VI. *The Reproductive Processes of Certain Mammals. Part* VI.—*The Reproductive Cycle of the Female Hedgehog.*

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[PLATES 27–33.]

CONTENTS.

I. *Introduction.*

THE hedgehog (*Erinaceus europæus*) is a common British and North European mammal, but no thorough investigation appears to have been made of the reproductive cycle of the female. The present account is designed to fill this gap and as a contribution to the comparative physiology of reproduction. Ecological data are not included.

HUBRECHT (1889), working at Utrecht on the embryology of the hedgehog, gives the breeding season as June to August and the number of fœtuses as 4–8. He regards the hedgehog as a primitive type.

MILLAIS (1904) states that the hedgehog breeds twice a year in Great Britain, having its first litter in May or June and its second in August or September, the period of gestation being not more than one month. Five to seven young are born, which are blind at birth; after about three weeks their spines harden and they assume adult coloration. The young are three-quarters grown by the time winter sets in.

BARRETT-HAMILTON (1911) states that the earliest hedgehog pregnancies occur in April, but he does not include any records. Second litters are found between the middle of August and the end of September; a late pregnancy is recorded on September 23 in Ireland and an early post-partum animal on September 28 in Scotland. There are generally four or five young, though they may vary in number from 2–9. The length of gestation is given as 4–7 weeks, but as most probably seven weeks on the authority of LILLJEBORG (1874). Like MILLAIS, BARRETT-HAMILTON states that the young are well grown in the same season. Both these writers describe the hedgehog as hibernating from late in November onwards; the length and extent of hibernation are very variable, however, and the animal is not infrequently found walking about in the winter.

In view of the restricted breeding season it seemed likely that the reproductive organs of the female, no less than of the male hedgehog (MARSHALL, 1911), would show marked changes between the anœstrous and breeding season conditions.

II. *Material and Methods.*

(*a*) *Collection of Material and Records.*—Animals were collected between 1930 and 1933 (the majority dating from 1931) until the series was adequate. It was found that seasonal changes could only be studied satisfactorily in hedgehogs taken straight from the field, since the condition of the reproductive organs may become affected after only a few days in captivity. Animals taken during the breeding season often cease to ovulate, and may terminate pregnancy (*cf.* HUBRECHT, 1889); during anœstrus, on the contrary, premature activity and growth will often occur in ovaries, uterus, and vagina. Almost all hedgehogs kept in captivity for more than a few days have been discarded from the series illustrating seasonal changes, although records of their condition when they came in from the field can be included, when known with certainty. A few other animals, kept in the laboratory, provided useful histological material. Among these were some hedgehogs taken in February and March while still anœstrus, which, in due course, showed breeding season development of the reproductive organs and ovulated spontaneously and normally in captivity. These are not recorded in Table I or in the Appendices.

The hedgehogs were almost all sent into the laboratory alive. They came from many different districts, but a large proportion were received from near the following places :—

Bangor (N. Wales).
St. Neots (Huntingdonshire).
Hungerford (Berkshire).

Professor F. W. R. BRAMBELL dissected and fixed at University College, Bangor, most of the hedgehogs from that district.

Locality, body weight, and date of killing were recorded for each animal and, for some, macroscopic observations on the mammary glands or nipples. The animals were killed by chloroform and the whole reproductive tract fixed. The mammary glands were preserved from a number of hedgehogs.

(*b*) *Histological Technique, Sectioning, and Measurements.*—The histological technique was similar to that used for the grey squirrel (DEANESLY and PARKES, 1933), material being fixed in Bouin's fluid and transferred to 70% alcohol and dissected. At that stage the uterus and decapsulated ovaries were weighed on a torsion balance. The different parts of the reproductive tract were then embedded in paraffin and sections were cut (through the regions indicated by dotted arrows and lines on fig. 1) and stained with hæmatoxylin and eosin. One ovary of each hedgehog was cut and mounted serially, and both ovaries from 32 animals marked * in the Tables and Appendices. Serial sections were made of the Fallopian tube when the ovaries showed a recent ovulation. Follicles and corpora lutea were measured as previously described.

(*c*) *Method of Preparing Mammary Glands.*—To obtain a complete preparation it is necessary to slit the hedgehog skin up the middle of the back and remove it with the underlying tissues in one piece. The technique used for examining the glands is a modification of BOUIN and ANCEL'S (1909) method: The skin is well stretched on a board and floated in a dish of Bouin's alcoholic fluid for 24 hours and then transferred to 70% alcohol. The mammary gland, with a surrounding sheet of connective tissue, is then dissected away from the skin before staining. The dissection is not easy in the hedgehog, since the connective tissue on which the gland rests is very thin and the muscles of the skin and body wall are naturally abundant and lie at different levels. The gland is stained for 24 hours in borax carmine, differentiated in acid alcohol until the muscle and connective tissue is colourless, and further dissected if necessary. Finally, it is stored in alcohol or is dehydrated, cleared, and mounted in xylol.

III. *The General Morphology of the Reproductive Organs.*

The reproductive organs of the hedgehog were described by Owen (1868); fig. 1, and figs. 2–5, Plate 27, show their general morphology in the female and the differences between the anœstrous and the breeding season appearance, especially in the size of the uterus and vagina.

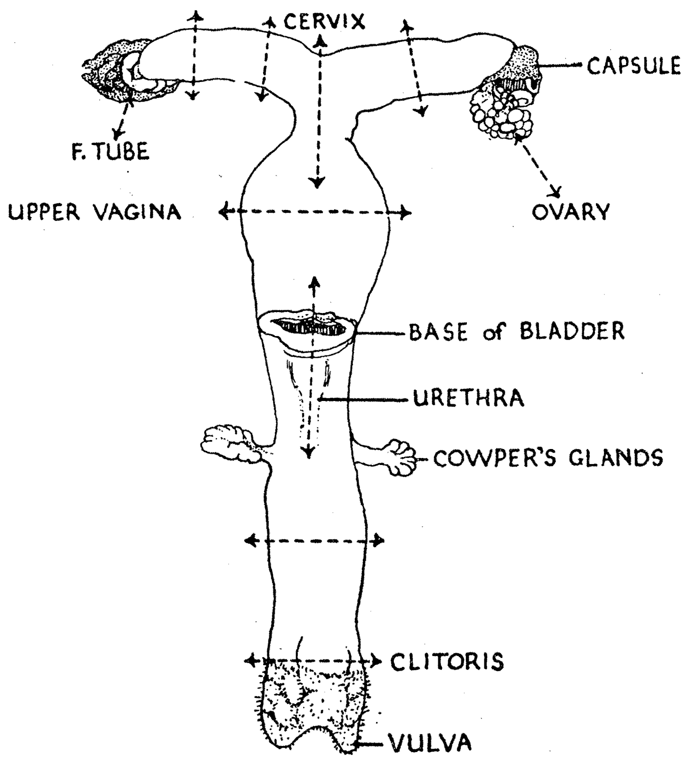


Fig. 1.— Diagram of the reproductive tract of the female hedgehog, after removal of the bladder, and dissection of one ovary from its capsule. The dotted lines and arrows show the regions through which sections were cut in each animal. In some, transverse sections were cut through Cowper's glands and the mid-vagina. Several transverse sections (2–6) were cut through each uterus.

The ovaries are roughly U-shaped bodies bent round a thick muscular hilus and exceptionally well vascularized. They resemble those of the rat in irregularity; their surface is always much indented, especially in the breeding season, when corpora lutea and follicles are prominent. The ovarian groundwork consists of fibrous tissue, including some fat-containing cells. There are no true interstitial cells, but degenerating follicles are numerous, and these sometimes form epithelial masses (see p. 258). Bodies of Call and Exner are common in small follicles, but not in the larger ones.

The ovary is completely enclosed in a tough peritoneal capsule supporting the Fallopian tube; the latter is about 50–80 mm. in length, and bent round so that it lies against the tip of the uterine cornu. The tube is fairly uniform in diameter except at the extreme end, where it narrows and plunges into the uterine muscle. This region of the Fallopian tube, within the uterine wall, is referred to as the tubal opening (pp. 248, 250) (fig. 24, Plate 30). Attached to the ovarian capsule near the hilus, but distinct from the tube, is a conspicuous parovarium consisting of tubules of ciliated epithelium lying in dense fibrous tissue, which show seasonal changes in size and activity.

The horns of the uterus are short, thick, and muscular and at their junction lie almost at right angles to the cervix and vagina, so that the whole structure is T-shaped. When fully developed each horn measures 1·5–2 cm. in length and 0·5 cm. in diameter. The uterine canals are continuous across the top of the cervix, fig. 3, where they open into a single cervical canal enclosed in a thick muscular wall and very small except at the extreme anterior end. The canal is lined by the uterine type of mucosa up to the os tincæ, which projects into the swollen region of the upper vagina, fig. 3, so that there are well-defined cervical fornices.

The hedgehog vagina is large and muscular, and undergoes seasonal size changes, but remains patent. For descriptive purposes it may be divided into three regions, which show a progressive decrease in the size of the lumen. In the first of these, or upper vagina, extending from behind and round the cervix to the point of junction of the urethra, the lumen is large and the wall relatively thin. This part of the vagina shows the most obvious changes during the reproductive cycle. It increases in size at the onset of the breeding season and becomes much dilated at œstrus, fig. 2, but is collapsed during most of pregnancy and lactation, as well as in anœstrus, figs. 31–33, Plate 31. In animals coming on œstrus after pregnancy the vagina is not as dilated as at the first œstrous periods. During the breeding season the upper vagina is often entirely filled by a thick fluid containing desquamated cornified epithelium mingled with the secretions of the cervical and vaginal glands (Courrier, 1924, *a*, *b*).

The mid-vagina, lying in the pelvis, has a more muscular wall and a much smaller lumen than the upper vagina. The urethra runs in the wall for about 2 cm. in the breeding season adult, and finally opens into the lumen at about the same distance from the vulva. The lower vagina, or urino-genital sinus, shows a further narrowing and simplification of the lumen; immediately below the epithelium there are several large lymph nodes. The clitoris, which sometimes contains a small cartilage, projects into the urino-genital passage. Sections through the clitoris show a paired epidermal infolding, and below this a mass of blood vessels and connective tissue homologous with the corpora cavernosa. The folds of epithelium merge finally with those of the vagina.

There are a number of accessory glands with ducts opening into the vaginal lumen. In the upper vagina, a small pair lie under the epithelium at the level of the base of the bladder. These are branched, tubular, mucous glands lined by a regular epithelium which varies in height according to its secretory activity, fig. 32, Plate 31.

In the mid-vagina there are larger paired glands extending dorso-laterally on either side of the urethra and a little behind its opening into the vaginal lumen. These glands show in section as masses of closely-packed small tubules with their ducts. Similar smaller glands are found near the clitoris.

The most conspicuous of the vaginal glands are those lying outside the muscle wall against the pelvic girdle; these are different in type from the preceding ones and probably homologous with Cowper's glands in the male. When dissected out they appear fan-shaped, figs. 2–5, Plate 27; in section they are composed of numerous very irregular tubules and ducts set in dense fibrous tissue. A single main duct opens into the vaginal lumen on each side. The tubules and ducts contain nuclear debris, especially during the breeding season; in this they resemble those of the male Cowper's and prostate glands.

The hedgehog has large mammary glands (Plate 33) situated somewhat laterally and ramifying round the bases of the legs. There are usually five pairs of symmetrically placed nipples, one pair thoracic and four pairs abdominal. In non-parous females the nipples are small and the glands undeveloped, but in parous females the nipples are larger and the mammary gland ducts form a widespread network which persists through anœstrus.

Pigment is very common both in the ovaries and uterus of the hedgehog, especially during the breeding season, when the organs receive an increased blood supply. It is especially abundant in Nos. 264 and 261, very early pregnancies. Pigmented debris is found in the vaginal lumen.

IV. *The Character of the Reproductive Cycle.*

(*a*) *Classification of Animals.*—The analysis of the reproductive cycle depended on the classification of all the available animals according to the functional condition of the reproductive organs, including the mammary glands. After a preliminary histological examination the animals were divided into groups, and from these the limits of the breeding season were determined. As a convenient distinction the term *post-partum* is used for all hedgehogs from June to the beginning of October which have had a litter in the current breeding season, and the term *parous* is restricted to hedgehogs whose last litter was in the previous breeding season. Both kinds of hedgehogs can be distinguished by the uterine blood vessels and musculature. The first three groups include parous and non-parous animals.

Group (1) *Anœstrus.*—Hedgehogs with small uteri and inactive ovaries. These comprise the majority taken between October and the end of March. (Appendices I and II.)

(2) *Approaching Œstrus.*—Hedgehogs which have not ovulated in the current season, but whose uteri are enlarging and becoming active. (Appendices I and II.)

(3) *Ovulating.*—Non-pregnant hedgehogs with recent corpora lutea. (Appendix III.)

(4) *Pregnant.* (Appendix IV.)

(5) *Early Post-partum.*—Hedgehogs whose uteri have not involuted and show marked traces of recent pregnancy. (Appendices V and VI.)

(6) *Lactating.*—Hedgehogs with well-developed mammary glands and involuted uteri. (Appendix V.)

(7) *Active Post-partum.*—Hedgehogs in which the uterine endometrium has been repaired after pregnancy and is again in an active condition. Some of these hedgehogs have ovulated since pregnancy and others are approaching œstrus. The group includes some which have recently been lactating. (Appendix VI.)

Once the general histological classification of the material has been accomplished, it was found that the weights of both ovaries and uterus varied with the condition of an animal, and were an index to the seasonal changes throughout the year. The final classification of the material, after measurement of the corpora lutea and examination of the uteri for spermatozoa, is given in Table I and Appendices I–VI.

(*b*) *Limits of the Breeding Season.*—On the basis of the preliminary classification of the hedgehogs the salient features of the breeding season could be determined. From the beginning of October till the end of April (with one possible exception) no animals contained recent corpora lutea or ruptured follicles, and up till the end of March uterus and vagina were small and inactive. The female hedgehog, therefore, has a well-marked anœstrus.

Pregnancies occurred in May (7), June (6), July (3), and August (2). Presumably there are also pregnancies in September, since a lactating hedgehog, with young weighing 110 gm., was killed on October 12. Litters in the late summer and autumn are probably more common than the figures in Table I suggest, though less abundant than in May and June ; several of the parous hedgehogs taken in winter show signs in their uteri of recent pregnancy (presumably during August and September). Lactation may continue late into the year (see p. 268). Most of the lactating animals (Appendix V) show marked uterine involution, but no animals are definitely in post-lactation anœstrus in August.

It is generally supposed, from the distribution of pregnancies, that hedgehogs may bear two litters in a year. The present material provides conclusive evidence of this, since it includes an early pregnancy associated with a well-developed, recently functional mammary gland, fig. 48, Plate 33 ; in June, July, and August nine animals recently pregnant have ovulated, so that they would presumably have been able to breed a second time in the season.

It is unlikely that all hedgehogs have two litters a year, since some, including parous animals, do not come into their first œstrus until June or even later. Animals born in the preceding August or September might not be ready to breed until nearly a year old, and these would account for some of the pregnancies in the second half of the breeding season.

Although young hedgehogs grow rapidly, females do not seem to reach maturity (*i.e.*, become capable of breeding) in the season in which they are born. The present

TABLE I.—The Reproductive Cycle of the Female Hedgehog.

This table shows the condition of 136 hedgehogs recorded throughout the year; eight of these were not histologically examined and are not included in the Appendix Tables.

	Jan.	Feb.	Mar.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
I.—*Animals which have not bred in the current year*—												
First year young	—	—	—	—	—	1	—	2	4	9	1	1
Anœstrous: non-parous	3	—	1	9	2	—	—	—	—	—	—	—
Anœstrous: parous	4	4	4	2	—	—	—	—	—	—	—	—
Nearing first œstrus	—	—	1	4	9	3	1	1	—	—	—	—
In diœstrous cycle	—	—	—	—	6	5	1	—	—	—	—	—
In pseudo-pregnancy cycle	—	—	—	—	6	1	1	1	—	—	—	—
II.—*Pregnant animals*	—	—	—	—	7	6	3	2	—	—	—	—
III.—*Animals which have bred in the current year*—												
Early post-partum and lactating, no ovulation	—	—	—	—	—	5	4	2	1	1	—	—
Nearing first ovulation since parturition ...	—	—	—	—	—	—	—	1	—	—	—	—
In diœstrous cycle	—	—	—	—	—	—	3	—	—	—	—	—
In pseudo-pregnancy cycle	—	—	—	—	—	1	3	2	—	—	—	—
Anœstrous	—	—	—	—	—	—	—	—	—	4	3	1
Total	7	4	6	15	30	22	16	11	5	14	4	2

material suggests that by the time the hedgehog first reaches adult body weight, anœstrus is setting in. Sexually mature females in spring which have passed their first ovulation weigh 320 gm. and upwards; two such animals were recorded under 400 gm., and one in early pregnancy of 400 gm. The other pregnant hedgehogs weigh about 450–680 gm. (exclusive of the uterus), and older females may weigh 700–1000 gm. Immature hedgehogs of 400–500 gm. are found in September and early October, but their uteri are very small, although one animal has follicles of almost œstrous size (Table III), and another shows a solitary corpus luteum (Table IV). Apparently ovulation may occur in first season animals, but it is more than doubtful if it could be followed by pregnancy (see pp. 251–253).

(*c*) *Litter Size and Number of Ova.*—Table II shows the available data on the number of ripening follicles, ruptured follicles, recent corpora lutea, fœtuses, placental sites, and nest young. Under each category are given the frequencies of the numbers in the left-hand column. The average number is five, which corresponds with the litter records of earlier writers.

TABLE II.

Number.	Frequency Distribution.					
	Ripening follicles.	Ruptured follicles.	Recent corpora lutea.	Fœtuses.	Placental sites.	Nest young.
1	—	—	—	1*	—	—
2	—	—	—	—	—	—
3	2	1	—	—	1	—
4	1	—	4	2	1	1
5	2	3	3	7	4	3
6	—	2	2	—	—	—
7	—	—	—	1	—	—
8	—	—	—	—	—	—
9	—	1	—	—	—	—
10	—	1	—	—	—	—

* In No. 131 pregnant at the end of lactation.

The investigation of the number of ova shed at one ovulation presented certain difficulties. Groups of maturing follicles were seldom a reliable fertility index, owing to their tendency to degenerate at or near the œstrous size. Many counts of developing and fully-formed corpora lutea were attempted, but in comparatively few ovaries, and those mainly at the beginning of the breeding season, could complete sets of corpora lutea belonging to the same ovulation be clearly distinguished. In eight hedgehogs, however, counts could be made of recently ruptured follicles. Corpora lutea accumulate very rapidly in the hedgehog ovary and regress very slowly; frequently, especially in pregnancy, they merge with adjacent ones, not always of the same cycle, and for this reason the corpora lutea of pregnancy cannot be counted and compared with the fœtuses. The ovarian records in Table II, however, show that the two ovaries can mature 3–10 ova at one time, the most common number being five, which corresponds to the fœtus number.

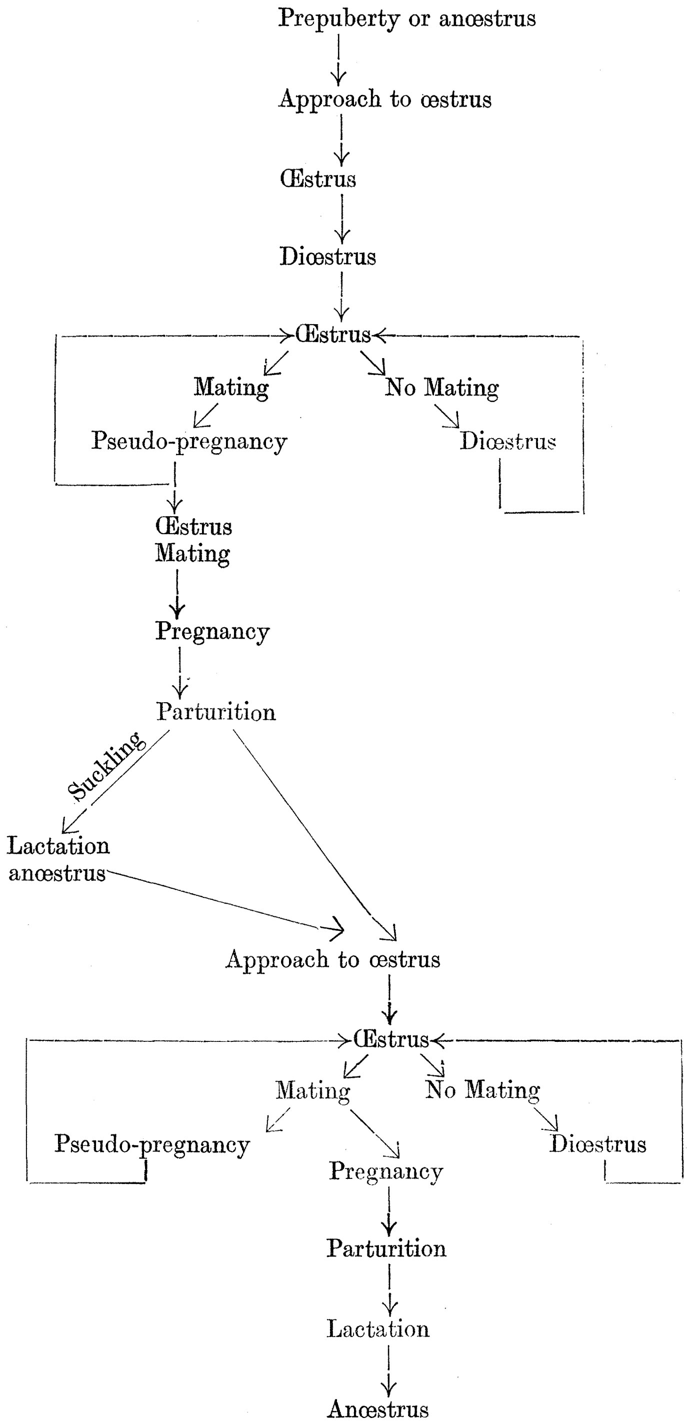
(*d*) *Ovulation, Copulation, and Pseudo-pregnancy.*—The accumulation of corpora lutea, referred to above, is found in both pregnant and non-pregnant hedgehogs. In the breeding season corpora lutea increase in number continuously, except during pregnancy and the lactation anœstrus, and products of recent and old ovulations persist side by side. It is accordingly possible to estimate the least number of times that an animal has ovulated before death, allowing an average of 2–3 corpora lutea in one ovary for each cycle. On this basis there can be no doubt that successive ovulations take place in the hedgehog before it gets pregnant—a very unusual infertility in a wild mammal. Ovulation is clearly spontaneous; some hedgehogs ovulated normally in a 24-hour interval between capture and death, and others when isolated in the laboratory. In non-pregnant animals taken from the field, however, some of the successive ovulations have been accompanied by mating. The male hedgehog is known to be fertile from the end of April till August, and in the present series two-thirds of the hedgehogs in May, which have ovulated, have mated (Table I and Diagram). There appears to be no vaginal plug in the hedgehog to provide evidence of copulation, but spermatozoa persist at the opening of the Fallopian tube, as well as in the uterine and cervical glands for considerable periods; they can actually still be found half-way through pregnancy. (Appendix IV.)

