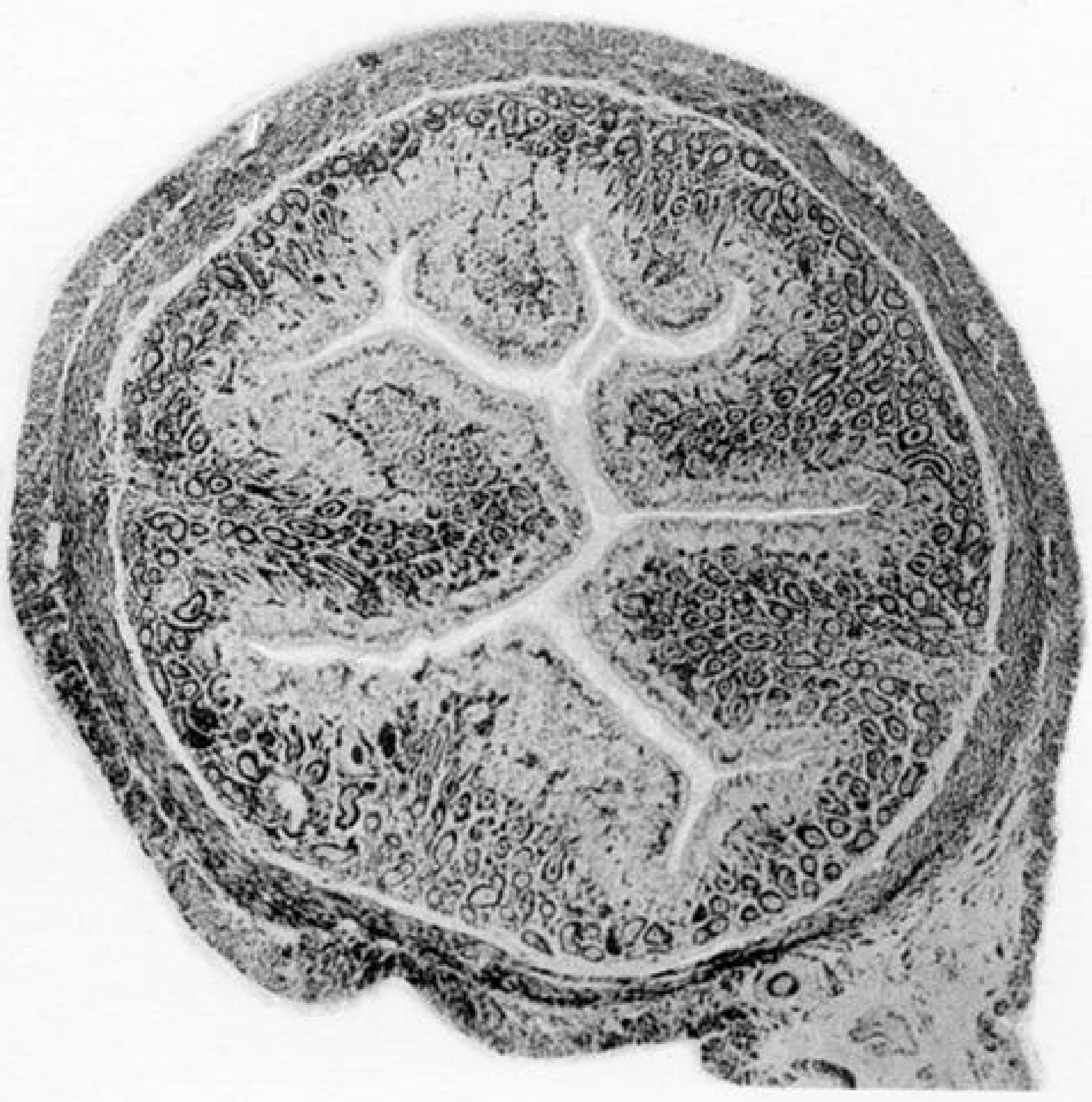

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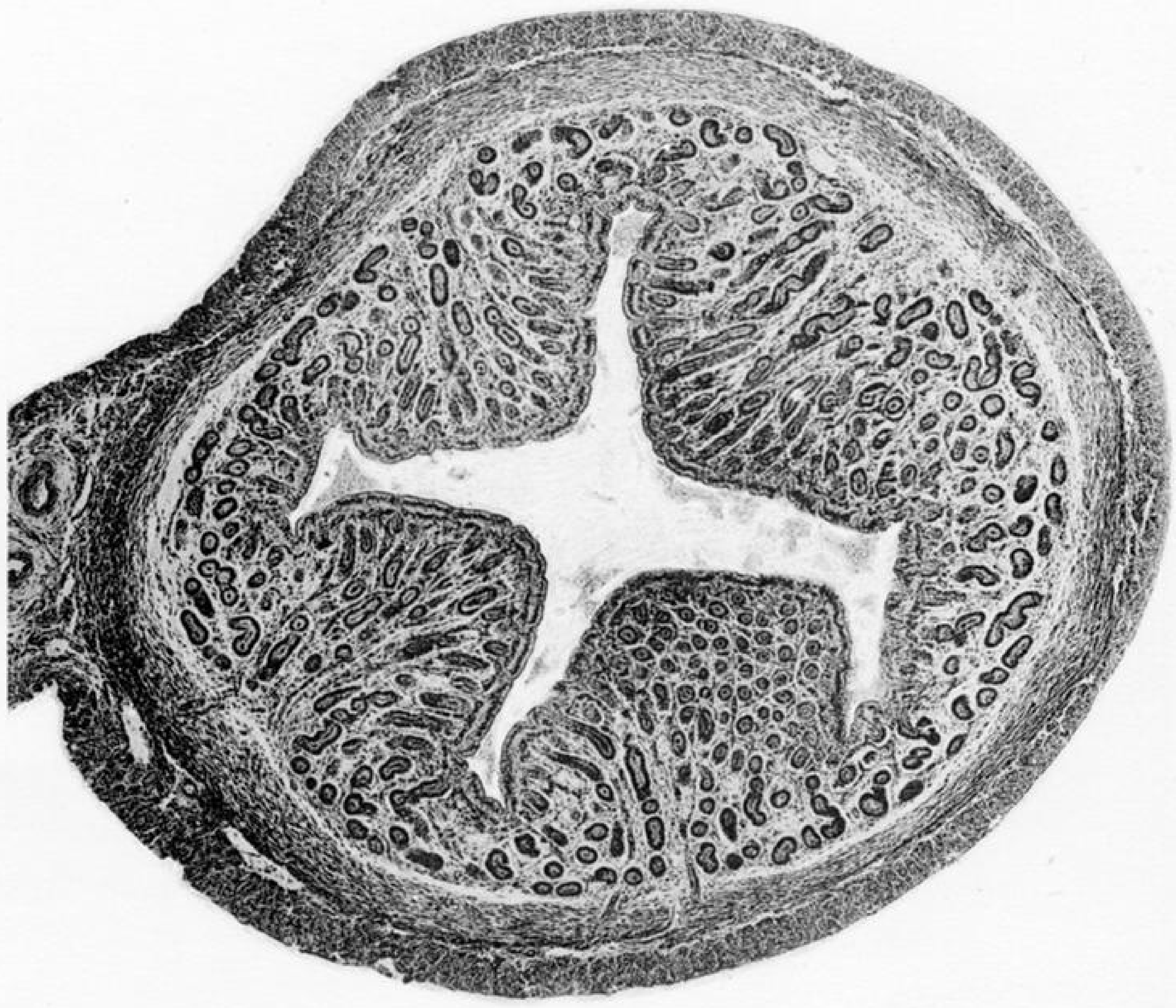

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PLATE 30.

Transverse sections through stoat uteri. X 47, except fig. 30, X 37.

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FIG. 26—No. 443 : June 20th. Pseudo-pregnant uterus from a mated first year stoat ; the mucosa is much denser than in fig. 25, and the epithelium has proliferated.