Two types of corpora lutea, comparable to those described in the rat by LONG and EVANS (1922), can be distinguished in the non-pregnant hedgehogs. In animals without spermatozoa in the uterus, the corpora lutea are small, fibrous, hardly luteinized bodies. Two or three sets are generally present, including ruptured follicles. Following LONG and EVANS' terminology, these may be called the corpora lutea of ovulation, since they develop in the short diœstrous interval in the absence of mating. In the mated, but non-pregnant hedgehogs, on the other hand, there are large, or well-vascularized, developing corpora lutea, totally different from those of ovulation and indistinguishable from those of pregnancy. The ovaries also contain old corpora lutea of ovulation, indicating that copulation does not generally occur at the first œstrus, though in one animal it occurred at the second. (No. 163.)

The numbers of large corpora lutea in hedgehogs in May and June, whose uteri show no trace of recent pregnancy, make it clear that a succession of two or three pseudo-pregnancy cycles is by no means uncommon before implantation takes place. All ovaries from pregnant hedgehogs contain at least one set of older corpora lutea of pseudo-pregnancy, and often enough corpora lutea to indicate two or three previous copulations, fig. 6, Plate 28.

In spite of the growth of corpora lutea of pseudo-pregnancy, most of the corresponding uteri differ little from those found in the diœstrous cycle. Only in animals which have

DIAGRAM OF THE REPRODUCTIVE CYCLE OF THE FEMALE HEDGEHOG.



had several sterile matings does there appear to be an attempt at progestational proliferation of the uterine epithelium (see p. 263). The earliest pregnancies, the first of which contained segmenting tubal ova in association with a very congested uterus, form an entirely distinct group.

(*e*) *Causation of Temporary Infertility.*—It is difficult to suggest any satisfactory explanation of the temporary infertility of the female hedgehog. MIRSKAIA and CREWE (1930) record a low percentage of pregnancies from first matings in mice, and suggest that the reproductive organs in these young animals are generally not physically capable of pregnancy, although puberty has been attained. They offer no explanation of the exact point at which the chain of processes normally leading to pregnancy is broken. HARTMAN (1931) has also discussed the relative sterility of the adolescent organism with special reference to Primates. It is very unlikely, however, that the sterile cycles of the hedgehog are analogous to those mentioned above, since the temporary infertility is found in parous as well as non-parous animals (Appendix III). Pseudo-pregnancy does not seem to be associated with age, low body weights, or low uterus weights.

Among adult animals of other species, a small proportion of matings are commonly infertile; in mice, for instance, only four out of five matings on an average result in pregnancy (PARKES, 1926), (MIRSKAIA and CREWE, 1930), and in rats about 88% (LONG and EVANS, 1922).

The infertility of the hedgehog, however, cannot be casual infertility of this kind, since it relates specifically to the early attempts to get pregnant after both the winter anœstrus and the lactation anœstrus. No animal was found which had become pregnant at its first mating in the season, and six animals had mated after lactation without becoming pregnant. (Appendix VI.)

It must be emphasized that the pseudo-pregnancy observed in the hedgehog is not necessarily comparable to the standard condition produced in laboratory animals after vasectomy or salpingectomy. No direct evidence is available as to whether fertilization of the ova takes place at the beginning of any of the hedgehog pseudo-pregnancies; in such an event the condition would be that of a pregnancy undergoing very early reabsorption. All except two of the pseudo-pregnancies were too late for finding ova in the Fallopian tube, since they pass rapidly into the uterus. Nos. 99 and 125 have ruptured follicles in their ovaries, but, in the former, ova have apparently not reached the tube and in the latter they are unfertilized. No spermatozoa were found in the Fallopian tubes in pseudo-pregnancy, except at the tubal opening; probably they cannot persist long in the tube, since hardly any were seen in association with the fertilized tubal ova belonging to the earliest pregnancy (No. 264). Under these circumstances fertilization can only be regarded as a possibility, on the evidence that the male hedgehogs are known to be fully fertile at the time of these sterile matings. The manner in which the processes leading to pregnancy are interrupted is uncertain and probably variable. If the eggs are sometimes fertilized, then the failure to become implanted must be attributed to lack of sensitivity on the part of the uterus; in the absence of a regular pseudo-pregnancy proliferation, this seems a possible explanation. The hedgehog uterus after sterile mating shows a variable reaction which is most marked, histologically, in animals which have mated several times (see p. 263). The apparent increase in sensitivity after repeated matings is perhaps comparable to the increase in sensitivity of the uterus of the ovariectomized mouse after a priming dose of œstrin (KAHNT and DOISY, 1928).

(*f*) *The Time Relations of the Cycle.*—Although the time relations of the cycles cannot be definitely ascertained from field material, certain inferences may be drawn from the available data. Ovulation is probably uncommon before the middle of April, but a hedgehog on May 13 had ovulated at least four times and had been pseudo-pregnant at least twice. Another hedgehog, with 4–5 mm. embryos, was killed on May 18; this had passed through several cycles before pregnancy. It may be concluded that the intervals between successive ovulations are fairly short, which is also suggested by the absence of histological regression in the corpora lutea of pseudo-pregnancy at the time of the next ovulation. The interval is probably increased by sterile copulation, which leads to the formation and persistence of larger corpora lutea, as in the rat and mouse. On this basis the length of time between sterile mating and the next ovulation may be put at 7–10 days. The first pregnancies were found in May and the first post-partum hedgehogs dated from early in June, so the duration of pregnancy may be estimated at about one month. BARRETT-HAMILTON's (1911) suggestion of seven weeks is almost certainly too long, in view of the sterile cycles before pregnancy and the absence of ovulation in fifteen hedgehogs killed in April (Table I).

(*g*) *Pregnancy and Lactation.*—Details of pregnant hedgehogs are given in Appendix IV; No. 262 was probably near parturition. No hedgehog showed any signs of an immediate post-partum œstrus, such as occurs in the rat and mouse. No. 177 (Appendix V), with a uterus weight 3·1 gm., was probably killed soon after having a litter. Most of the hedgehogs with well-developed mammary glands are in lactation anœstrus (see later), so that the most recent corpora lutea belong to the first pregnancy of the season in nineteen animals; these comprise hedgehogs pregnant in May and June, or post-partum or lactating in June and July. Almost all of them have passed through 3–5 sterile cycles previous to pregnancy, and their ovaries are large and full of corpora lutea. Often the latter have become confluent, and are so numerous (15–30 in one ovary) as to make exact counts difficult. Since the average number of fœtuses corresponds with the average number of ova liberated (Table II) it may be assumed that there is little loss through ova not becoming implanted. There are no data to compare the distribution of corpora lutea of pregnancy in the two ovaries with the distribution of fœtuses, but it may be noteworthy that no uterine horn contained more than one fœtus in excess of the other, although in 10 out of 22 pairs of ovaries recorded there is an excess of at least two follicles or corpora lutea on one side. In view of the shape of the cervix in the hedgehog, migration of ova, such as takes place in the shrew (BRAMBELL)*, must be considered a possibility.

There is no direct evidence on the length of lactation or of the lactation anœstrus. Probably, as in the mouse, the latter varies with the number of young suckled (PARKES,

* BRAMBELL.—" Œstrous cycle of the shrew." *In preparation.*

1926). Appendices V and VI show the dates of the anœstrous lactating hedgehogs and those whose reproductive organs are again active after breeding. The first post-partum hedgehog was taken on June 8, and a pregnant hedgehog which had been recently lactating on July 9. It seems probable that the duration of the lactation anœstrus in the middle of the breeding season is often not more than a month. Some of the active animals recorded in Appendix VI had well-developed mammary glands, so that lactation was continuing or had only just ceased, though the animals had recommenced ovulation. Diœstrous and pseudo-pregnancy cycles both occurred in post-lactation hedgehogs, the latter being succeeded by the former in at least one animal. It is impossible to estimate how many times these animals normally ovulate before becoming pregnant again. Copulation may take place at the first post-partum œstrus.

(*h*) *Seasonal Variation.*—Table I shows in concise form the condition of the hedgehogs throughout the year. Details of the individual animals are given in the Appendices. The first hedgehog of the year in which the reproductive organs resembled those in the breeding season was a non-parous one taken at the end of March (Table III). None of the 15 hedgehogs taken between April 14 and April 26 had ovulated, but the majority showed a definite approach to the œstrous condition. It is probable that hedgehogs do ovulate in April, since some of those in the early part of May have passed through several cycles, including pseudo-pregnancies (Appendix III), and at least one must have become pregnant very early in May (Appendix IV). Pregnancy in April (mentioned by BARRETT-HAMILTON, 1911) is almost certainly rare. There is no difference between non-parous and parous females in the time of onset of breeding season activity; for both kinds of animals this may vary from May to July. The first litters are born early in June; a lactating hedgehog with five young about three weeks old (adult coloration, weight 80 gm.), was obtained on June 24. In July and August together only 5 out of 27 animals have not yet become pregnant, and of these 2 are pseudo-pregnant and 1 has ovulated. In July, 6 out of 16 animals have ovulated since pregnancy, and would probably have been capable of having a second litter. Hedgehogs of several kinds were taken in August, but none were anœstrus; one as late as August 15 had just mated. Only one adult hedgehog, which was lactating, was taken in September, so that it is impossible to say how far anœstrus has set in by that month. Lactation continues to October and perhaps later (see p. 268). From October onwards the uteri of adult hedgehogs show a decrease in size (Appendix II) and marked glandular regression. Ovulation has ceased and the ovaries are smaller owing to the gradual degeneration of the accumulated corpora lutea, but there is no constant anœstrous level and partial follicular growth seems to occur sporadically all through the winter. Immature hedgehogs weighing 270 and 280 gm. were collected in August, and others in September and October (Appendix I) up to 560 gm. Uterus and vagina were very small in these animals, but some of the ovaries were active. In No. 223 there is a large follicle up to œstrous size, and in No. 230 there is a single corpus luteum of ovulation. Most of these ovaries contain numerous degenerating follicles. Evidently sporadic ovulations may occur in first season hedgehogs, but almost certainly uterus and vagina do not reach the full œstrous condition, and mating would be extremely unlikely.

Anœstrus seems to check the growth of the reproductive organs of the immature hedgehogs at about the same time as those of the adults.

V. *The Ovary.*

(*a*) *Seasonal Changes in Size and Appearance.*—The hedgehog ovary is bent round the large hilus in such a way that it is often impossible to remove the hilus completely without damaging the ovary. There is consequently a higher proportional error in the weights of the dissected ovaries than in those of the uteri. The records indicate a difference in weight in anœstrus between the ovaries, averaging 0·035 gm., of prepubertal animals and those of parous animals, averaging 0·086 gm., although the parous ones vary considerably. In the early spring prior to the breeding season, when the uteri are enlarging, the ovaries are hardly bigger than in anœstrus and there is little change in them during the first diœstrous cycles, but they gain in weight in mated animals owing to the increased vascularity and the formation of larger corpora lutea. In pregnancy there is much variation, since the size of the ovaries depends partly on their size at the end of anœstrus, partly on the number of ovulations before implantation, and partly on the follicular development. During lactation, when there is no regular cycle, the ovaries remain large, and when ovulation recommences they increase again. The largest recorded are those of No. 131, fig. 8, Plate 28, in July (known to be a second pregnancy) and No. 177, probably similar, killed just after parturition in August; these ovaries weigh 0·22 and 0·27 gm. respectively and contain very many corpora lutea. The size and appearance of the anœstrous ovary in parous animals depends largely on the rate at which the old corpora lutea regress; in some hedgehogs, shrunken but intact luteal bodies persist as late as March; in others, at the end of October, only fibrous patches mark the position of the former corpora lutea, fig. 9, Plate 28; these may still be traced at the beginning of the next breeding season. The most conspicuous features of the anœstrous ovary are degenerating follicles of various kinds (see p. 258). Follicular growth continues sporadically during anœstrus, but degeneration usually sets in at or before 0·9 mm. diameter is reached, no recent ovulation being found from the end of October to April.

The change from the anœstrous to the breeding season ovary seems quite abrupt; during the first cycle the only difference consists in the presence of ruptured follicles or corpora lutea. There are no conspicuous changes in the stroma, and follicular degeneration is still common. In April large follicles about 1 mm. in diameter become fairly numerous, but these fail to ovulate, and degenerate.

During the diœstrous and pseudo-pregnancy cycles before the female breeds, successive sets of corpora lutea arise so that the ovary comes to resemble a mulberry. Well-vascularized corpora lutea of the maximum size may be found next to recently ruptured follicles and in the same ovary corpora lutea of earlier pseudo-pregnancy cycles are only slightly shrunken. A developing corpus luteum is often very irregular in shape ; it may become confluent with another of the same cycle or with an older one. In the domestic mouse and rat, which have somewhat similar ovaries to the hedgehog, corpora lutea of previous cycles degenerate abruptly in mid-pregnancy (LONG and EVANS 1922, DEANESLY, 1930), but this does not occur in the hedgehog. The corpora lutea of pregnancy are not readily distinguishable in any way once they are fully grown. (Appendix IV.) Large follicles are rather uncommon in the ovary during the breeding season ; the resting size varies from 0·65–0·80 mm. and follicles of 0·90 mm. or more are only found in about one in four ovaries except during pregnancy. There is less follicular atresia during the breeding season than in anœstrus, but degenerate follicles can always be found. Often these aggregate forming characteristic cell masses in the ovary, p. 259, fig. 9, Plate 28.

(*b*) *Follicular Growth during Prepuberty.*—The initial growth of the ovum and follicle resembles that of other mammalian species described by BRAMBELL (1928) and PARKES (1931) ; the ovum reaches its full size (70 μ in diameter) while the follicle is still only 180 μ in diameter. JENKINSON (1913) gives the diameter of the mature hedgehog ovum as 60 μ ; this agrees generally with the present observations, since there appears to be a decrease in the ova of follicles of more than 450 μ towards this size, probably owing to the greater shrinkage during fixation when the egg lies free in a large follicular cavity. The hedgehog ovum is exceptionally small for the body weight of the animal ; the diameter is only two-thirds of that of the grey squirrel (DEANESLY and PARKES, 1933), and about half that of the ferret (PARKES, 1931).

Small oöcytes about 14–17 μ in diameter are present, scattered in the ovarian stroma. These become surrounded by follicular epithelium and grow in the usual way ; the epithelium is about seven cells thick when the ovum is first fully grown. The smallest follicles with the beginnings of an antrum are 250 μ in diameter ; often, however, a diameter of 300–400 μ is reached before any antrum formation takes place and in one follicle of 470 μ diameter the antrum has only just appeared.

The follicle is by no means quiescent in prepubertal hedgehogs which are only 2–4 months old in the late summer and autumn. Follicles 0·8 mm. or more in diameter were found in six hedgehogs from 270 gm. upwards between August and October. The largest follicle found in this group of prepubertal hedgehogs before anœstrus was that of No. 223 (Table III). This was almost up to the maximum size, although the corresponding uterus, which may have undergone some regression, weighed only 0·14 gm. In anœstrous, prepubertal hedgehogs from November to March the follicles vary up to 0·85 mm. At the end of March one prepubertal hedgehog (No. 33, Table III) has large follicles and a well-developed uterus and looks almost ready to ovulate, but four prepubertal hedgehogs in April and two in May have small follicles below 0·6 mm., and in others the largest intact follicles vary from 0·66–0·93 mm. in diameter.

(*c*) *Maturation of the Follicle: Ovulation.*—The most striking feature of follicular growth in the hedgehog is the enlargement of the granulosa cells and nuclei during

TABLE III.—Hedgehogs with Large Follicles.

Number of animal.	Date.	Condition.	Diameter of follicles.
			mm.
223	October 21	Prepubertal	1·06.
33	March 26	Prepubertal	1·04, 0·70.
66*	May 4	Prepubertal	0·91, 0·93, 0·90, 0·90, 0·94, 0·91.
158	May 15	Prepubertal	1·02, 0·90.
259	June 2	Parous : not yet ovulated ...	0·99.
154*	June 19	Parous : not yet ovulated ...	1·07, 1·17, 1·10, 1·14.
159*	June 7	Parous : ovulated once	1·04, 0·99, 1·02, 1·06, 1·17.
162*	June 19	Parous : just ovulated	1·25.
101*	May 18	Parous : just copulated ...	0·94, 0·95, 0·98, 0·94.
104*	May 18	Pregnant	1·03.
130*	July 9	Pregnant	1·05, 0·98.
312	June 21	Post-partum, not lactating ...	1·02, 1·00, 0·98.
196*	August 15	Post-lactation ; just copulated...	0·98, 0·98, 0·99.

* Both ovaries sectioned.

the growth of the follicle (figs. 17 and 18, Plate 29). Even in small follicles the granulosa cells show distinct cell boundaries ; in a follicle of 0·66 mm. diameter the cells averaged 9–12μ and the nuclei 4–5μ. The nuclei remain small in relation to the size of the cells during follicular enlargement. In 1 mm. follicles the cells measure about 16–17μ and the nuclei 6–7μ. Follicles of this size and over were not found in many hedgehogs ; they are recorded in Table III, which gives the diameters of the largest follicles seen in non-pregnant animals. Degenerate follicles of about these dimensions were more common than normal ones, indicating that the large follicle is in an unstable condition. Table III records large follicles in five hedgehogs between March 26 and June 19 which have not yet ovulated, but which appear to be near œstrus. These follicles show no congestion of the thecal vessels and have not quite attained their pre-ovulation size. The final maturation stages probably occur rapidly, as in many mammals. The pre-ovulation size is indicated by a follicle in No. 162 (diameter 1·25 mm.), which had not ovulated or obviously degenerated, although all other large follicles in the ovary were ruptured.

In the typical large follicle with a diameter of about 1 mm. (*e.g.*, in Nos. 154, 159) the ovum (diameter 60μ) is centrally situated in the discus proligerus, which retains its attachment to the rest of the granulosa, fig. 13, Plate 29. The latter is about six cells thick round the periphery, where the regular cuboid cells have a diameter of about 16μ, the nuclei measuring 6-7μ. The theca is of the type found in the rabbit and there is no distinct theca interna at this stage. Two animals (Table III) appear to have copulated just before death, but their follicles are well below full size. Further follicular enlargement after copulation has been observed in several mammals, notably in the rabbit (WALTON and HAMMOND, 1928) and in the ferret (ROBINSON, 1918), in which ovulation is dependent on copulation.

Ovulation is accompanied by a marked congestion of thecal blood vessels ; as the hedgehog ovum is expelled, a stream of granulosa cells are normally carried out through the ovulation point, fig. 14, Plate 29. Some of these cells accompany the ovum into the Fallopian tube ; others remain connected to the developing corpus luteum, which in consequence often becomes very irregular in shape. The present material includes seven animals with very recently ruptured follicles, showing as yet no ingrowths of vascular tissue from the theca. Typically such ruptured follicles are round or flask-shaped. At first there is a small cavity, but this is soon reduced and traversed by spindle-shaped granulosa cells. The eggs from ruptured follicles were frequently found free and unfertilized in the ovarian capsules and in the Fallopian tubes. The granulosa cells are slightly smaller and more spindle-shaped than in the ripe follicle, but otherwise unchanged. The theca interna, once the initial congestion has subsided, shows no special features.

(*d*) *The Corpus Luteum of Ovulation.*—The development and regression of the corpus luteum of ovulation can be studied in a dozen or more hedgehogs (killed mainly in May or June), which have not yet bred or copulated. In the absence of mating, the granulosa fails to become luteinized, although normal vascularization takes place. Both cells and nuclei are shrunken in comparison with those of the ripe follicle, fig. 15, Plate 29. The central cavity is not filled by enlarged lutein cells, but by extravasated blood and fibrous tissue. The fully-formed corpus luteum of ovulation is a much less conspicuous object than the just ruptured follicle ; its diameter is often only 0·7 mm., though it may reach 1 mm. (Table IV). It seems to contract steadily up to the time of the next ovulation, and afterwards remains stationary with a diameter of about 0·5 mm. Since they do not enlarge, these corpora lutea seldom become confluent like those of pregnancy and pseudo-pregnancy. Recent ones can often be distinguished by the fresh blood clot in the centre, or by their size.

(*e*) *Corpora Lutea of Pseudo-pregnancy and Pregnancy.*—There are no definite histological differences between corpora lutea of pseudo-pregnancy and pregnancy, figs. 6–8, Plate 28, although the latter must be functionally distinct. Table IV and Appendix IV show that the mean diameters of corpora lutea of each kind vary from 1·1 to 1·4 mm. They suggest that the corpora lutea of pregnancy tend to be smaller than the others. It is probable that by examination of the lutein cell inclusions different secretory cycles might be traced in the corpora lutea, but this work has not been undertaken. A few ovaries fixed in Flemming's fluid show little osmicated fat.

Copulation, which is followed by a greatly increased vascularization of the whole ovary, seems to have an immediate effect on the development of corpora lutea ; instead of subsiding after ovulation has occurred, the increased blood supply continues, so that even the old corpora lutea in the ovary contain dilated blood sinuses, while the developing ones are strikingly congested, fig. 7, Plate 28. The large epithelial cells of the ripe follicle hardly gain in size during luteinization, but their nuclei show a slight average increase, figs. 18 and 20, Plate 29. Cells and nuclei, however, are very variable in the fully-grown corpus luteum, the diameter of the cells being 13–20 μ and those of the nuclei 6–10 μ. Cell enlargement being slight and mitosis not in evidence, it

TABLE IV.—Mean Diameters of Corpora Lutea.

Number of animal.	Description.	Mean diameters.
	Corpora lutea of ovulation.	mm.
152*	Just ruptured follicles	0·87, 0·90, 0·85.
125*	Just ruptured follicles	0·91.
100*	Early stage of vascularization: corpora lutea hollow ...	0·87.
106*	Early stage of vascularization: corpora lutea hollow ...	0·73.
126	Recent, fully-formed: egg has passed into uterus ...	0·77.
308	Recent, fully-formed	0·93.
103	Recent, fully-formed	0·79.
159*	Near end of diœstrous cycle: large follicles in ovary ...	0·67, 0·77.
331	Near end of diœstrous cycle: large follicles in ovary ...	0·99, 0·87.
162*	End of diœstrous cycle: ruptured follicles in ovary ...	0·88, 0·99.
152*	End of diœstrous cycle: ruptured follicles in ovary ...	0·78.
98*	End of diœstrous cycle: ruptured follicles in ovary ...	0·64, 0·62.
230*	Recent, fully formed, in first season October hedgehog ...	0·75.
	Corpora lutea of pseudo-pregnancy.	
105*	Developing	0·94, 0·93, 0·85.
163*	Developing	1·04, 0·99, 0·98, 1·05.
115	Developing	1·01, 1·06, 1·04.
101*	Fully-formed	1·22, 1·20, 1·29, 1·26.
133*	Fully-formed	1·29, 1·44.
198	Fully-formed	1·26.
196*	End of cycle: large follicles in ovary	1·40, 1·35, 1·34.
99*	End of cycle: ruptured follicles in ovary	1·36, 1·33, 1·42, 1·44, 1·24, 1·32.
308	End of cycle: new corpora lutea developing	1·29, 1·41.
264*	End of cycle: new corpora lutea developing	1·33, 1·25, 1·17, 1·31, 1·20.
	Corpora lutea of pregnancy. *See Appendix IV.*	
	Corpora lutea of pregnancy: post partum.	
312	Early post-partum	1·37.
177	Early post-partum	1·22, 1·38.
313	Post-partum: follicles enlarging	1·12.
126	Post-partum: recent ovulation	1·08, 1·16.
	Corpora lutea of pregnancy during lactation.	
170	Not shrunken, but showing histological changes	1·37, 1·45, 1·35, 1·47.
144	Not shrunken, but showing histological changes	1·25.
192	Regressing	1·05.
135	Regressing	1·18, 1·08, 0·93.

* Indicates that both ovaries were sectioned. The records in column 3 are those of typical corpora lutea, but they do not necessarily include the diameters of all corpora lutea from one ovulation.

must be concluded that most of the space occupied by liquor folliculi in the ripe follicle (about half its volume, fig. 13, Plate 29), is taken up by blood sinuses and vascular connective tissue in the fully-formed corpus luteum. This corresponds to the histological appearance of these bodies, fig. 20, Plate 29. No shrinkage or regressive change is apparent in the corpus luteum at the end of the pseudo-pregnancy cycle or just after parturition. During lactation the old corpora lutea shrink very gradually and their diameter goes down to about 1 mm. or less, but they persist at about this size and the lutein cells do not degenerate for some time. Owing to their long duration, 20–30 corpora lutea may be found in a 10 μ horizontal section through an ovary in July, when a hedgehog has recommenced ovulation after lactation.

(*f*) *The Follicle during Pregnancy and Lactation.*—Follicular activity has been observed in pregnancy in several mammals; follicles enlarge and often reach œstrous size, but instead of ovulating, they degenerate. This occurs in the hedgehog ovary. The diameters of the largest follicles in each pregnant animal range from 0·61 mm.–1·05 mm., exclusive of many other large follicles which are obviously degenerating.

If no young are suckled, follicles probably mature normally soon after parturition (Nos. 312 and 125). During most of lactation (Appendix V) there seems to be little growth or activity, but follicular enlargement prior to the next œstrus may begin before lactation has quite ceased.

(*g*) *Follicular Degeneration and Follicular Masses.*—Follicular degeneration is very common in the hedgehog ovary. It is found in follicles of all sizes and at all times of the year, but especially in anœstrus. In many follicles the granulosa nuclei become pycnotic and the ovum fragments, leaving the follicle as a cyst containing debris. More rarely partial luteinization of small follicles occurs.

In addition to these common types of follicular degeneration, such as have been described in other mammals (references in GARDE, 1930), there is a third type, found in the parous hedgehog ovary, which results in the formation of epithelial or follicular masses of varying size, often larger than corpora lutea of pregnancy. These masses arise through the coalescence of several small follicles (diameters ranging from about 130–400 μ) from which the ova have disappeared. When such follicles begin to degenerate, the ovum becomes eccentric and large vacuoles appear in the epithelium, but do not fuse to form an antrum. In the next stage several small follicles of this kind are crushed together; the epithelium receives small vascular ingrowths, but there is no active invasion from all round the theca, such as occurs in luteinizing follicles or after normal ovulation. The epithelial cells increase slightly in size and at their maximum the nuclear diameter is 5–6 μ and the cell diameter about 10 μ; this is smaller than that of the cells of the ripe follicle or large corpus luteum. The cytoplasm becomes markedly eosinophil so that it resembles luteal rather than follicular cytoplasm, although quite distinct from both. The fully-formed cell mass is irregular, and generally shows remains of the thecæ of the component follicles, fig. 9, Plate 28. Vacuoles, containing a substance resembling liquor folliculi in section, may be seen in the cell mass. The vascularization appears active and there are often congested blood sinuses, but the vascular network is not nearly as well developed or regular as in the corpus luteum. No mitoses have been observed, but the cells look healthy and probably persist for a long time. Although follicles degenerate in all parts of the ovary, there are usually only one, or, more rarely, two follicular masses, often situated near the hilum. This suggests that their formation is dependent on local vascular conditions, and that they only arise when connection is established with an adequate blood supply. This might possibly account for their observed absence or rarity in the prepubertal ovary.

There is no evidence that these active, glandular-looking cell masses have any special function, since they are found in the middle of anœstrus and during pregnancy, and at other stages of the reproductive cycle in the parous animal.

VI. *The Fallopian Tube.*

The microscopic appearance of the Fallopian tube is shown in figs. 10–12, Plate 28; there is little variation along it until the non-ciliated uterine isthmus. Sections were examined through tubes at all phases of the reproductive cycle, but the difference between the anœstrous and œstrous condition is very slight. The usual cyclic changes (SNYDER, 1923, etc.), growth of the epithelial cells towards œstrus and secretion and cell sloughing after ovulation, can just be traced in the hedgehog Fallopian tube, but the maximum variation in the height of the epithelium is from 10–15 μ up to 15–20 μ and very little secretion is found. The tube, however, swells somewhat in the breeding season, the sub-epithelial stroma becoming more œdematous than in anœstrus.

Fallopian tubes from all animals with ruptured follicles were cut serially; fig. 11, Plate 28, shows a section through such a tube containing two ova; the epithelium does not appear very active, but some cytoplasmic sloughing is taking place. In the diœstrous interval the surface of the epithelium reforms and the tube remains quiescent until the next ovulation. The most active Fallopian tube is that of No. 264, which contains segmenting eggs. The epithelium is irregular in some parts owing to the cytoplasmic sloughing accompanying secretion, but elsewhere it is still ciliated. The segmenting eggs lie among much nuclear and cytoplasmic debris, some of which is degenerate follicular epithelium, fig. 12, Plate 28. Close examination only shows one or two spermatozoa in this Fallopian tube, although fertilization has recently occurred: either few of them penetrate beyond the tubal opening, or else they are rapidly washed out or autolysed. No spermatozoa are found in the Fallopian tube of No. 104, the earliest implantation stage, or in tubes of any other animals. Their absence from this region contrasts markedly with their persistence at the tubal opening into the uterus. Probably spermatozoa which do not attach themselves are soon carried towards the exterior.

VII. *The Uterus.*

(*a*) *General.*—HUBRECHT (1889) has described the appearance of the hedgehog uterus during the breeding season and at the beginning of pregnancy. In the non-pregnant, fully-developed uterus, fig. 23, Plate 30, the lumen, though sometimes irregular, generally forms a wide slit surrounded by uniform cuboidal or columnar epithelial cells about 13μ in height. The uterine glands extend up to the circular muscle layer; they grow out from the epithelium radially so that when first formed they resemble the spokes of a wheel, fig. 22, Plate 30; later the glands become coiled, beginning at their deeper ends and then gradually dispersed through the stroma, so that transverse sections through the uterus cut the tubules in all directions, figs. 27, 29, Plate 31. The stroma between the glands is denser adjacent to the lumen; the deeper region becomes somewhat œdematous as the uterus grows and approaches an active condition, but no striking change occurs during œstrus.

The muscle layers, especially the inner circular muscles, are thick and contain numerous blood vessels and large lymph spaces. After an animal has been pregnant these vessels remain enlarged and serve to distinguish the parous from the non-parous uterus. Lactation causes typical uterine regression, the glands atrophying and the stroma becoming dense. A fresh outgrowth of glands from the epithelium takes place in the spring after the winter anœstrus. Changes in the uterus are invariably accompanied by identical changes in the cervix.

(*b*) *Size Changes.*—The uterus increases with body weight in the immature hedgehog, but regresses during anœstrus if a sufficiently high level has been reached before the end of the breeding season. Appendix I gives the average uterus weights of 20 immature hedgehogs from 110–520 gm., killed between the beginning of August and the end of January, and presumably under eight months old; the uteri vary from 0·020–0·250 gm., or, excluding the smallest animals known to be still suckling, 0·055–0·250 gm. Between March and May, when the first ovulations are found, the weights of the uteri of similar non-parous animals show a marked increase (Appendix I), though they are still small in some individuals. The average weight of 11 non-parous uteri in April is 0·34 gm. and of 15 in May is 0·59 gm. (0·52 gm. for seven animals which have not ovulated).

Among the non-parous hedgehogs which have ovulated (Appendix III) the smallest uteri weigh 0·53 gm. and 0·55 gm.; the former contains spermatozoa, fig. 23, Plate 30. It is possible that growth of the uterus continues during the first sterile cycles before pregnancy occurs. Uteri showing progestational proliferation, but no external signs of implantation, weigh 0·94 gm.–1·2 gm (Appendix IV). In October parous uteri are intermediate in weight (Appendix II) between those of the breeding season and anœstrus. By November, however, the anœstrous level is reached, and the average weight of the uteri between November and January is 0·53 gm. In the present material the parous uteri, unlike the non-parous ones, show no significant increase until May; a parous hedgehog killed on April 21 has the smallest uterus of the series. The average weight of 17 uteri in May and June in non-pregnant, parous animals is 0·99, or nearly twice that of anœstrous uteri; the variation is from 0·7–1·66 gm. In 10 animals of this group which have ovulated (Appendix III) the average uterus weight is not significantly different—1·05 gm.

The largest non-pregnant hedgehog uteri in the series are naturally the early post-partum ones (Appendices V and VI). Very shortly after parturition a uterus weighed 3·4 gm., and another 3·1 gm. During lactation the weight of the uterus falls to 0·6–0·7 gm., a little above the anœstrous level.

In nine active post-partum hedgehogs (Appendix VI) the uteri have recovered after involution and have an average weight of 1·38 gm.; they are rather heavier than the parous uteri, listed in Appendix III, owing to the thicker musculature.

(*c*) *Prepuberty.*—The prepubertal hedgehog uterus may show a considerable degree of glandular development before the beginning of the first anœstrus. In a 280 gm. prepubertal hedgehog, taken in August, the uterine glands extend up to the circular muscle, although they are apparently not secreting. The uterus is almost the same size (0·13 gm.) in a 400 gm. hedgehog killed early in September, but the stroma is somewhat denser. At the end of September, in a similar animal, the uterine mucosa is histologically of the adult type; the lumen is wide, the stroma œdematous, and the glands regular and well developed. Anœstrous regression, however, has clearly set in; numbers of dilated blood sinuses can be seen in the sub-epithelial stroma, such as are found in parous uteri during lactation and early anœstrus. The gland tubules are small with a very narrow lumen.

In October, prepubertal uteri range from 0·09–0·25 gm. in animals 220 gm. body weight and upwards; the degree of development varies with the size of the animal, but all uteri appear inactive or regressing. In the larger hedgehogs the uteri are of the type described above, fig. 21, Plate 30, but in others the gland tubules are simpler. Between November and the end of January, prepubertal hedgehog uteri are small with dense vascular stroma and shrunken glands. No non-parous hedgehogs were taken between January 25 and March 23; most of those taken in April still have comparatively undeveloped uteri.

(*d*) *Approach to Œstrus.*—The gradual development of the non-parous uterus up to the breeding season level can be studied in hedgehogs taken in March (2), April (12), and May (15) (Appendices I and III). Ovulation has occurred in eight of the non-parous May animals. The uterus tends to be larger and better developed in the bigger females, but there is considerable variation between 350 and 450 gm. body weights, and the uterus weight ranges from 0·22 to 0·54 gm. In the smaller uteri of this group the endometrium still has the anœstrous appearance, although growth has taken place and the stroma is less dense. Up to a uterus weight of about 0·30 gm. and sometimes above, there is little fresh growth in the endometrium, but the degeneration of the old glands can be traced. Gradually new glands begin to form as epithelial outgrowths, and later they extend regularly and radially into the stroma. By the time the old glands have disappeared, the new ones have grown out to the muscle layer and have become coiled at their extremities, fig. 22, Plate 30. The degree of new glandular development varies in different regions of the same uterus, but fresh, well-grown glands, readily distinguishable from old ones, are generally found in non-parous uteri of 0·35–0·5 gm.; the earliest of these occurs at the end of March. Growth of the uterus is effected by generalized growth of the tissues and only to a lesser extent by œdema of the stroma.

The changes in parous uteri approaching œstrus are similar to those in non-parous ones ; ten hedgehogs taken in April, May, and June (Appendix II) have not yet ovulated, but show stages of growth and glandular activity in the uterus. Reorganization begins before there is any appreciable change in weight.

(*e*) *The Diœstrous Cycle.*—The appearance of the uterus during the diœstrous cycles at the beginning of the breeding season can be studied in six parous and six non-parous hedgehogs (Appendix III), which have ovulated one to three times, and have been killed in various phases of the cycle, *i.e.*, having large follicles, ruptured follicles, developing and recent corpora lutea in the ovaries. No cyclic changes could be distinguished in the uteri. The glands are well developed, but not different from those of pro-œstrous hedgehogs which have not yet ovulated, and the uterine epithelium is also similar. It is probable that the uterus becomes slightly more œdematous at œstrus, but the difference is inadequate to show clearly in sections. The absence of changes during the diœstrous cycle makes the hedgehog uterus comparable to that of the guinea-pig (STOCKARD and PAPANICOLAU, 1917), although there seems to be a rather more definite œstrous swelling in that animal.

(*f*) *The Pseudo-pregnancy Cycle.*—Under this heading uteri will be described which contain spermatozoa, but show no indications of pregnancy (Appendices III and VI).

Although spermatozoa persist a long time in the hedgehog uterus, they are not readily seen even shortly after copulation, and they are rarely found in the uterine or cervical lumen. BAUMEISTER (1913) observed, however, that they tended to congregate in the tips of the uterus at the points of entry of the Fallopian tubes, figs. 24, Plate 30, and his observation was repeatedly confirmed in the present material. Spermatozoa are often abundant in this region when scanty or absent elsewhere. They also penetrate into the deeper-lying tubules of the uterus and cervix, so that they are less liable to be washed out. This would partly account for their unusually long survival in the female hedgehog, compared with other mammals which have been investigated (WALTON and WHETHAM, 1933). WHITE (1933) finds that spermatozoa lose their fertilizing power and disappear very rapidly from the rat uterus, and HAMMOND and ASDELL (1926) have made similar observations on the rabbit. In the hedgehog, unlike these two animals, the testes are abdominal so that spermatozoa are presumably not subjected to a higher temperature in the uterus ; this would be favourable to their survival, although there is no evidence that their fertilizing power lasts exceptionally long.

Owing to the persistence of spermatozoa it is sometimes difficult to say whether a hedgehog is at the beginning or end of a pseudo-pregnancy cycle and the determination has to be made from the amount of spermatozoa and the appearance of the vagina ; Nos. 99, 101, and 196 were in this category (Appendices III and VI). Pseudo-pregnant uteri can readily be distinguished from the early progestational ones (Nos. 264, 104, and 261), which show distinctive changes, only found in association with developing ova and blastulæ (see p. 264), but they do not form a homogeneous group. There is no regular epithelial growth or congestion of the uterine mucosa after sterile copulation, and the extent of the histological reaction in the uterus seems to vary with the previous history of the animal. Pseudo-pregnant hedgehogs at the beginning of the breeding season are listed in Appendix III; four are parous and four non-parous. Some of these have had a sequence of sterile cycles, since their ovaries contain numerous large corpora lutea. The only one in its first pseudo-pregnancy cycle is No. 163 (non-parous), which copulated at the second œstrus; fig. 23, Plate 30, shows that its uterus is not conspicuously different from that of unmated animals; in some parts, however, the epithelium has become thrown into small regular folds and the stroma immediately below it is œdematous. This "notched" appearance of the epithelium, though seen in section to a very varying extent, is undoubtedly characteristic both of the uterus and cervix of inseminated hedgehogs. It does not seem to be brought about by growth or mitosis. Probably the uterus is swollen at the time of copulation and the uterine epithelium stretched; later it collapses, producing more or less the appearance illustrated in fig. 30, Plate 31. It is noticeable that actual rupture of the epithelium is not uncommon in such uteri, fig. 27, Plate 31. No. 99, killed just after ovulation, shows a wide lumen and stretched regular uterine epithelium. Others killed in the luteal phase of the cycle have the notched type of uterine epithelium. There is an attempt at progestational proliferation, indicated by slight growth and secretion in the epithelial cells of the uterus and cervix, in some pseudo-pregnant animals which have not bred, notably Nos. 99 and 101. The significance of these changes has been discussed on p. 250. In No. 99, where there is disorganization of the uterine stroma, a small group of cells in the cervix have become irregular and elongated and resemble the corresponding cells in the early pregnancy, No. 104; the majority of the cervical epithelial cells, however, have remained cuboidal and uniform. Some animals show a slight localized reaction of this kind near the tip of the uterus and traces of secretion from the epithelial cells.

The most interesting uterus, a very large one (1·66 gm.), is that of No. 101. This animal apparently mated just before death after a succession of pseudo-pregnancy cycles; the ovaries contain four large follicles. The uterus is exceptionally œdematous and the uterine and cervical epithelium have grown out everywhere into a series of fronds which resemble a withered progestational proliferation, fig. 35, Plate 32. No secretion is taking place and there are no indications of true pregnancy. It may be assumed that the uterine mucosa proliferated in the last cycle, but implantation of ova failed to occur.

Animals becoming pseudo-pregnant after lactation tend to have a slightly more active uterine endometrium (Nos. 132, 128, 129, Appendix VI) than those at the beginning of the breeding season, but they are similarly variable. Owing to the accumulation of older corpora lutea it is impossible to state the maximum number of times a post-partum animal has copulated without becoming pregnant, but it is clear that it may do so at least twice, so that a further sensitization of the uterus seems to be often necessary after the lactation anœstrus. In one animal (No. 133) the uterus looked pseudo-pregnant, but did not contain spermatozoa ; in the ovaries were recent corpora lutea of ovulation and also corpora lutea of pseudo-pregnancy from the previous cycle. The uterus seems to have been unaffected by the beginning of the next cycle.

(*g*) *Implantation and Pregnancy.*—The earliest progestational changes were observed in three uteri, which showed no external swellings. In the first of these (No. 264, Appendix IV) both ovaries and uterus were greatly congested, figs. 7, 24, 36, Plates 28, 30 and 32, the latter showing a close resemblance in section to the one described and illustrated by HUBRECHT (1889 : p. 398 : Plate 20, fig. 37). The corpora lutea were still developing and two 4–8 cell eggs and some spermatozoa were found in the Fallopian tube adjacent to the uterus, fig. 12, Plate 28. BAUMEISTER (1913) states that hedgehog ova generally pass into the uterus before the eight-cell stage. The tip of this uterus was sectioned serially, but no eggs were found.

Prior to the actual proliferation, therefore, the uterus becomes somewhat œdematous, and there is a great congestion of the sub-epithelial stroma which is not found in any other uterus. In some regions the epithelial lining is destroyed and blood and pigment derived from it, pour into the uterine cavity and partially fill it, fig. 36, Plate 32. This also happens in the cervix.