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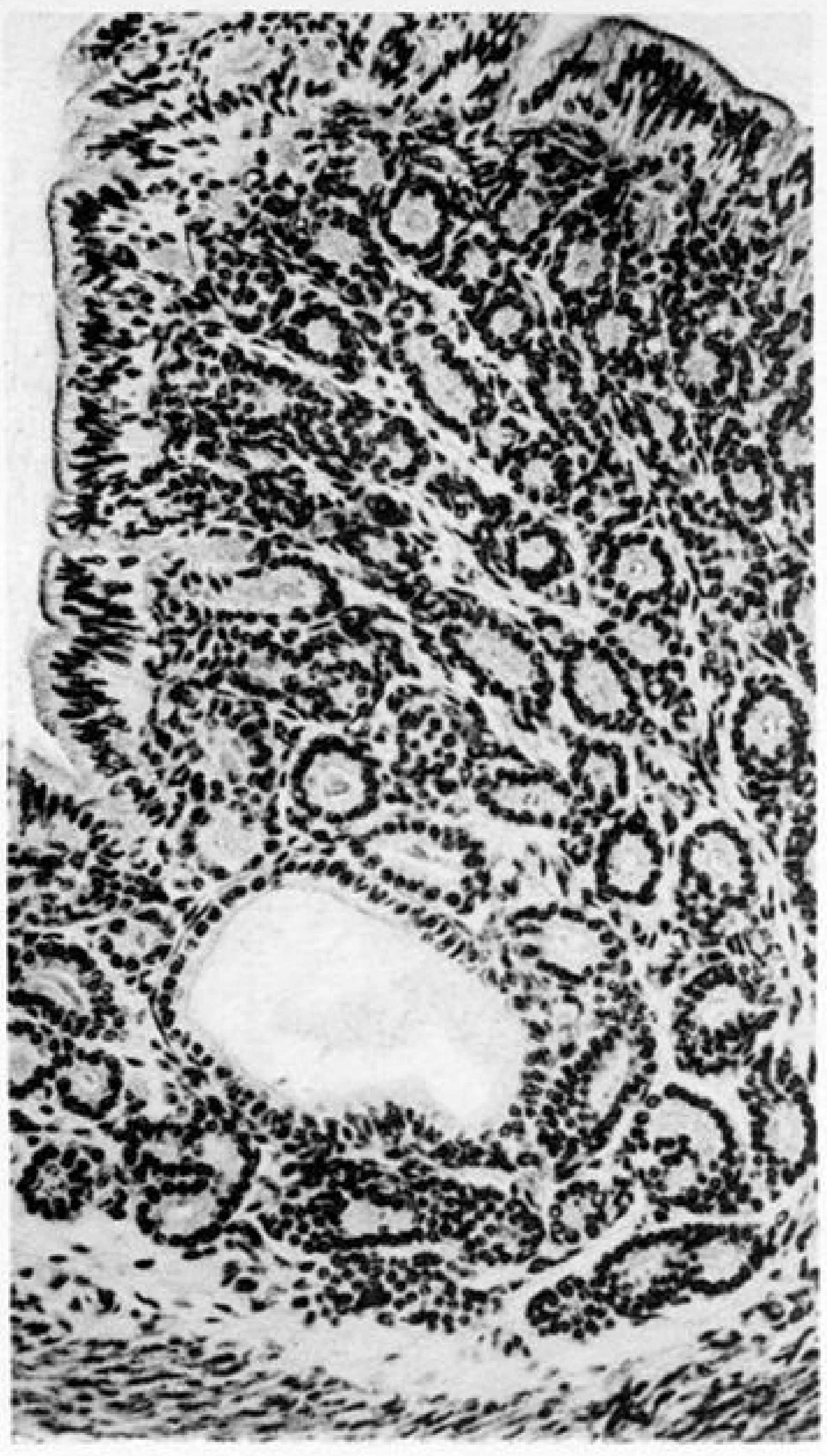
FIG. 28—No. 18 : April 21st. Oestrus uterus in a lactating stoat which has just mated.

FIG. 29—No. 246 : February 7th. Parous uterus showing pseudo-pregnant proliferation.

FIG. 30—No. 347 : March 4th. Section through the uterus in very early pregnancy. The epithelium has begun to grow.