The earliest proliferative stage is No. 104, which has a small, probably non-parous uterus (0·94 gm.), which is not particularly congested. Here there are the beginnings of epithelial activity, figs. 28, 37, Plates 31, 32 ; two very small blastulæ lie free in the lumen and contain 15 and 10 nuclei respectively in their largest sections. Near these blastulæ, and also at the tip of the uterus, the epithelium has grown out into a fringe of irregular papillæ, the active cells having increased in number and size. Adjacent to them, however, there are others, often in the anti-mesometrial part of the epithelium, which are only just beginning to change and divide. BAUMEISTER (1913) describes the early blastulæ as lying in eosinophil lymph, but since such a substance is found in the region of epithelial activity, it would appear to be the secretory product of the epithelial cells into which many of the polymorphs, abundant in the epithelium and stroma, have migrated, fig. 28, Plate 31. No. 104 is an earlier implantation stage than those of HUBRECHT (1889), but already the closing of the gland tubules next the lumen, which he describes, is taking place and the stroma and small blood vessels are proliferating (COSTA, 1929).

In No. 261, a later stage of progestational proliferation than No. 104, the blastulæ are larger and lie free at the anti-mesometrial end of the lumen. They contain about 20 cells in their largest sections, and are 70 μ in length. Active proliferation of the stroma, mainly on the anti-mesometrial side, has altered the shape and position of the lumen, as HUBRECHT has related, and carried it near to the mesometrium. The uterine epithelium has grown into folds and crypts and the lumen is filled with secretion, blood, and pigment, fig. 38, Plate 32, except in one region, where the epithelium is less developed and active.

The next stage of pregnancy is illustrated by No. 107, which had the smallest uterus (1·07 gm.) with definite pregnancy swellings and placentæ. Between the placental sites the uterine epithelium forms a complex glandular network. In No. 131, in which fertilization occurred before the mammary gland had regressed, only one pregnancy swelling was found in the uterus, but elsewhere the uterine epithelium has reacted and formed glandular crypts. The lumen contains leucocytes and glandular secretion. The stroma is denser than in the other specimens, probably owing to the recent uterine regression during lactation.

In No. 317, approximately a mid-pregnancy, the regions between the placental sites show active secretion from the epithelial crypts. The uterine glands which lie deeper in the stroma are not affected and do not hypertrophy or secrete (*cf.* the guinea-pig).

Late in pregnancy, when the whole uterus is stretched and there is little space left between the embryos, the epithelium appears as an irregular multi-cellular layer with small projections and shallow crypts of secreting cells. Spermatozoa, presumably dating from the time of fertilization, were found in almost all the pregnant uteri (Appendix IV), except very late in pregnancy, when little or no material between the fœtuses was available for examination.

(*h*) *The Post-partum Phase.*—The appearance and size of the uterus just after parturition is shown by No. 312 (Appendix V), which had a litter in the laboratory, and was killed about one day later. Parturition was presumably normal, since the mammary gland was fully developed. The endometrium is completely disorganized and very vascular and œdematous; a few glands persist in the deeper layers of the mucosa. The greater part of the section is occupied by the thick muscle walls. In No. 177, which has a uterus of similar size, there are only three placental sites and the regions between them show rather less disorganization than in No. 312. The mucosa is not so œdematous and more glands persist; the epithelial cells are still large and irregular and there is much pigment in the stroma.

Two of the three other large post-partum uteri (Nos. 166, 125, 126) belong to animals which have ovulated since parturition (Appendix VI). The musculature is still very thick and the endometrium œdematous and disorganized at the placental sites, although elsewhere the gland tubules are comparatively regular. No. 125 shows no definite placental sites, but has clearly been pregnant, fig. 29, Plate 31. Comparison with the uteri of lactating hedgehogs indicates that none of the animals mentioned above could have lactated for long, since this would have led to uterine involution as in other species. Appendix V shows the size of the uterus in six lactating animals; the average weight is 0·66 gm. The endometrium is extremely dense and the gland tubules have dwindled till their diameter is only 15–20 μ. Near the thick circular muscle the stroma is less dense and comparatively free from glands. Large, occluded blood vessels, pigment, etc., can be found at the old placental sites, fig. 25, Plate 30.

In nine post-partum hedgehogs the uteri have recovered after involution; the whole endometrium has grown and is less dense. Abundant mitoses in both gland cells and stroma are found in the uterus of No. 313, which has ceased lactation. The majority of glands no longer appear radial, but as cross-sections of ramifying tubules. The condition of the endometrium in these post-partum uteri varies not only with the functional condition of the animal (length of time since pregnancy or lactation, recent copulation, etc.), but also according to the situation of the sections relative to the old placental sites. The majority of the uteri are pseudo-pregnant, fig. 30, Plate 31.

(*i*) *Anœstrus.*—In anœstrus the uteri show a somewhat greater atrophy than during lactation, but they are not essentially different. The endometrium becomes very dense and contains dilated blood sinuses and atrophying glands, fig. 36, Plate 32. At the old placental sites the remains of blood vessels, etc., may persist late into the winter ; a new epithelium forms which sends out small projections into the stroma, but no fresh growth of glands takes place till the spring.

VIII. *The Vagina.*

(*a*) *Changes in the Vaginal Epithelium.*—There is a distinct cycle in the hedgehog vagina, as COURRIER, (1924, *a*, *b*,) has already pointed out. It enlarges at the beginning of the breeding season and becomes greatly dilated at œstrus. The distention does not vary perceptibly during the short diœstrous cycles, but it subsides in pseudo-pregnancy. During most of pregnancy and lactation, as well as in anœstrus, the vagina is small. The gross changes are accompanied by alterations in the vaginal epithelium and in the accessory glands. The epithelial cycle is of the usual type—stratification and cornification followed by sloughing and fresh growth. It is best seen in the upper vagina ; farther down the epithelium varies according to its position and the changes, though similar, are less easily traced.

During the winter the thickness of the upper vaginal epithelium shows individual differences, since not all animals reach the extreme point of anœstrus simultaneously; those in which the epithelium has been recently cornified are slower to pass into the resting condition than those which have been lactating up to the beginning of anœstrus. In a hedgehog killed in January the vaginal epithelium is fairly thick and has a ragged edge of vacuolated and swollen cells invaded by polymorphs. The outer epithelial layers were probably sloughed shortly before death. In the resting condition of the vagina there are only one or two rows of squamous cells next to the lumen above the transitional and basal layers, fig. 43, Plate 32. Although the epithelium becomes very low, growth probably does not cease completely during anœstrus, since there are generally traces of epithelial debris in the lumen.

In prepubertal hedgehogs, before or during their first winter, the vaginal epithelium is 30–100 μ thick and shows cell-sloughing. It does not become typically stratified, however, fig. 39, Plate 32, until the spring, in the majority of hedgehogs, although one in September shows a partial stratification and much sloughing of nucleated vaginal cells. In most prepubertal hedgehogs between October 2 and March 23 the vaginal epithelium shows little activity. By April, however, the vagina and vaginal epithelium are growing rapidly in parous and non-parous hedgehogs. In some of the latter the vaginal epithelium is still irregular, but in the majority it is both stratified and cornified ; once growth starts in the spring it proceeds fairly rapidly. Wholesale sloughing begins, however, before the epithelium has reached its full thickness, when the cornified layer, from which the pycnotic nuclei may or may not have disappeared, is about 20–30 μ thick, and the whole epithelium varies from 120–180 μ. At this thickness or less the vaginal epithelium alternately presents a ragged and a cornified surface. Leucocytes are not abundant. The intermittent growth and sloughing coincides with the formation and degeneration of large follicles in the ovary, before any ovulation has taken place, and before either the uterine or the vaginal enlargement is complete.

Two of the parous hedgehogs in April have cornified vaginal epithelium, but the other is still quiescent. Stages between the anœstrous and the breeding season condition are also found in parous and non-parous hedgehogs in May and June, which have not yet ovulated.

The condition of the early breeding season vagina at œstrus is shown in figs. 31, 40, Plates 31, 32 ; comparison with the prepubertal or anœstrous vagina indicates the total increase in the epithelium. When the ovaries contain large or just ruptured follicles the upper vagina has a layer of cornified epithelium 60–120 μ thick. This cornified layer apparently persists throughout the diœstrous cycle, only slight sloughing occurring after ovulation in absence of mating. A much greater sloughing of cornified epithelium takes place after copulation, fig. 41, Plate 32 ; the regular cornified layer disappears in some parts and the whole of the upper vagina becomes filled with fluid containing cornified debris. Sloughing is intensified in early pregnancy and successive cell layers are shed, so that by the time placental swellings have formed in the uterus the vaginal epithelium is much lower than it is during a sterile cycle. In later pregnancy the epithelium is often vacuolated, fig. 42, Plate 32. After parturition and during lactation the vaginal epithelium remains low and irregular, though it is a little thicker than in late pregnancy. The appearance of the vagina does not suggest a regular post-partum œstrus such as occurs in the mouse. When activity recommences, cornification is seldom as pronounced as it is at the beginning of the breeding season. Sloughing of the epithelium may occur before the first post-partum œstrus. Most of the active post-partum hedgehogs show various stages of sloughing, but one killed just after copulation has a well-defined cornified layer 50–80 μ thick. (Appendix VI.)

(*b*) *Changes in the Accessory Glands.*—Seasonal changes can be seen in the vaginal glands, but the variations in the secretory activity of different tubules make it impossible to trace a detailed correspondence with the reproductive phases of the animal. In general it may be said of all the glands that they regress in anœstrus ; the tubules shrink and the secretory epithelium becomes inactive.

The upper vaginal glands show the greatest changes in the height of the secretory epithelium and in the size of the gland tubules. In anœstrus most of the epithelium is only 6–8 μ in height, but near the beginning of the breeding season the same cells have increased up to 24μ—about the same height as at œstrus. Columnar epithelium of this kind is found during the diœstrous and pseudo-pregnancy cycles even when the vaginal epithelium is low, but there is some evidence that the cells temporarily lose their cytoplasmic border just after œstrus, owing to active secretion. In pregnancy and lactation the upper vaginal glands regress: the epithelium is only 10–14μ or less in height.

Cowper's glands also change in size between anœstrus and the breeding season; during the latter the tubules enlarge and contain secretion with masses of nuclear debris. In anœstrus the tubules are small and the epithelium is only half as high as during the breeding season.

The large diffuse mid-vaginal glands and the clitoral glands undergo seasonal variations comparable to those described above, but no definite glandular cycle could be traced. There is some evidence that these mid-vaginal glands are active during pregnancy.

IX. *The Mammary Glands.*

There is no prepubertal development of the mammary glands in the hedgehog, nor was any growth observed in non-parous or parous females at the beginning of the breeding season. The mammary glands of the parous hedgehogs, Nos. 259 and 261, are indistinguishable; the former was approaching its first œstrus since the previous year, while the latter had ovulated several times and had just become pregnant. Both glands consist of a thin, diffuse network of ducts which have persisted through anœstrus from the last breeding season. No. 317, an early pregnancy (with 4 mm. fœtuses) showed a very similar gland, fig. 44, Plate 33, hardly distinguishable except for a slight thickening round the nipples; from the appearance of the gland and from the animals's body weight (650 gm.) No. 317 was probably a parous adult. It is doubtful, by analogy with other species, if the nipple areas would have been fused at this stage of a first pregnancy. The only other mammary glands of pregnant hedgehogs are those of Nos. 130 and 262 in the latter half of pregnancy, figs. 45, 46, Plate 33. These show a definite thickening; in No. 262 the gland is continuous, but more compact than in No. 130; probably the former had not previously been pregnant.

In No. 312, which had just had a litter, the mammary gland is much thicker than in No. 262; the animal was large and the mammary gland forms two strips of secretory tissue 19 cm. long and 1·5–3·5 cm. wide, fig. 47, Plate 33. A further thickening of the gland takes place during lactation until the whole secretory area is solid. No. 131, a very early pregnancy, had a gland of this type, showing that it had already suckled one litter, fig. 48, Plate 33.

The mammary gland regresses at the end of lactation and in the absence of further pregnancy it gradually dwindles to the network of ducts already described; this persists right through the winter, and, together with the enlarged nipples, suffices to distinguish parous from non-parous females. Two of the nipple areas from a hedgehog taken on

January 10 were not completely regressed, so that evidently suckling of an autumn litter may continue for some time, fig. 49, Plate 33.

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X. *Summary.*

(1) Female hedgehogs were collected during 1930–1933 in order to ascertain the limits of the breeding season and the nature of the reproductive cycle; 136 animals taken straight from the field, mainly in 1931, were examined and recorded.

(2) Pregnancy occurs in May, June, July, August, and September, and probably lasts about one month. Hedgehogs in England and Wales generally breed in May or June, and many have a second litter later in the year (Table I). The most common number in a litter is five; this corresponds with the usual number of ova at ovulation.

(3) The hedgehog ovulates spontaneously and undergoes one or more short diœstrous cycles unaccompanied by mating; in these circumstances the corpora lutea are small and hardly luteinized.

(4) Mating, detected by uterine spermatozoa, begins after one or more cycles, but no hedgehog became pregnant at its first mating, and repeated pseudo-pregnancy cycles (after sterile matings) are common. (Diagram, p. 249.)

(5) In pseudo-pregnancy the corpora lutea are much larger than those of the diœstrous cycle, but there is little uterine change.

(6) The succession of infertile diœstrous and pseudo-pregnancy cycles leads to accumulation of corpora lutea, which persist through pregnancy and lactation up to anœstrus in the following autumn.

(7) Fertile mating, shown by segmenting ova or blastulæ, is associated with progestational changes not found in pseudo-pregnancy.

(8) The development of the corpora lutea of pregnancy does not exceed that occurring after sterile mating.

(9) There is no immediate post-partum œstrus and no cycle during the first part of lactation.

(10) At the end of the lactation anœstrus the cycle recurs as at the beginning of the breeding season; animals may copulate at the first œstrus after pregnancy, but first copulations are often infertile as before. (Table I.)

(11) Second pregnancies occur from July onwards. Lactation may continue late into the year.

(12) Hedgehogs have ceased to ovulate in October and the anœstrous period lasts till April. Ovaries, uterus, and vagina are all reduced in size during anœstrus. Fresh growth takes place in the spring.

(13) A description is given of the functional changes in the reproductive organs during the year.

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DESCRIPTION OF PLATES.

Abbreviations.—Blast., blastocyst; *c.e.*, congested endometrium; *C.g.*, Cowper's gland; *c. preg.* corpus luteum of pregnancy; *c. psp.*, corpus luteum of pseudo-pregnancy; *f.m.*, follicular mass; *F.t.o.* Fallopian tube opening; *g.c.*, glandular cyst; *lym.*, lymph node; *mv. g.*, mid-vaginal glands; *os.* os tincæ; *s.ov.*, segmenting ovum; *u.l.*, uterine lumen; *uv.g.*, upper vaginal glands.

PLATE 27.

Dissections of the reproductive tract, natural size, description as in Fig. 1, p 242.

FIG. 2.—No. 259. Reproductive tract of parous hedgehog in June about to ovulate for the first time in the season. The bladder, urinogenital sinus and vulva have been cut away. Cowper's and the mid-vaginal glands have been exposed by removal of the muscle wall. One ovary has been slit out of its capsule, to show prominences and large follicles.

FIG. 3.—No. 332. Reproductive tract of non-parous hedgehog in May which has ovulated but not mated. The uterine wall has been sliced away to show that the lumen is continuous between the two horns, although partially interrupted on the ventral side. The upper vagina has been slit open, and the vaginal fluid drained off, to reveal the corrugated lining and the projecting os tincæ. The ovarian capsules have been stretched to show the Fallopian tube on the right and the parovarium on the left. The mid-vaginal glands have been dissected out as before.

FIG. 4.—No. 261. Reproductive tract during early implantation. The upper vagina is beginning to collapse. The mid-vaginal muscle walls have been reflected. The clitoris can be seen posteriorly as a slight prominence.

FIG. 5.—No. 270. Reproductive tract of parous hedgehog in anœstrus, showing the decrease in size of the organs.

PLATE 28.

Ovary, × 12. Fallopian Tube, × 68.

FIG. 6.—No. 101. Ovary with recent and old corpora lutea of pseudo-pregnancy.

FIG. 7.—No. 264. Ovary with corpora lutea of pseudo-pregnancy and two developing corpora lutea of pregnancy, markedly congested.

FIG. 8.—No. 131. Ovary from second pregnancy, showing recent and old corpora lutea not very different in size.

FIG. 9.—No. 271. Anœstrous ovary (January), with fibrous remains of corpora lutea and large follicular masses.

FIG. 10.—No. 192. Fallopian tube in anœstrus.

FIG. 11.—No. 152. Fallopian tube with unfertilized ova and follicular epithelium.

FIG. 12.—No. 264. Fallopian tube with segmenting ovum.

PLATE 29.

Follicles and corpora lutea.

FIG. 13.—No. 159. Œstrous follicle. × 45.

FIG. 14.—No. 152. Just ruptured follicle. × 45.

FIG. 15.—No. 126. Corpus luteum of ovulation with central blood clot. × 45.

FIG. 16.—No. 104. Corpus luteum of pregnancy. × 45.

FIG. 17.—No. 114. Part of a 0·74 mm. diameter follicle, showing enlargement of epithelial cells. × 183.

FIG. 18.—No. 159. Part of the œstrous follicle in fig. 13, showing theca and follicular epithelium. × 183.

FIG. 19.—No. 331. Part of a corpus luteum of ovulation. × 183.

FIG. 20.—No. 104. Part of a corpus luteum of pregnancy, fig. 16. × 183.

PLATE 30.

Uterus × 16 (except fig. 24 × 12).

FIG. 21.—No. 169. Prepubertal uterus (0·14 gm.) in September.

FIG. 22.—No. 153. Prepubertal uterus in May (0·35 gm.), fresh glands fully developed.

FIG. 23.—No. 163. Non-parous uterus (0·53 gm.) in first pseudo-pregnancy cycle. Spermatozoa in the glands. Sub-epithelial tissue slightly œdematous.

FIG. 24.—No. 264. Section showing the tubal opening and progestational congestion, fig. 36.

FIG. 25.—No. 136. Lactation uterus (0·71 gm.).

FIG. 26.—No. 272. Anœstrous parous uterus (0·42 gm.) in January.

PLATE 31.

Uterus × 11. Vagina × 2·8.

FIG. 27.—No. 99. Non-parous uterus of hedgehog which has just mated and ovulated at the end of pseudo-pregnancy.

FIG. 28.—No. 104. Early implantation stage in non-parous uterus, *cf.*, fig. 37.

FIG. 29.—No. 125. Uterus (2·1 gm.) which has not involuted after parturition. No. 125 had ruptured follicles and uterine spermatozoa, like No. 99 (fig. 27).

FIG. 30.—No. 129. Pseudo-pregnant uterus (1·65 gm.) which has recovered from lactation involution. The uterine mucosa is " notched."

FIG. 31.—No. 162. Upper vagina just after ovulation in an unmated animal.

FIG. 32.—No. 132. Upper vagina in pseudo-pregnancy, following lactation, showing upper vaginal glands.

FIG. 33.—No. 192. Upper vagina in lactation anœstrus.

PLATE 32.

Uterus × 87. Upper vaginal epithelium × 337.

FIG. 34.—No. 264. Accumulation of spermatozoa at tubal opening. × 250.

FIG. 35.—No. 101. Epithelial proliferation in pseudo-pregnancy after repeated infertile matings, *cf.* fig. 38.

FIG. 36.—No. 264. Congestion of uterine stroma in very early pregnancy before the eggs have reached the uterus (*cf.* Hubrecht, 1889, p. 398 : Plate XX, fig. 37).

FIG. 37.—No. 104. Progestational proliferation and secretion in the region of a blastocyst.

FIG. 38.—No. 261. A slightly later stage of progestational proliferation. The blastocyst lies free in the lumen which is filled with blood and pigment.

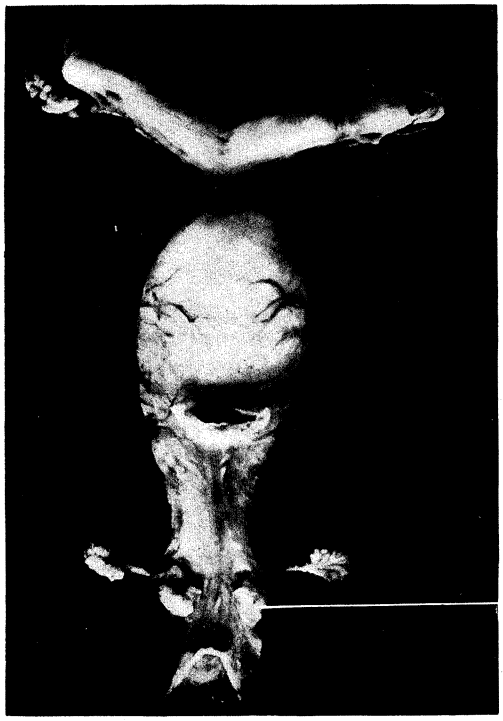
FIG. 39.—No. 286. Prepubertal October hedgehog. Vaginal epithelium not flattened.

FIG. 40.—No. 156. Hedgehog which has just ovulated but not mated. Vaginal epithelium high and cornified.

FIG. 41.—No. 105. Pseudo-pregnant hedgehog ; vaginal epithelium cornified and sloughing.

FIG. 42.—No. 155. Pregnant hedgehog ; vaginal epithelium low, vacuolated, and infiltrated by leucocytes.

FIG. 43.—No. 192. Lactating hedgehog ; vaginal epithelium low as in anœstrus.