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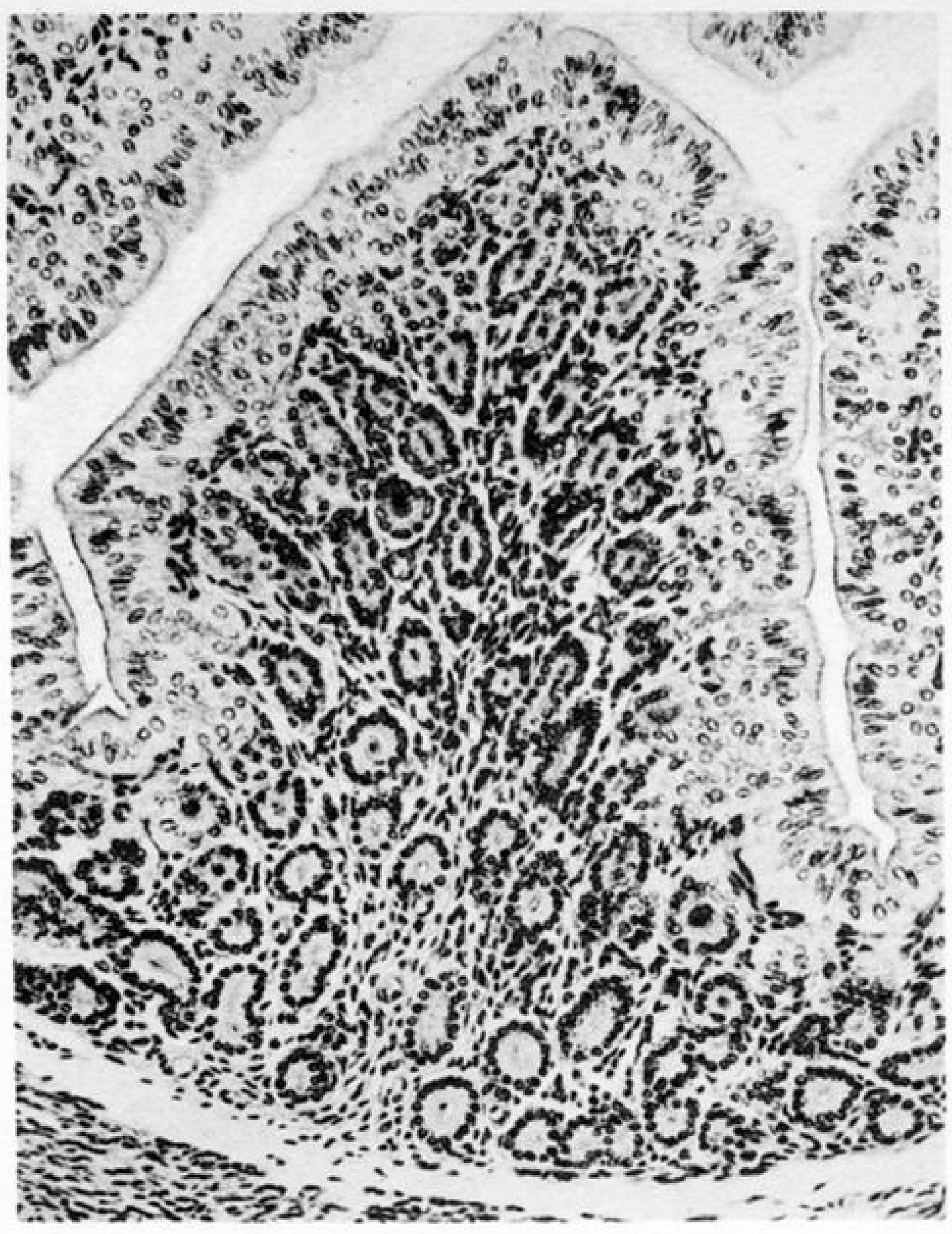