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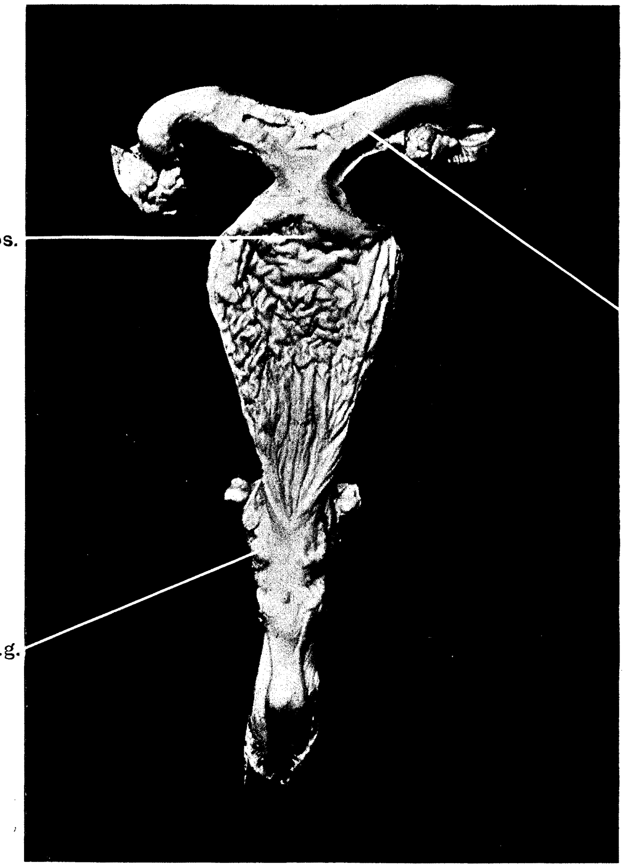

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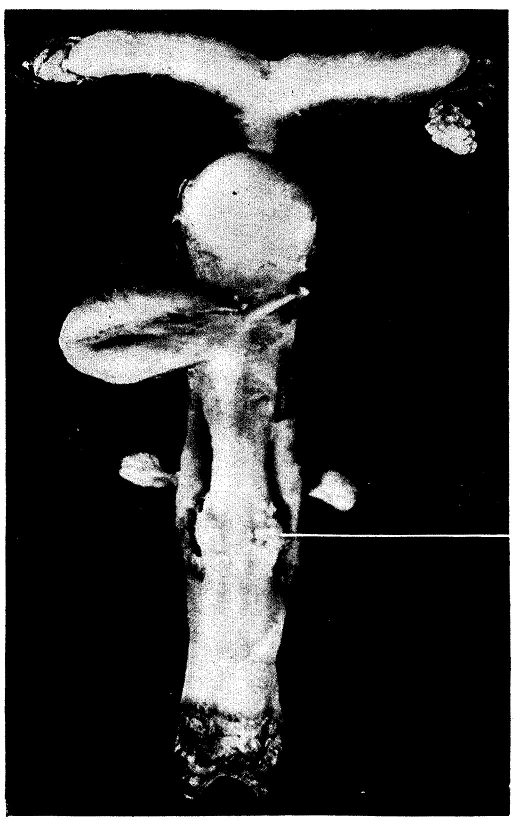

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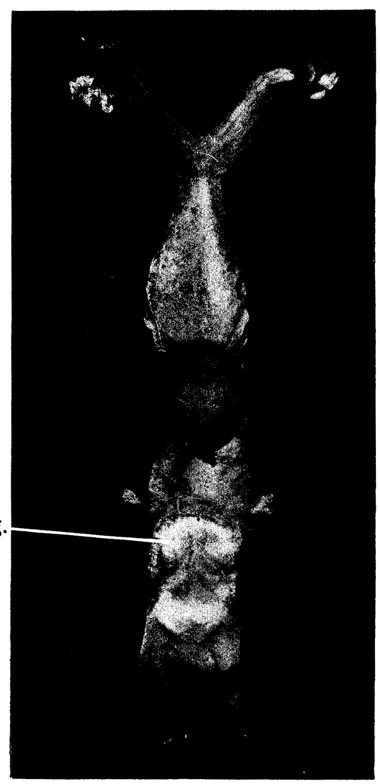

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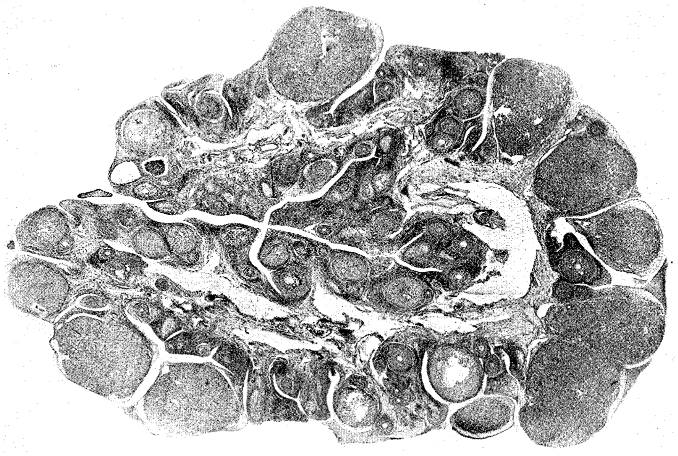

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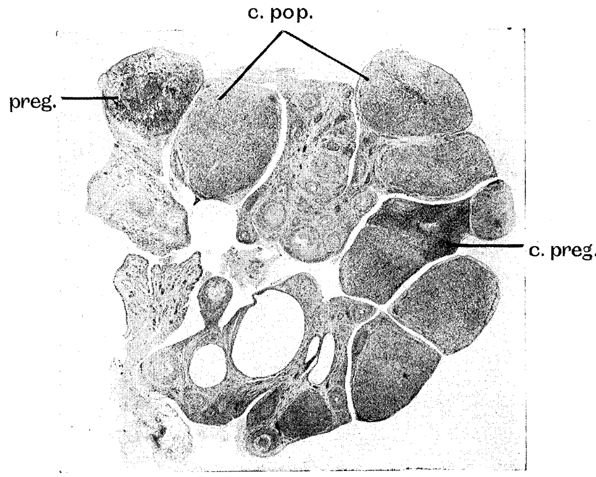

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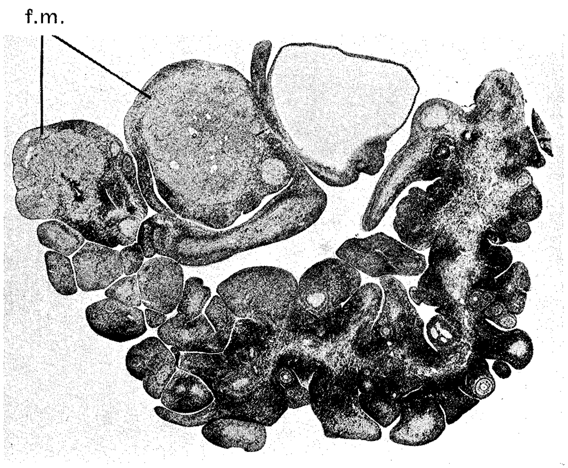

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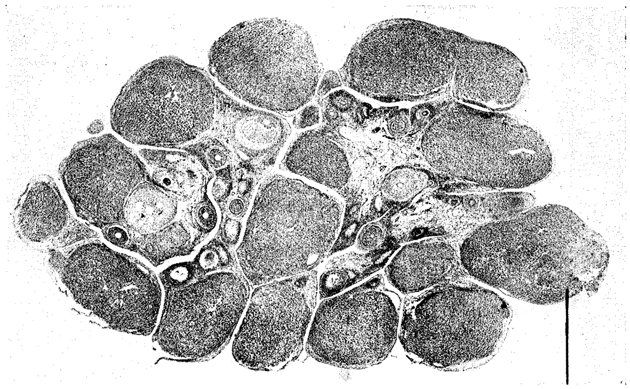
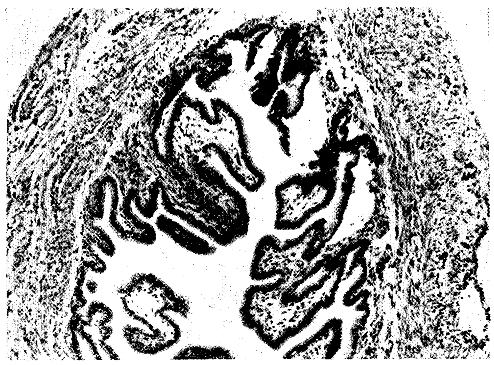


Fig. 8.

Fig. 11.



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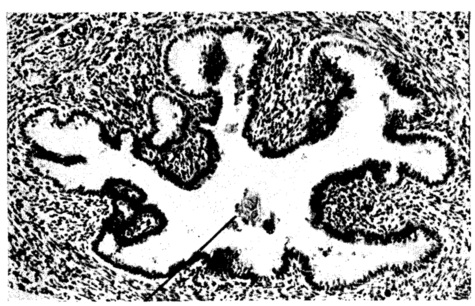

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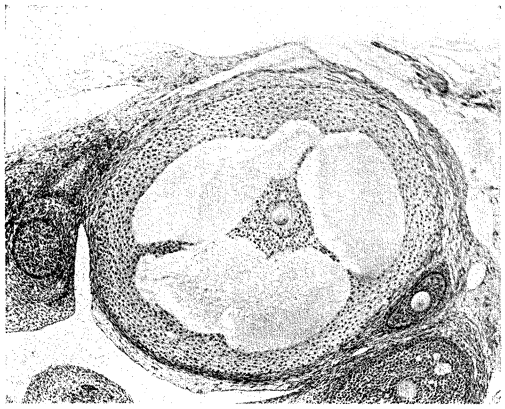
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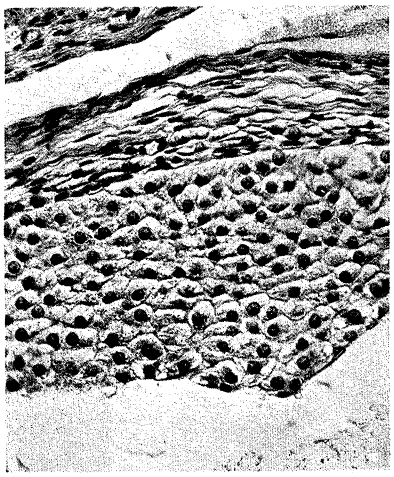
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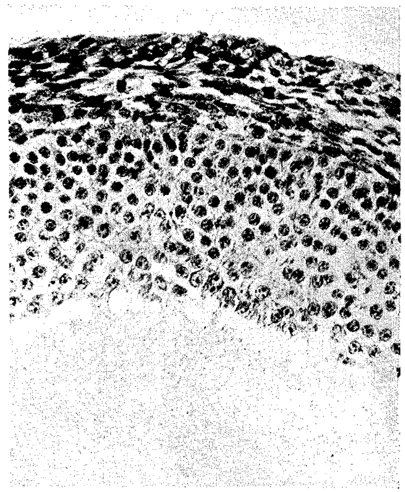
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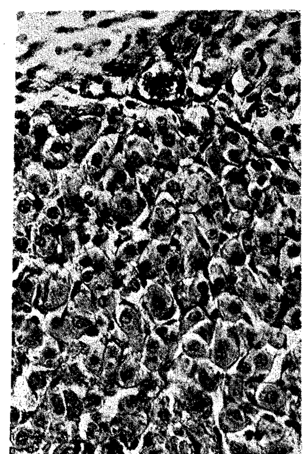
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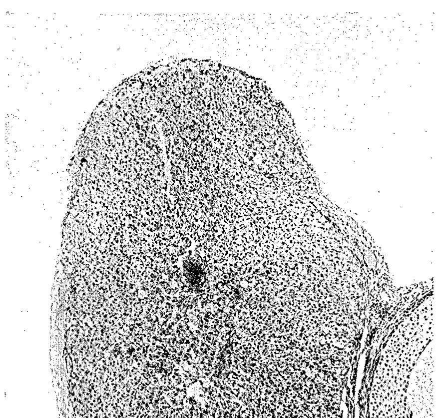
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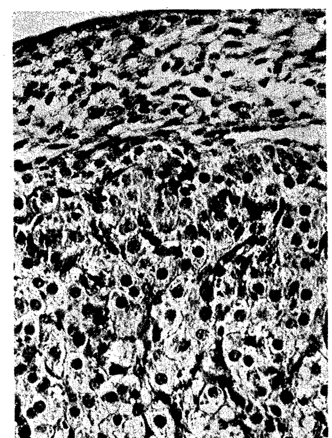
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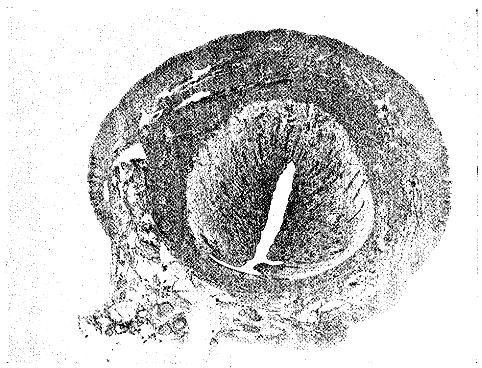

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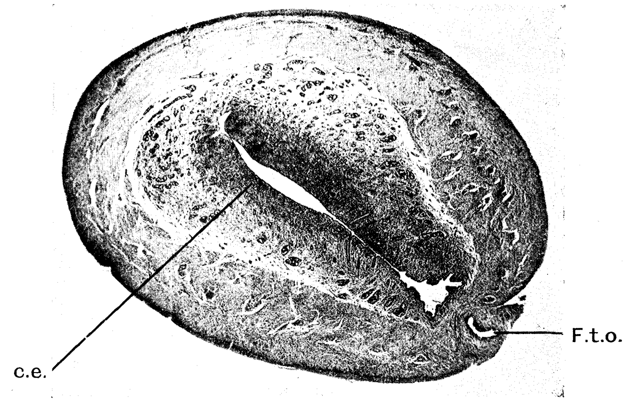

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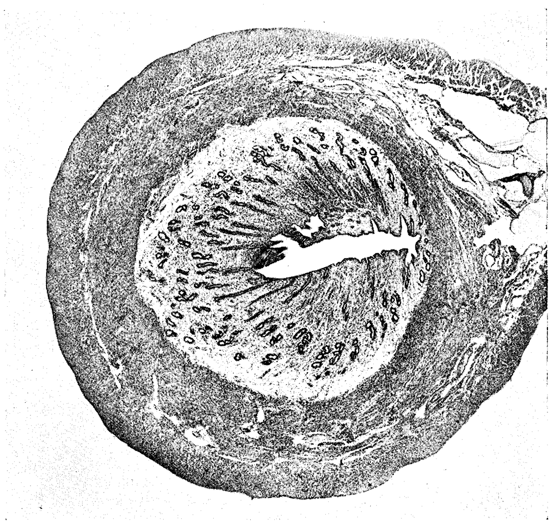

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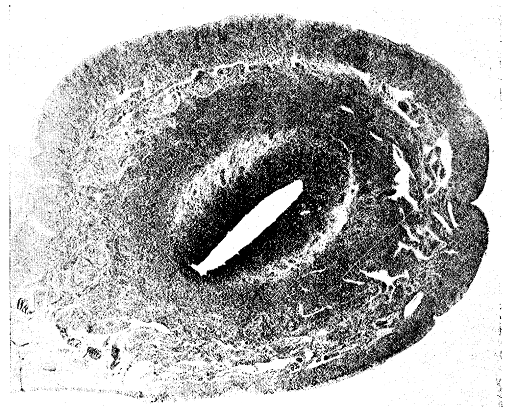

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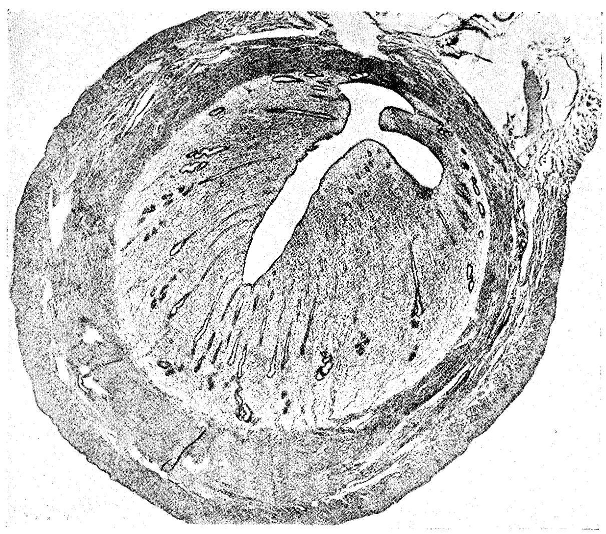

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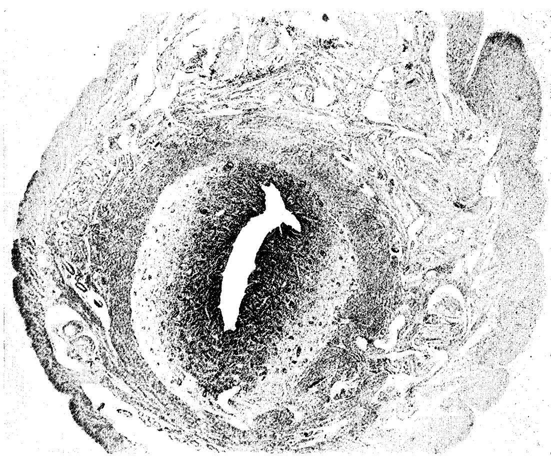

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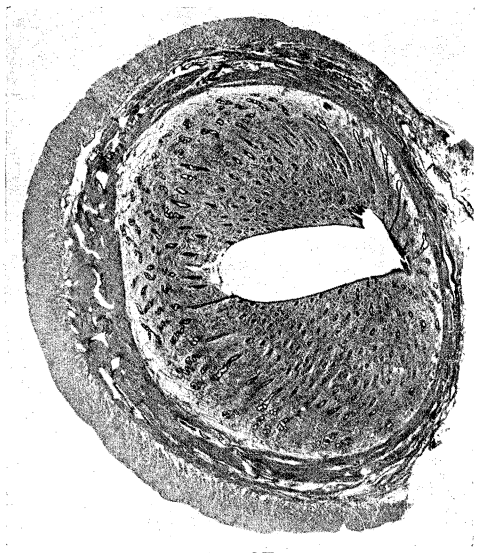

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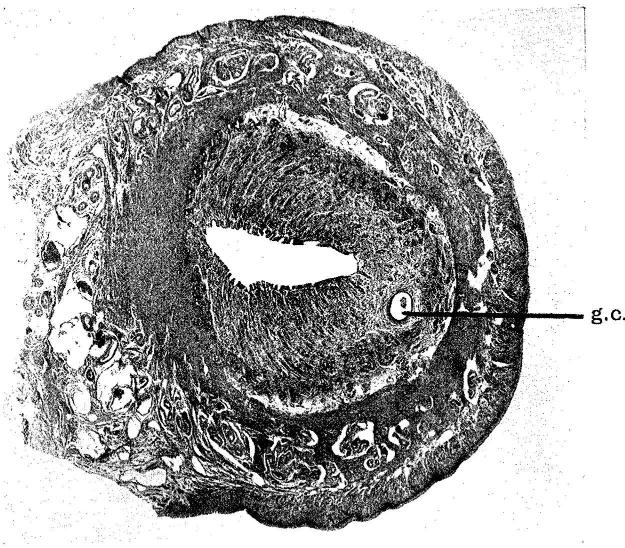

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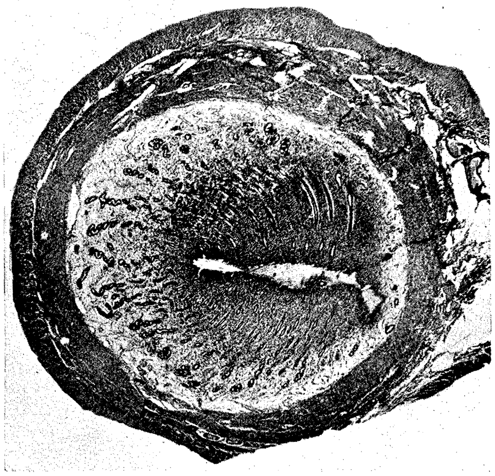

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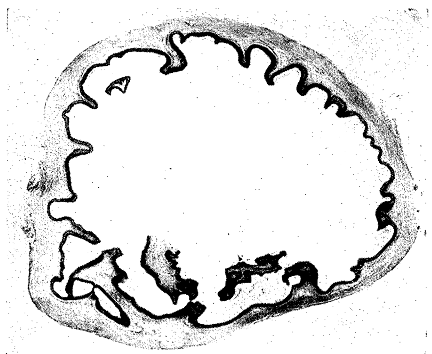

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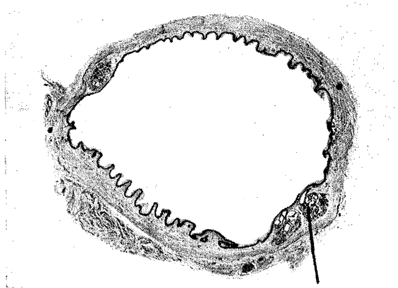

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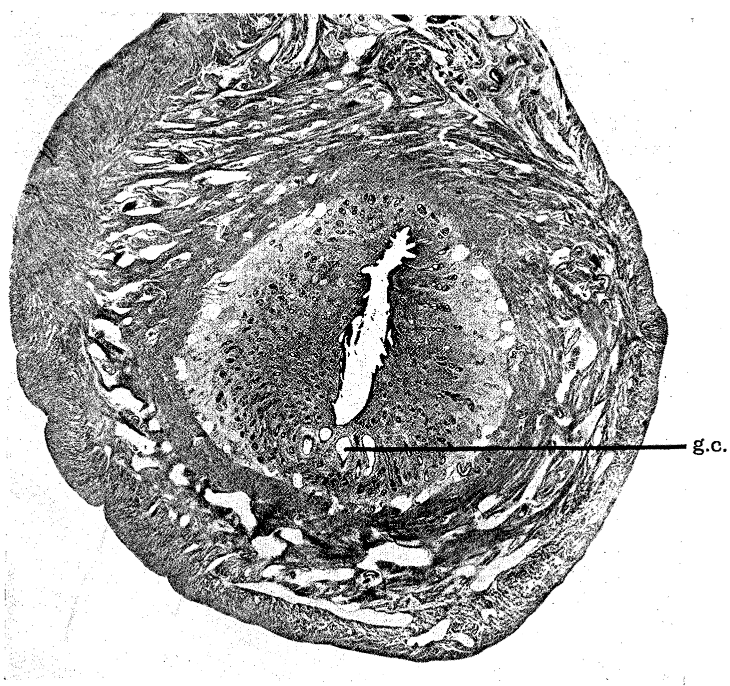

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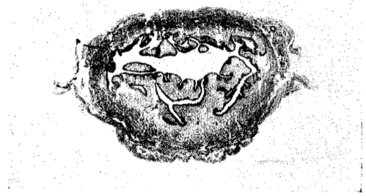
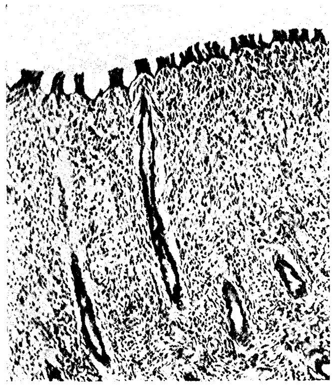


Fig. 33.