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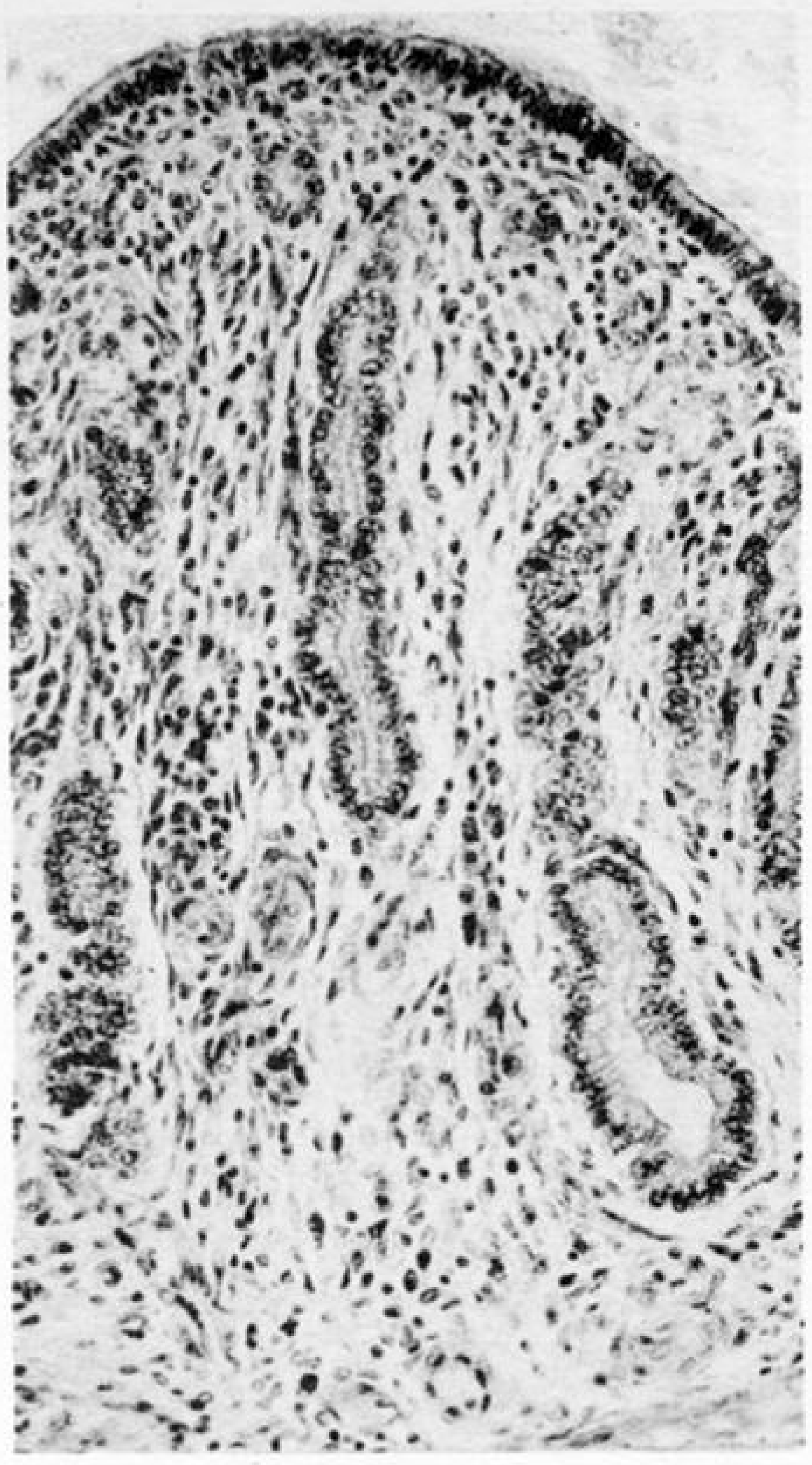

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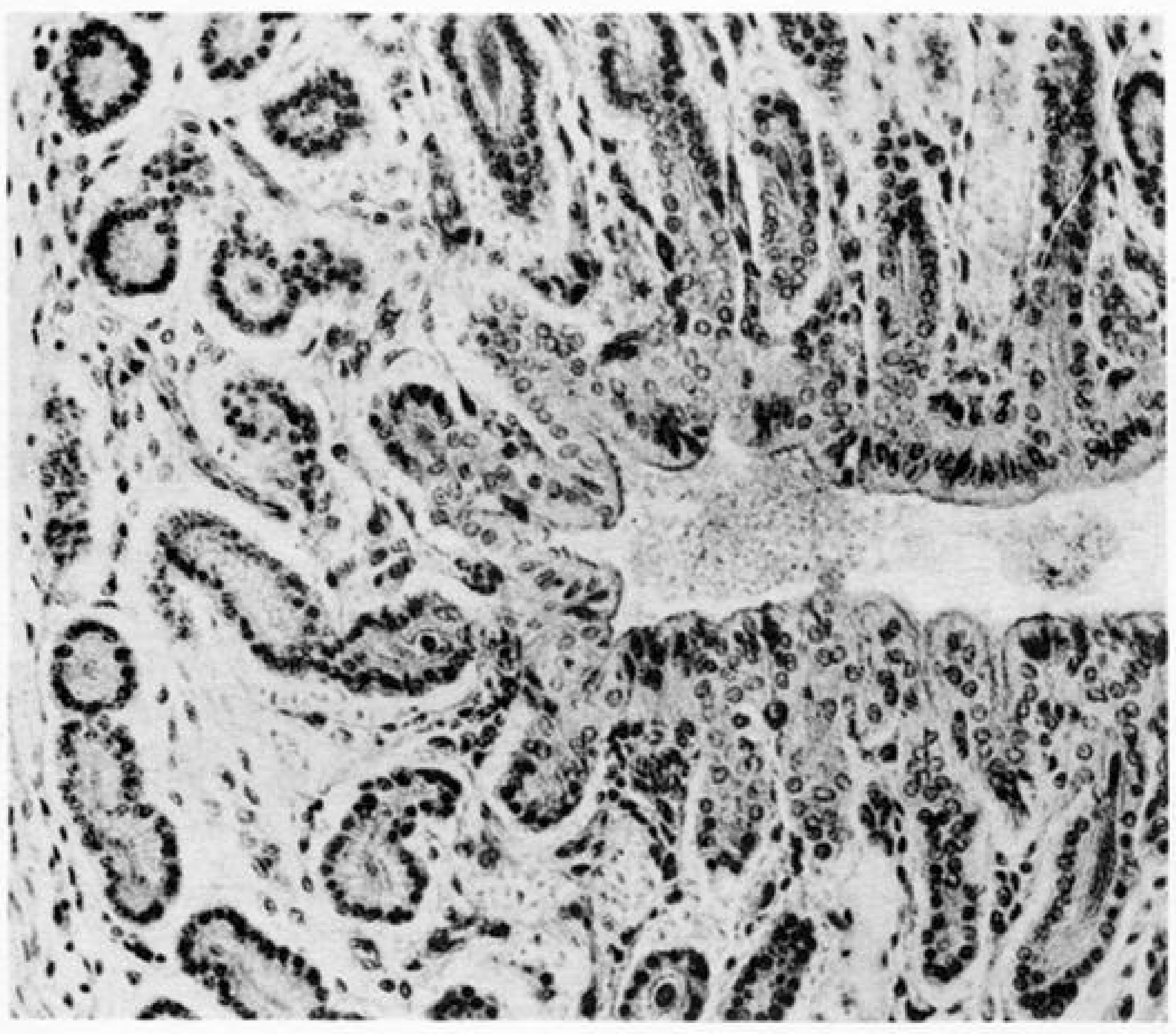

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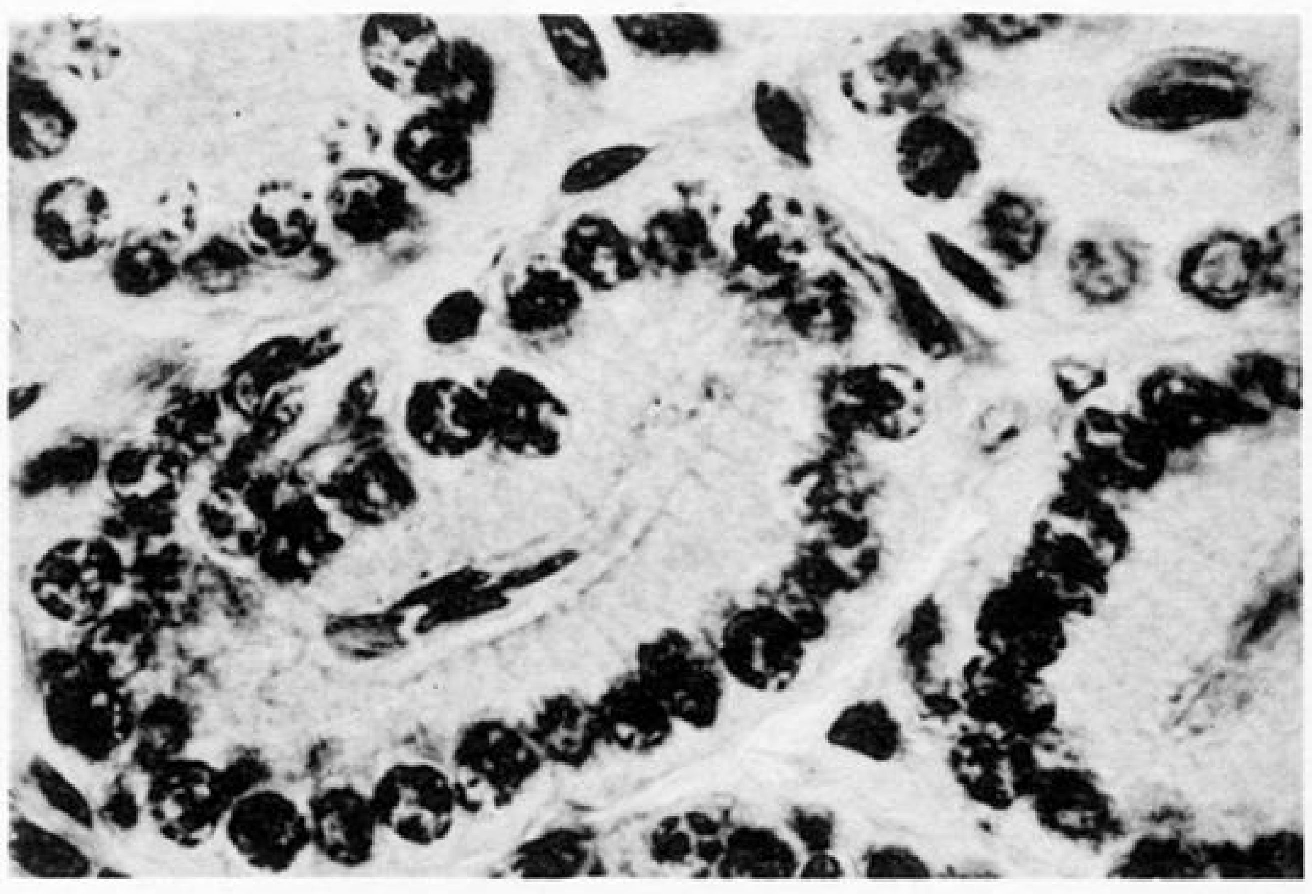