Fig. 34.



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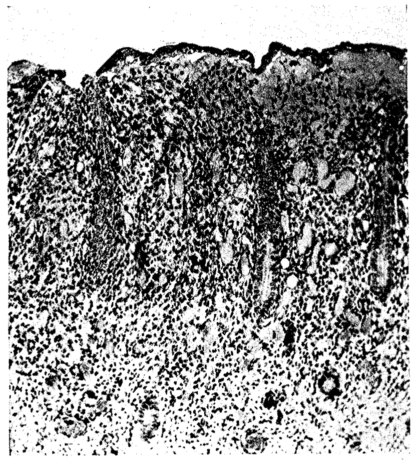
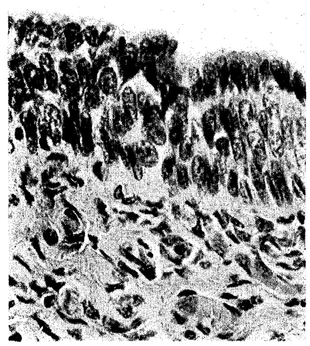


Fig. 36.

Fig. 37.

Fig. 38.



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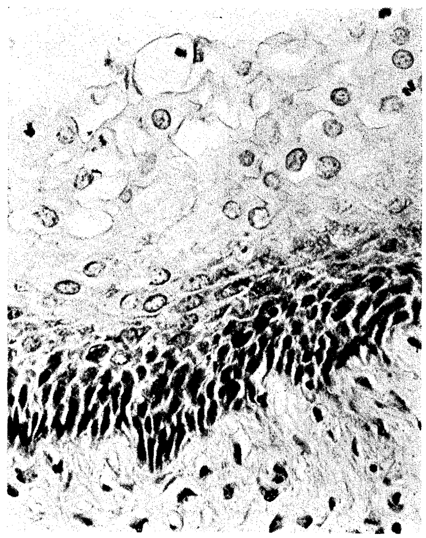

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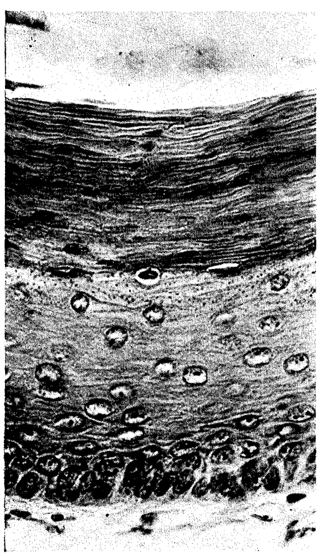

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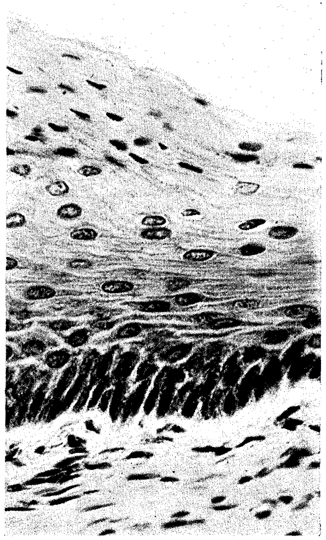

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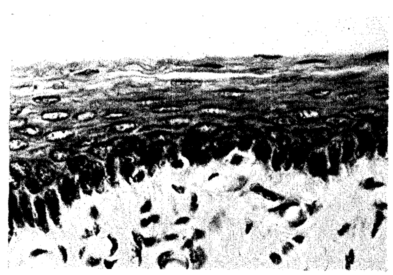


Fig. 43.


Fig. 45.


Fig. 44.


Fig. 47.


Fig. 46.


Fig. 48.


Fig. 49.

PLATE 33.

Mammary glands.

FIG. 44.—No. 317. Part of mammary gland from parous hedgehog in early pregnancy. Natural size.
FIG. 45.—No. 130. Mammary gland in mid-pregnancy. × $\frac{2}{3}$.
FIG. 46.—No. 262. Mammary gland (both sides) in late pregnancy. × $\frac{1}{2}$.
FIG. 47.—No. 312. Mammary gland immediately after parturition. × $\frac{3}{5}$.
FIG. 48.—No. 131. Mammary gland from hedgehog recently lactating and now pregnant. × $\frac{3}{5}$.
FIG. 49.—No. 271. Part of mammary gland from anœstrous hedgehog in January; not fully regressed. Natural size.

APPENDICES.

NOTE.—The appendices record details of normal hedgehogs which have been histologically examined, and grouped according to their condition. * indicates that both ovaries were sectioned.

APPENDIX I.—Prepubertal Hedgehogs.

Forty-two prepubertal hedgehogs, all those which have not yet ovulated, arranged in order of date.

Time of killing.	Number of hedgehogs.	Uterus weights.	Average uterus weight.
		gm.	gm.
August-September	6	0·02–0·14	0·12†
October	9	0·02-0·25	0·13†
November-January	5	0·05–0·09	0·07
March	2	0·12–0·51	—
April	12	0·12–0·53	0·33
May	7	0·35–0·70	0·52
July	1	0·38	—

† The average weights of the uteri in August, September, and October are exclusive of those of four suckling young (110–115 gm.).

APPENDIX II.—Anœstrous Parous Hedgehogs.

Thirty-one parous hedgehogs from the end of the breeding season up to the time of the first ovulation in the following year.

Time of killing.	No. of hedgehogs.	Uterus weights.	Average uterus weight.	Time of killing.	No. of hedgehogs.	Uterus weights.	Average uterus weight.
		gm.	gm.			gm.	gm.
October	4	0·40–1·22	0·74	April	3	0·34–0·76	0·55
Nov.-Jan. ...	8	0·38–0·71	0·53	May	4	0·69–1·02	0·81
February ...	4	0·36–0·78	0·55	June	3	0·87–1·15	1·00
March	4	0·41–0·83	0·59	August	1	1·0	—

Appendix III.—Diœstrous and Pseudo-pregnant Hedgehogs.

Non-pregnant hedgehogs which have ovulated, but have not bred in the current season. They are arranged in two groups, (*a*) non-parous and (*b*) parous, for comparison of the weights of uteri. These groups are again subdivided into unmated and mated (pseudo-pregnant) animals, the latter containing sperm in their uteri and large corpora lutea in their ovaries. Animals marked as "just ovulated" had recently-ruptured follicles. No. 101, which has had several previous pseudo-pregnancy cycles, appears to have just mated, but not ovulated.

Date.	No. of animal.	Uterus weights.	No. of cycles.	Condition at death.
		(*a*) *Non-parous.*		
Unmated.		gm.		
May 8 ...	98*	0·66	2	Just ovulated.
May 13 ...	100*	0·85	3	Just ovulated.
May 18 ...	106*	0·61	3	Just ovulated.
May 25...	167	0·55	2	Diœstrous; recent corpora lutea.
June 20...	156*	0·78	2	Just ovulated.
July 3 ...	194*	0·58	2	Pro-œstrous; large follicles and recent corpora lutea.
Mated.				
May 13 ...	99*	0·87	4 or more	Just ovulated; several matings.
May 15 ...	163*	0·53	2	Pro-œstrous; large follicles; one mating.
May 18 ...	105*	0·59	3	Pseudo-pregnant; developing corpora lutea; second mating.
May 19 ...	115	0·55	3 or more	Pseudo-pregnant; developing corpora lutea; several matings.

Date.	No. of animal.	Uterus weights.	No. of cycles.	Condition at death.
		(*b*) *Parous.*		
Unmated.		gm.		
May 14 ...	168*	0.99	2 or 3	Just ovulated.
May 18 ...	103	0.86	2 or 3	Diœstrous; recent corpora lutea.
June 7 ...	159*	1.03	1	Pro-œstrous; large follicles and recent corpora lutea.
June 19	162*	1.10	3	Just ovulated.
June 20	152*	1.10	3	Just ovulated.
June 22	164	1.15	1	Diœstrous; recent corpora lutea.
Mated.				
May 18 ...	101*	1.66	4 or more	Œstrous; large follicles; several matings.
May 31 ...	308	0.78	3 or more	Pseudo-pregnant; developing corpora lutea; several matings.
June 8 ...	260	1.12	3 or more	Pseudo-pregnant; developing corpora lutea; several matings.
July 14	197	0.70	—	Pseudo-pregnant; ovaries missing.

Appendix IV.—Pregnant Hedgehogs.

Pregnant hedgehogs arranged in order of size of fœtus. The corpora lutea of No. 264, which contains segmenting eggs in the Fallopian tube, are irregular and still developing. Nos. 104 and 261 do not show placental swellings, but these are present in No. 107, although not counted. No. 131 is a second pregnancy, having recently lactated. Spermatozoa occur in the uteri in Nos. 264, 104, 261, 107, 131, 121, 160, 161, 317, and 122.

Month.	Number of animal.	Diameter of corpus luteum of pregnancy.	Uterus weight.	Distribution and number of fœtuses.	Average crown-rump length of fœtuses.
		mm.	gm.		mm.
May 30	264*	—	1·20	—	—
May 18	104*	1·33	0·94	—	—
June 9	261	1·10	1·38	—	—
May 18	107*	1·11	1·07	—	—
July 9	131	1·35	1·25	0 L + 1 R	—
May 27	121*	1·12	—	2 L + 3 R	—
June 3	160*	1·18	—	2 L + 3 R	2·0
May 25	161*	1·04	—	3 L + 2 R	3·6
June 20	317	1·28	—	3 L + 2 R	4·0
May 18	102*	1·13	—	2 L + 3 R	4·6
May 26	122*	1·30	—	2 L + 2 R	6·1
June 1	155*	1·07	—	3 L + 2 R	10·0
July 9	130*	1·31	—	3 L + 4 R	12·0
June 10	262	1·23	—	3 L + 2 R	29·8

Appendix V.—Early Post-partum and Lactating Hedgehogs.

This Table shows the seasonal distribution of early post-partum and lactating hedgehogs, none of which have ovulated since parturition. The uterus undergoes involution during lactation, but the ovaries remain large. The condition of the mammary gland was not recorded in Nos. 165, 166, and 177; in the other animals it was well developed.

Date.	No. of animal.	Uterus weight	Notes.	Date.	No. of animal.	Uterus weight	Notes.
		gm.				gm.	
June 11	165*	1·40	5 placental sites.	July 29 ...	136	0·71	Lactating.
June 18...	166	1·75	Post-partum uterus.	Aug. 14	144	0·49	Lactating.
June 21...	312	3·40	5 placental sites; just had litter.	Aug. 19	177	3·10	3 placental sites.
				Sept. 30	170	0·76	Lactating; 5 young, average weight, 110 gm.
July 8 ...	192	0·60	Lactating.				
July 21 ...	135	0·66	Lactating.	Oct. 12 ...	182	0·75	Lactating; 5 young, average weight, 115 gm.

APPENDIX VI.—Active Post-partum Hedgehogs.

This Table includes hedgehogs which have ovulated or are nearing œstrus since pregnancy, arranged according to date. No. 313 is listed as post-partum in Table I, since it probably became pro-œstrus in captivity. Hedgehogs listed as pseudo-pregnant contain spermatozoa in the uteri. Nos. 125 and 126 show no sign of lactation involution of the uterus; the former has mated at its first post-partum œstrus. At least three hedgehogs (Nos. 128, 129, 196) have mated more than once since pregnancy. The condition of the mammary gland was not always recorded, but in four hedgehogs there was evidence of recent lactation and No. 132 was thought to be still lactating.

Date.	No. of animal.	Uterus weight	Notes.	Date.	No. of animal.	Uterus weight	Notes.
		gm.				gm.	
June 8 ...	125*	2·10	Pseudo-pregnant; ruptured follicles of first post-partum ovulation; no evidence of lactation.	July 14	132	1·35	Pseudo-pregnant; large corpora lutea; mammary gland well developed.
June 24	313	1·28	Nearing œstrus after 15 days in laboratory; mammary gland involuting; 5 placental sites.	July 14 ...	133*	1·81	Diœstrus after pseudo-pregnancy; recent corpora lutea of ovulation.
July 1 ...	126	2·40	Diœstrus; first post-partum ovulation; no evidence of lactation.	Aug. 4 ...	138	1·02	Nearing œstrus; mammary gland regressed.
July 5 ...	128*	1·83	Pseudo-pregnant; developing corpora lutea.	Aug. 4 ...	139*	1·09	Pseudo-pregnant; follicles enlarging; mammary gland well developed.
July 5 ...	129	1·65	Pseudo-pregnant; developing corpora lutea.	Aug. 15	196*	1·35	Pseudo-pregnant; has just copulated after a previous pseudo-pregnancy.
July 7 ...	321	1·08	Diœstrus; developing corpora lutea; mammary gland regressing.				

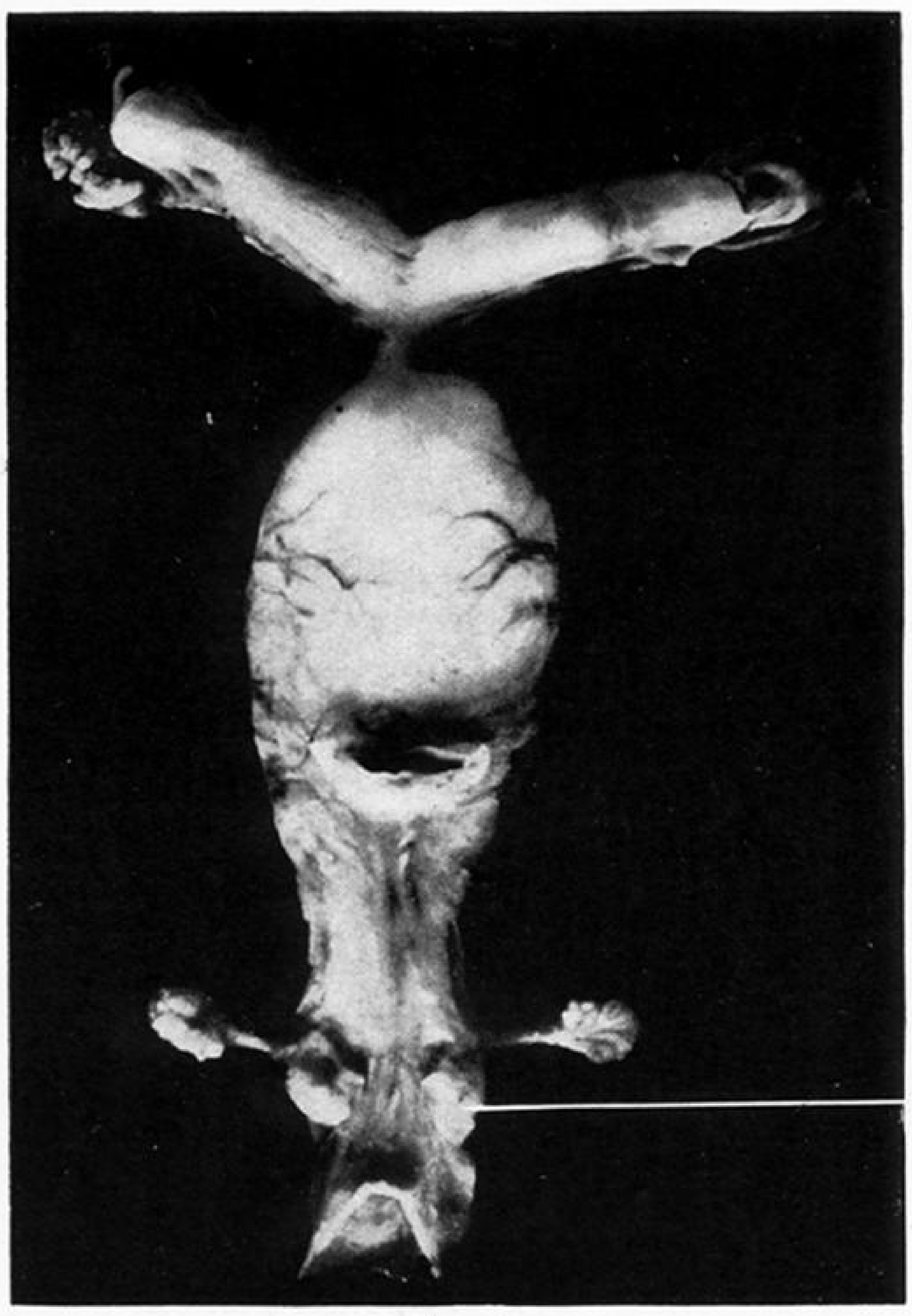
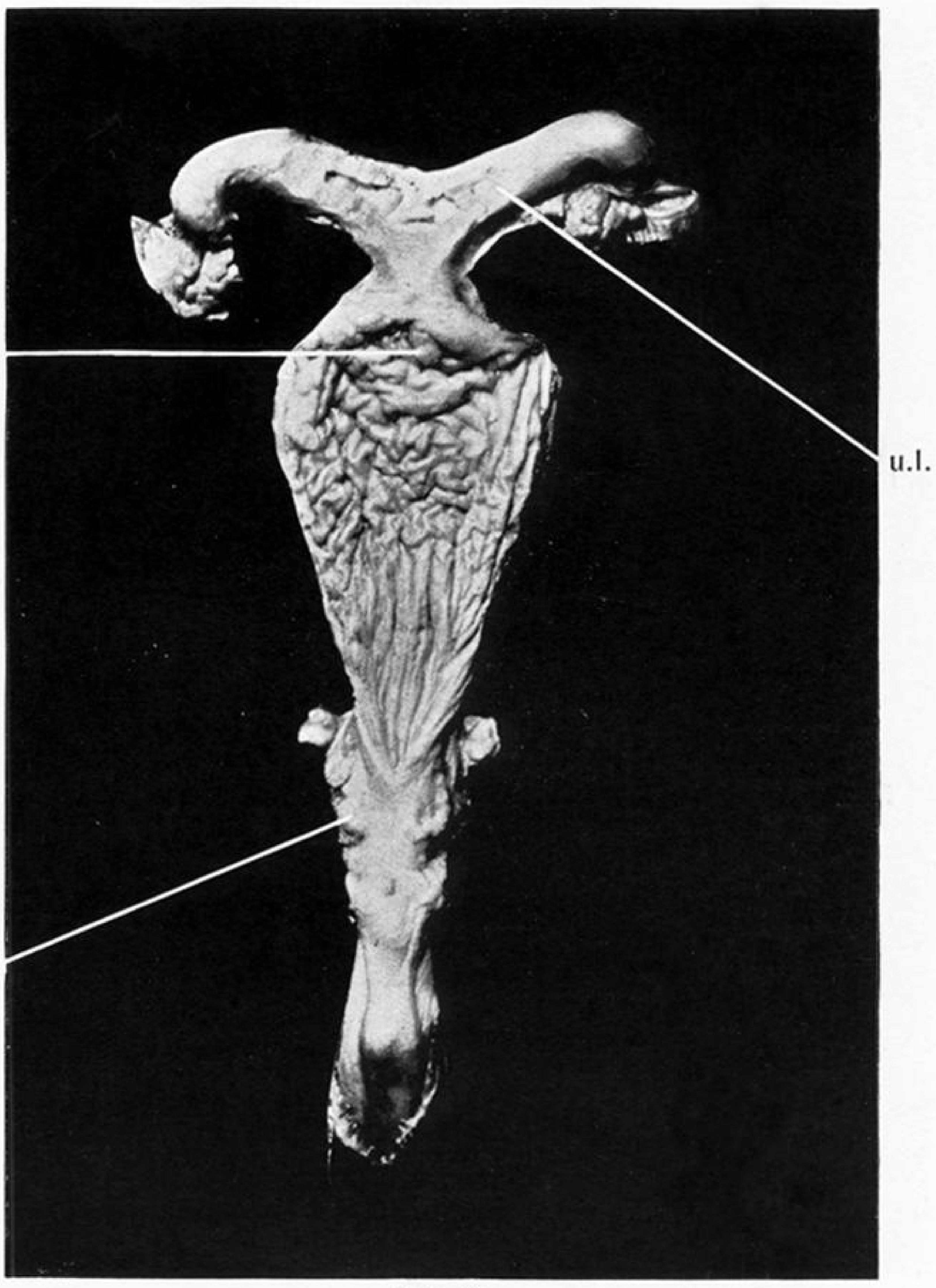


Fig. 2.