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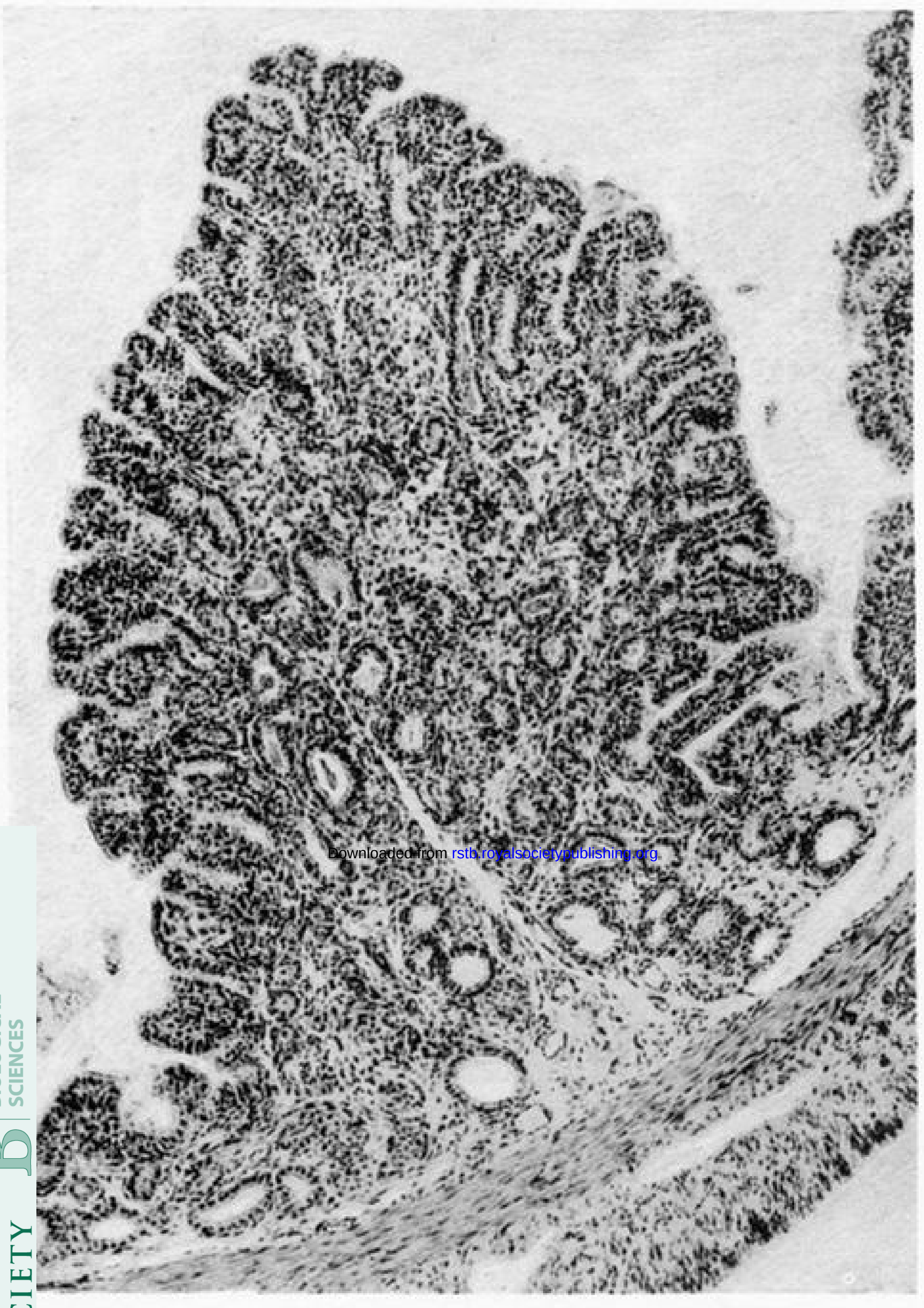

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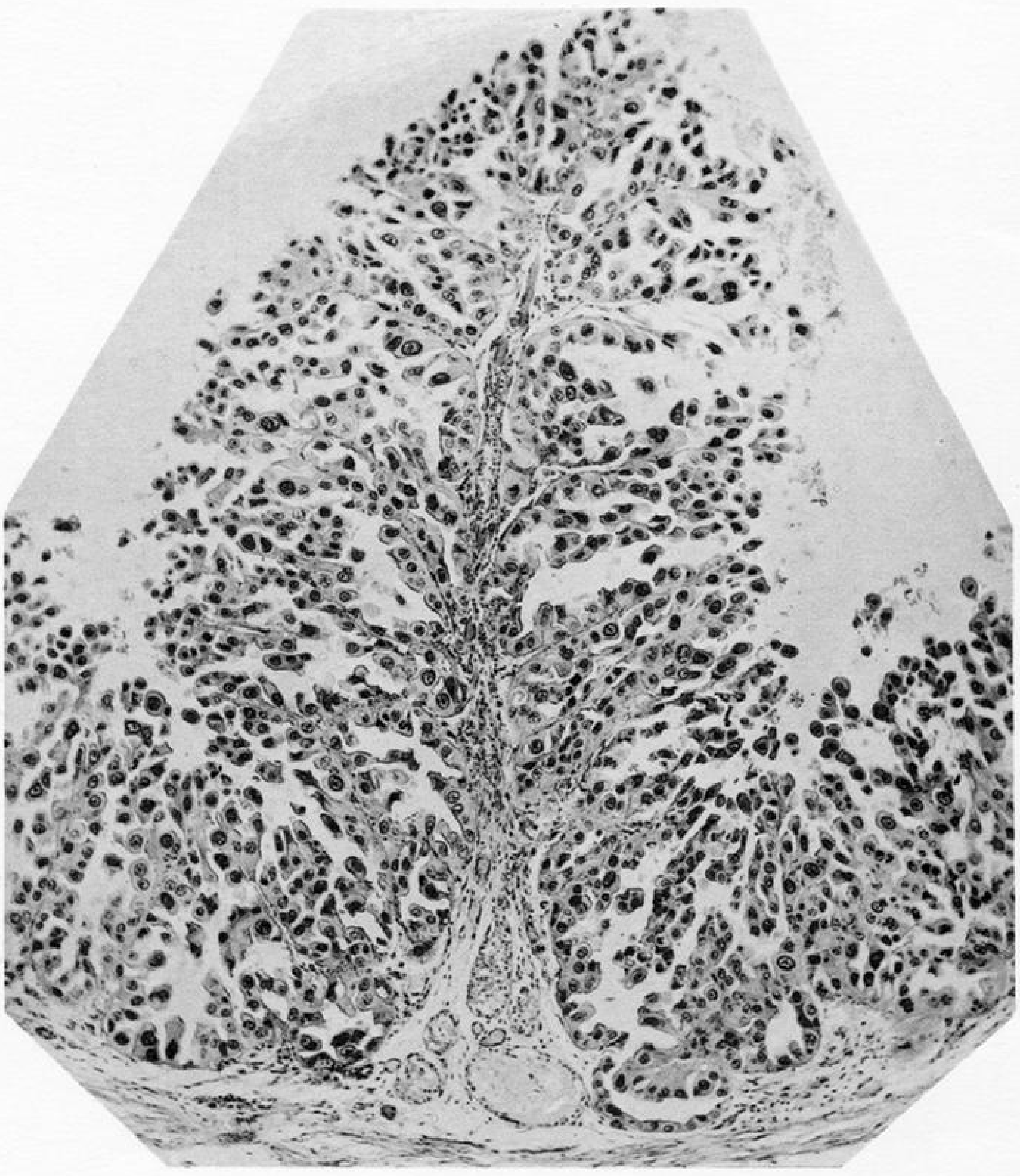

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FIG. 35—No. 269 : March 17th. Uterine mucosa in mid-pregnancy between the embryos. The epithelium is becoming syncytial. X 60.

FIG. 36—No. 287 : March 26th. Syncytial proliferation of the uterine mucosa, between the embryos, in late pregnancy. X 60.

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