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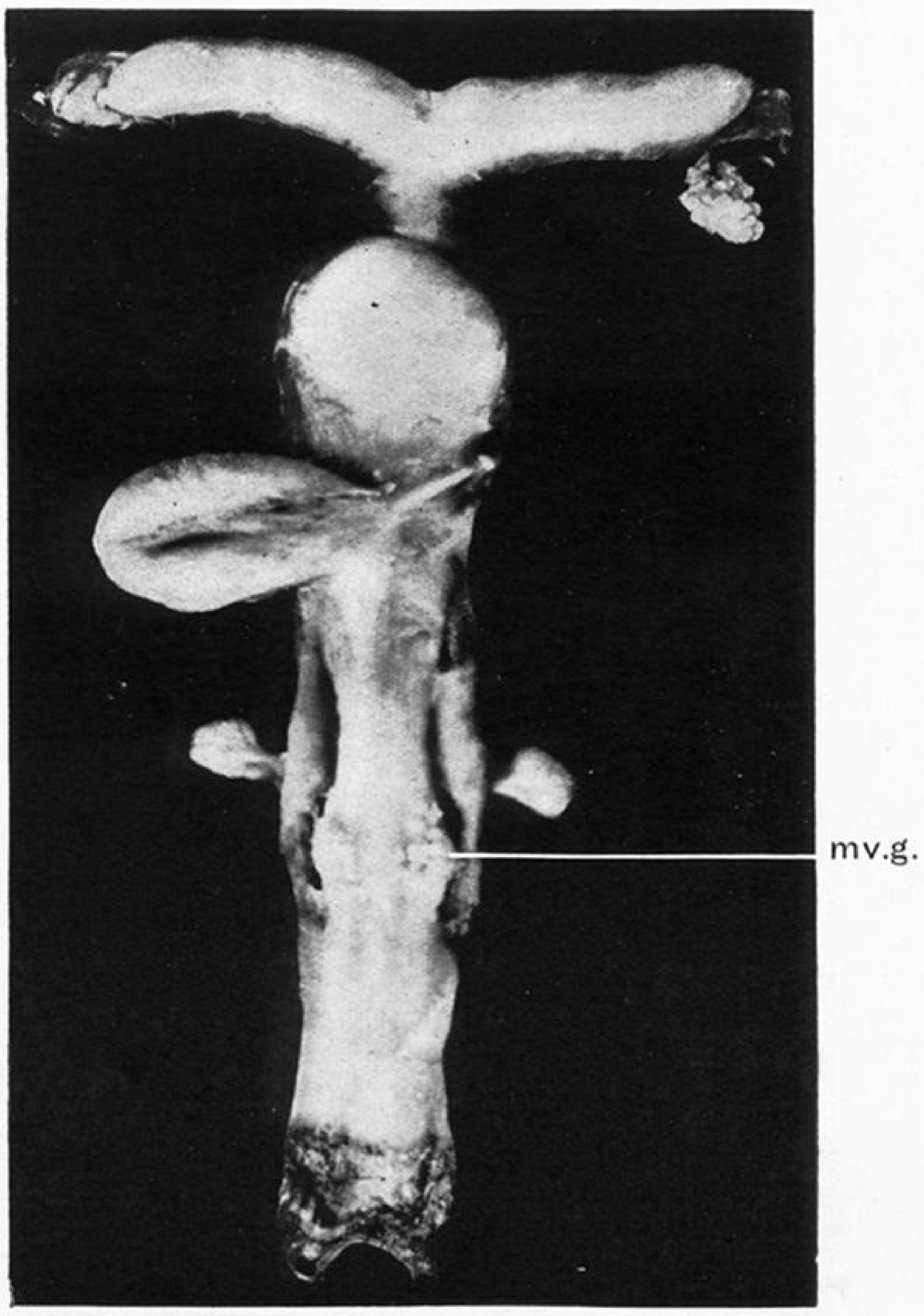

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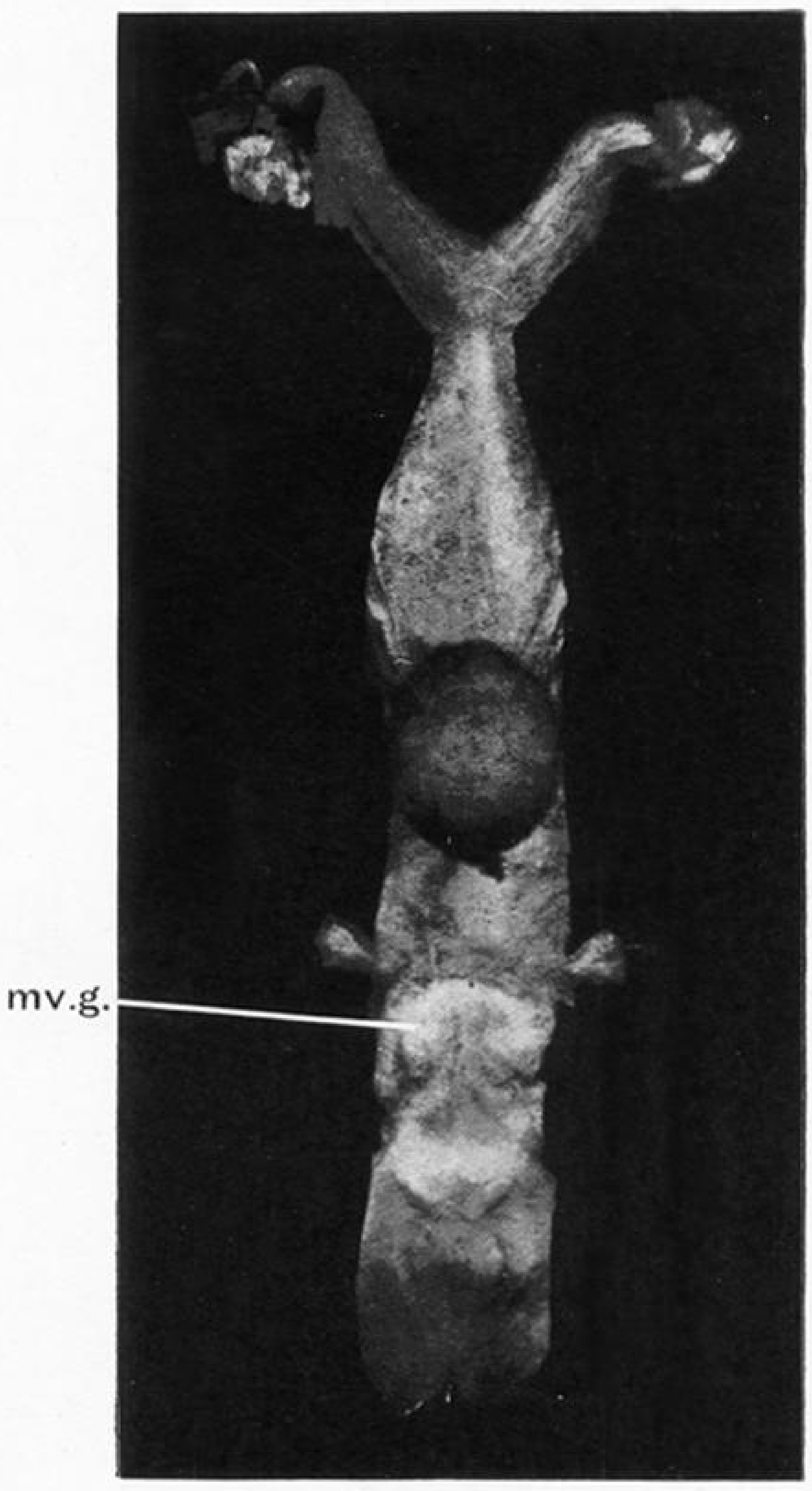

Fig. 5.

PLATE 27.

Dissections of the reproductive tract, natural size, description as in Fig. 1, p 242.

FIG. 2.—No. 259. Reproductive tract of parous hedgehog in June about to ovulate for the first time in the season. The bladder, urinogenital sinus and vulva have been cut away. Cowper's and the mid-vaginal glands have been exposed by removal of the muscle wall. One ovary has been slit out of its capsule, to show prominences and large follicles.

FIG. 3.—No. 332. Reproductive tract of non-parous hedgehog in May which has ovulated but not mated. The uterine wall has been sliced away to show that the lumen is continuous between the two horns, although partially interrupted on the ventral side. The upper vagina has been slit open, and the vaginal fluid drained off, to reveal the corrugated lining and the projecting os tincæ. The ovarian capsules have been stretched to show the Fallopian tube on the right and the parovarium on the left. The mid-vaginal glands have been dissected out as before.

FIG. 4.—No. 261. Reproductive tract during early implantation. The upper vagina is beginning to collapse. The mid-vaginal muscle walls have been reflected. The clitoris can be seen posteriorly as a slight prominence.

FIG. 5.—No. 270. Reproductive tract of parous hedgehog in anœstrus, showing the decrease in size of the organs.

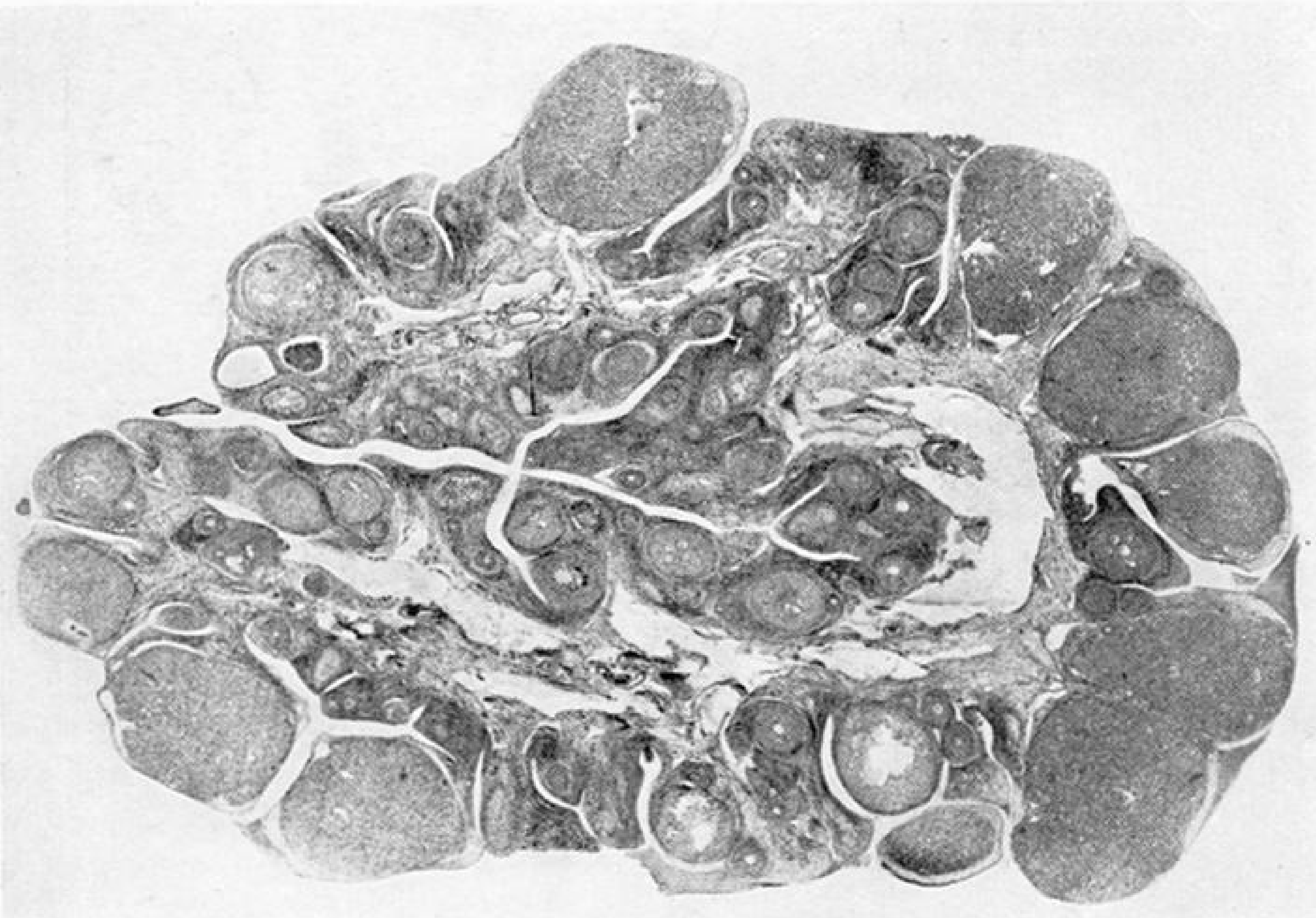

Fig. 6.

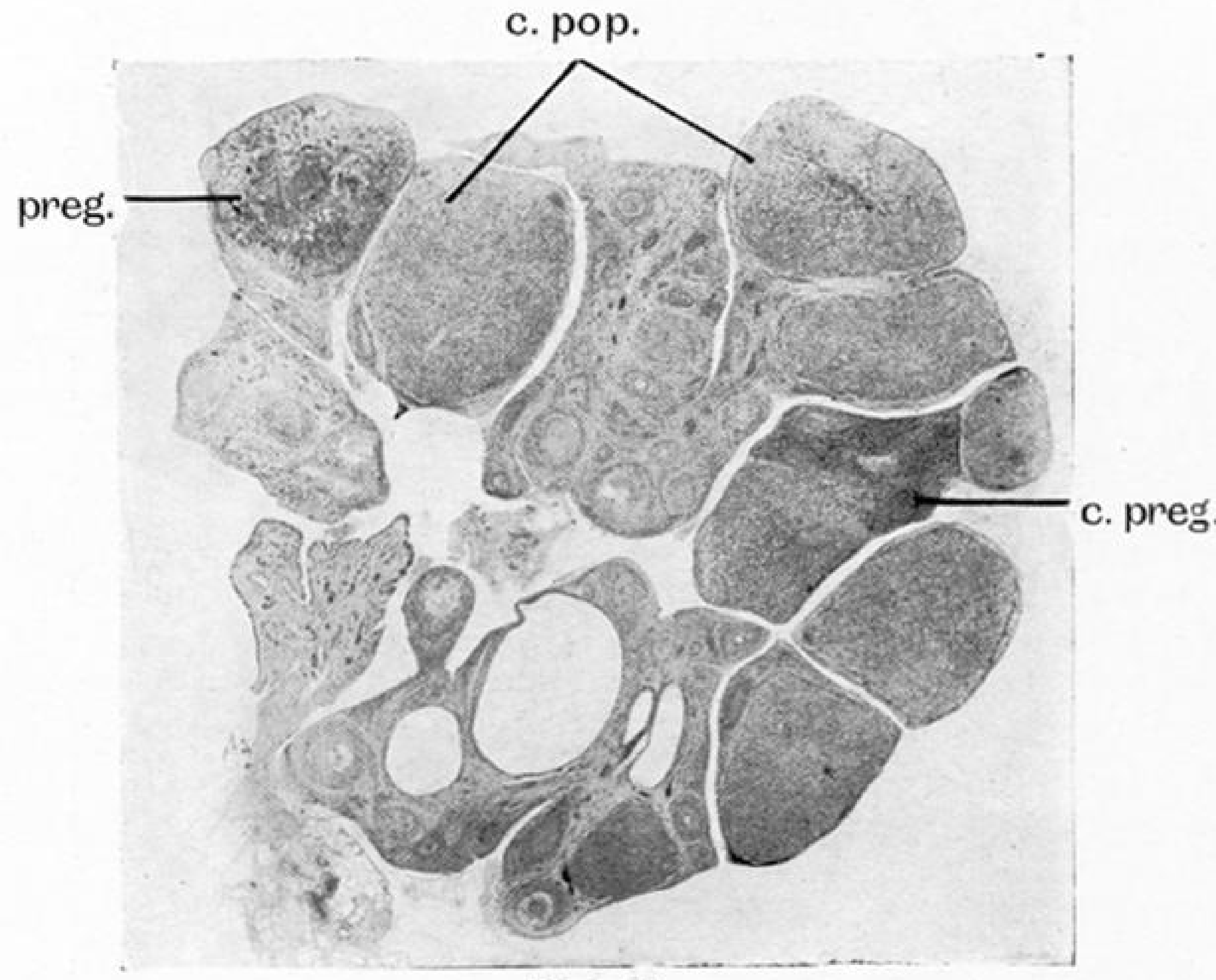

Fig. 7.

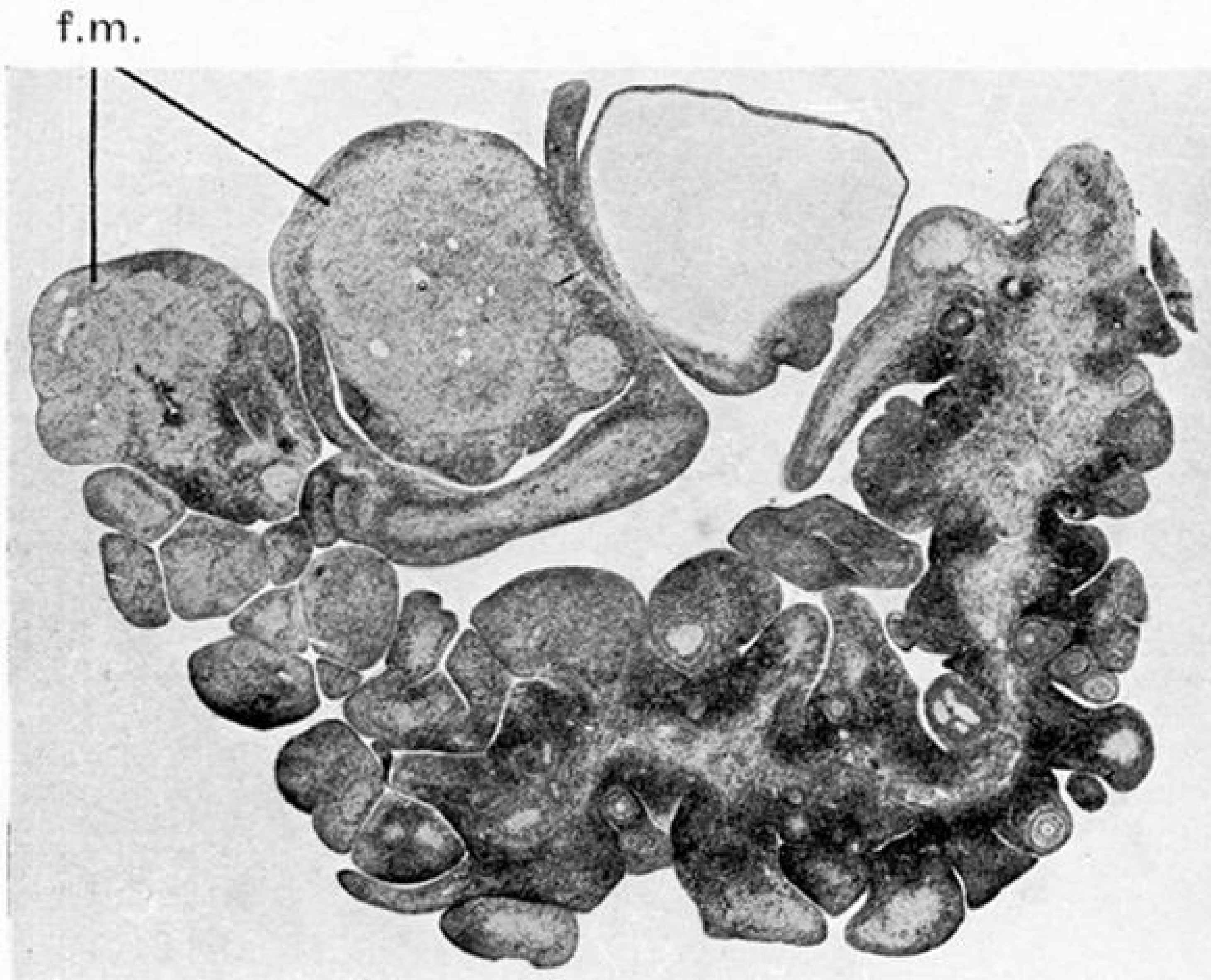

Fig. 9.

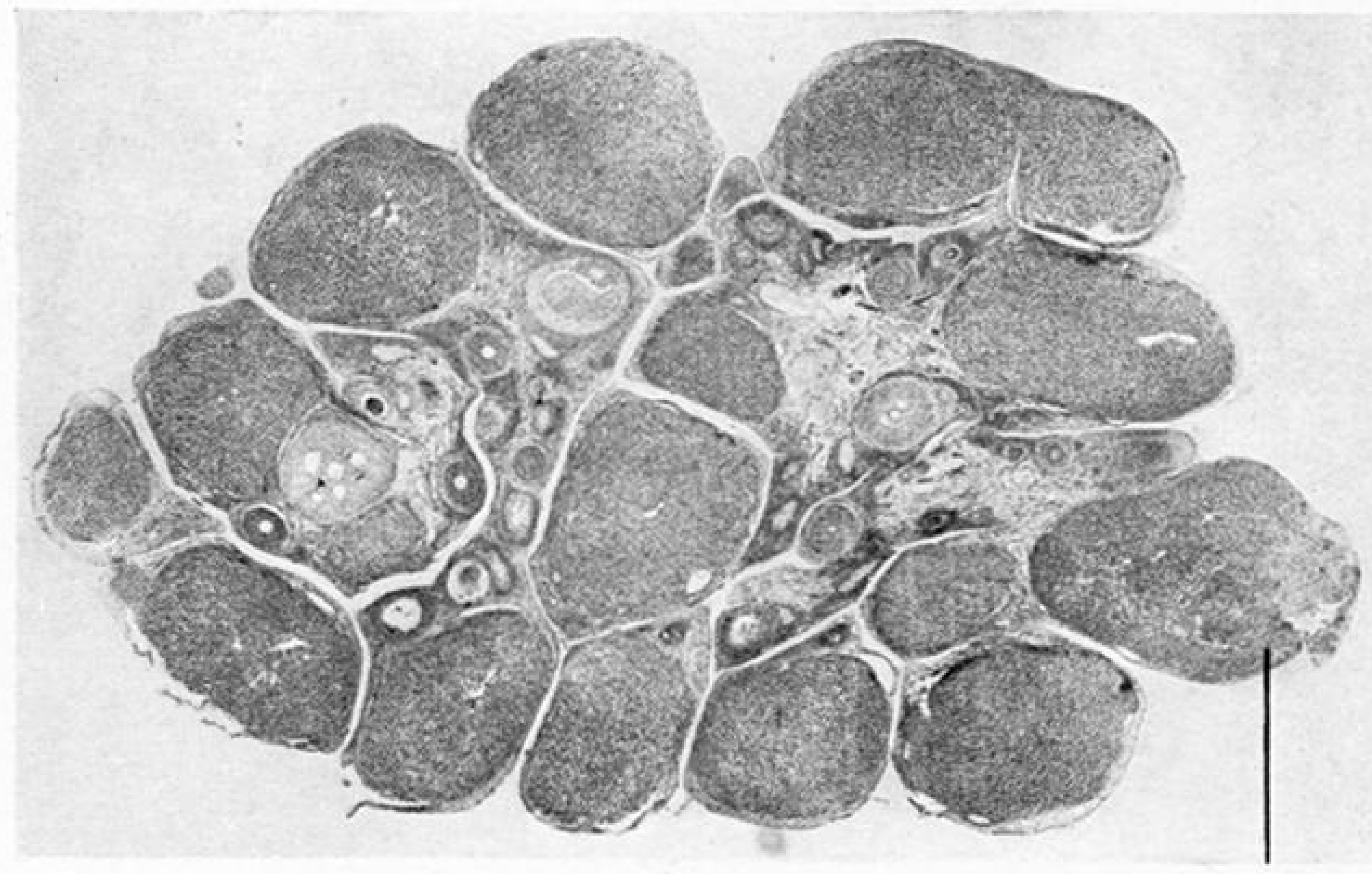

Fig. 8.

Fig. 11.

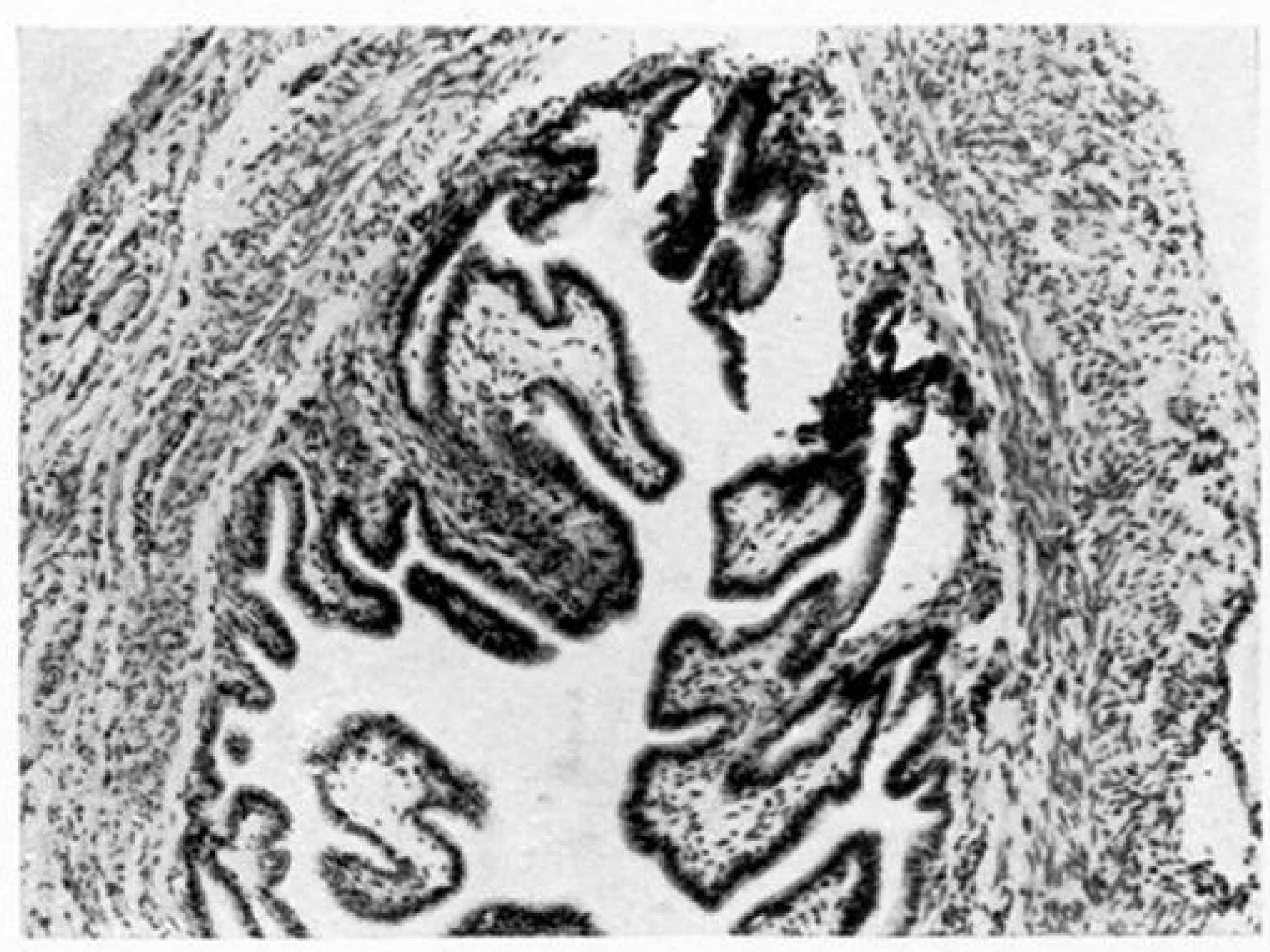

Fig. 10.

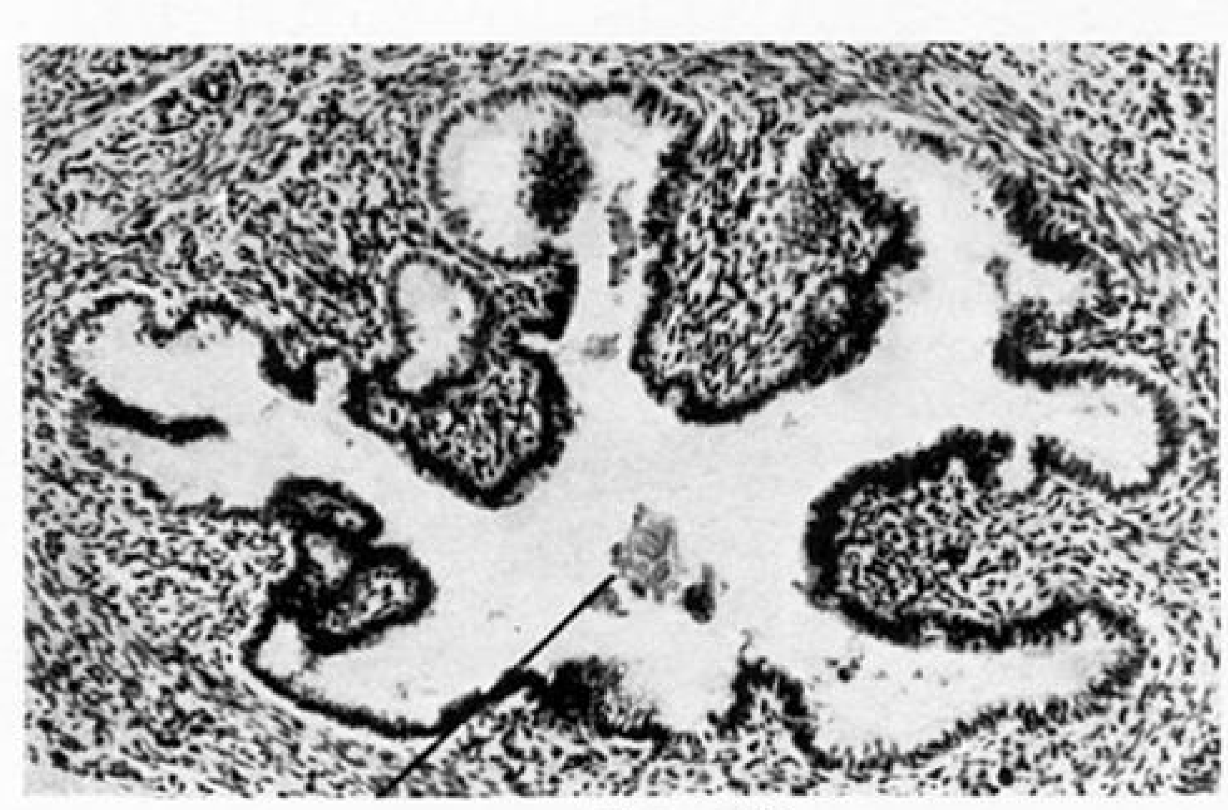

Fig. 12.

PLATE 28.

Ovary, × 12. Fallopian Tube, × 68.

FIG. 6.—No. 101. Ovary with recent and old corpora lutea of pseudo-pregnancy.

FIG. 7.—No. 264. Ovary with corpora lutea of pseudo-pregnancy and two developing corpora lutea of pregnancy, markedly congested.

FIG. 8.—No. 131. Ovary from second pregnancy, showing recent and old corpora lutea not very different in size.

FIG. 9.—No. 271. Anœstrous ovary (January), with fibrous remains of corpora lutea and large follicular masses.

FIG. 10.—No. 192. Fallopian tube in anœstrus.

FIG. 11.—No. 152. Fallopian tube with unfertilized ova and follicular epithelium.

FIG. 12.—No. 264. Fallopian tube with segmenting ovum.

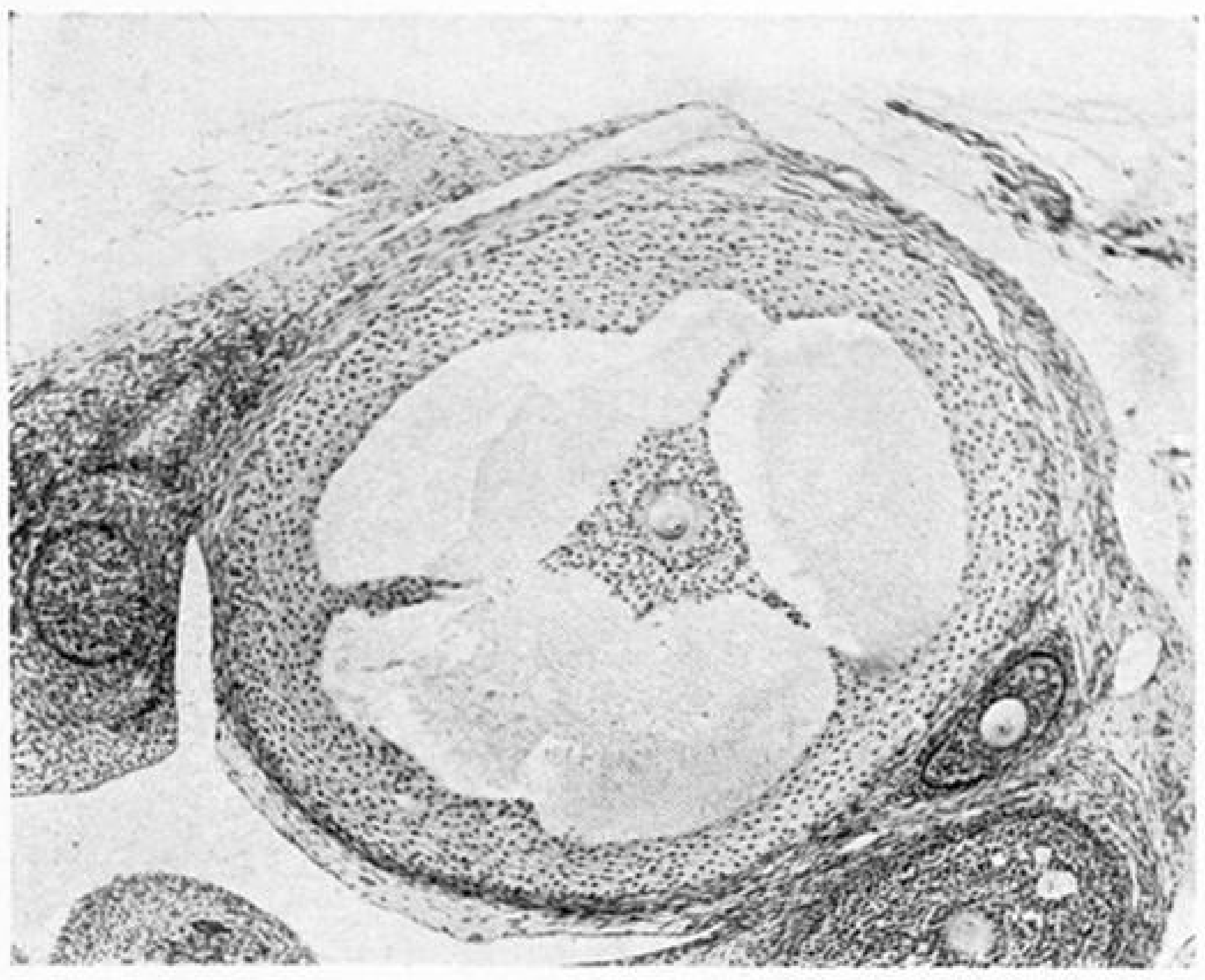

Fig. 13.

Fig. 15.

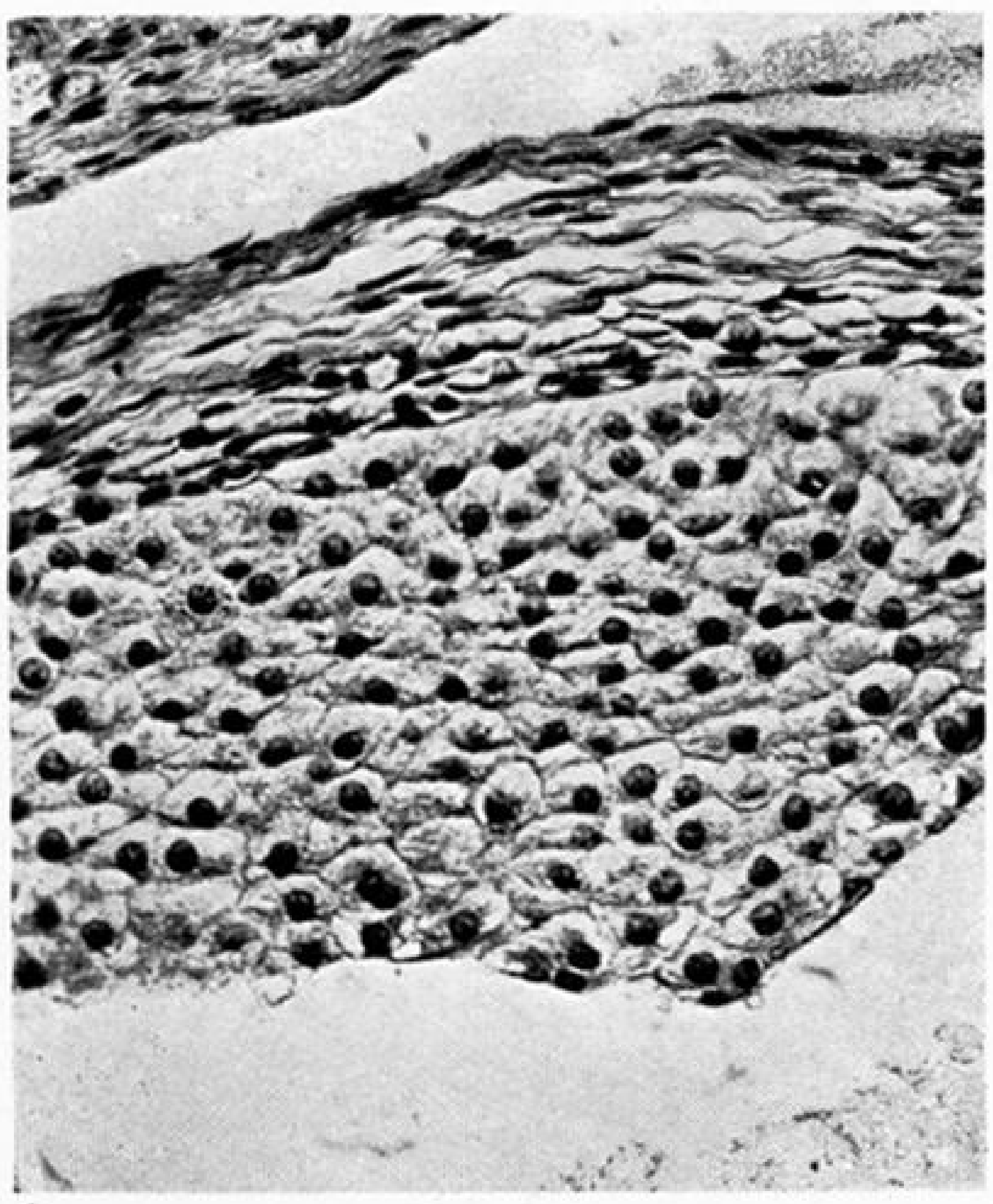

Fig. 18.

Fig. 14.

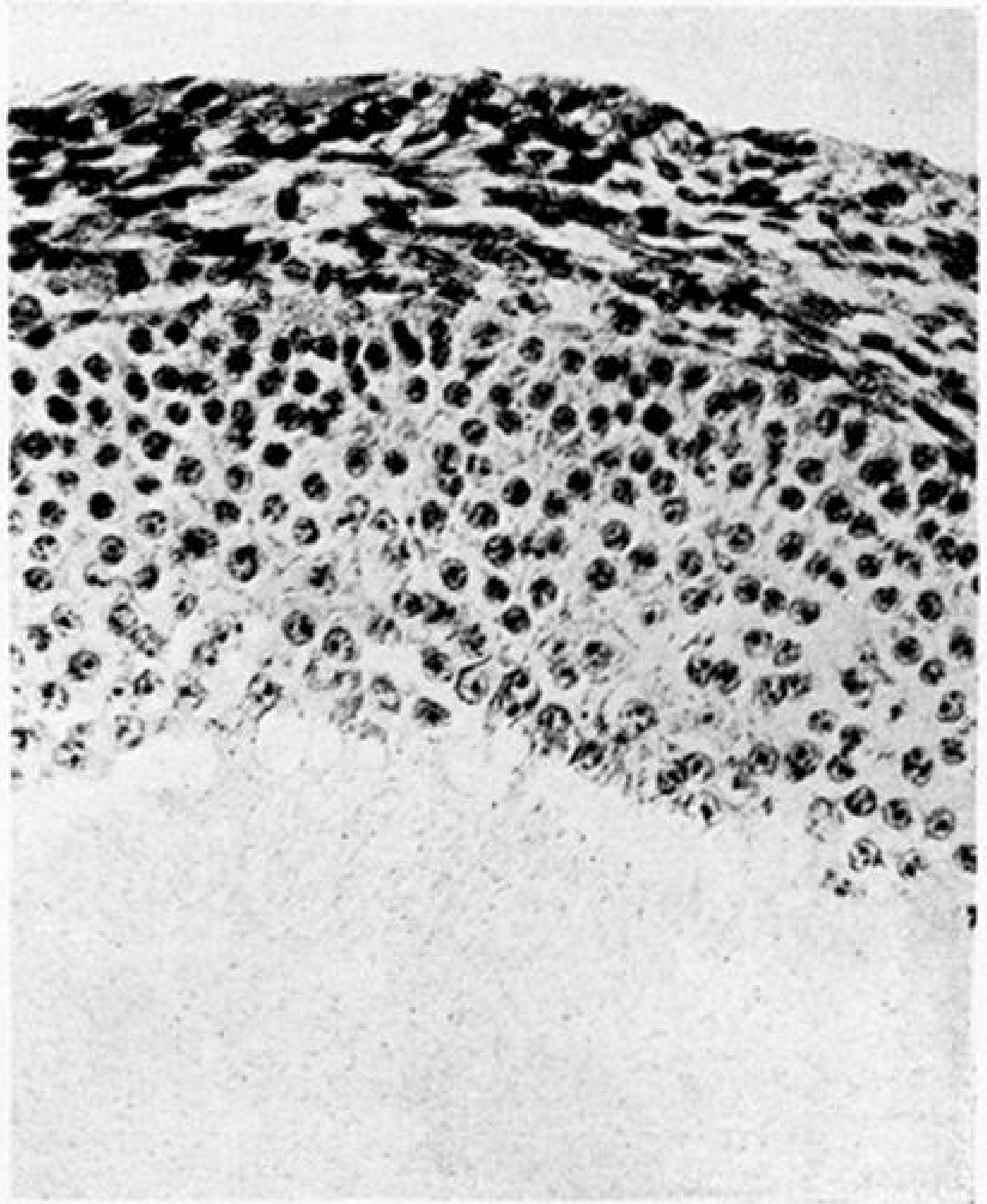

Fig. 17.

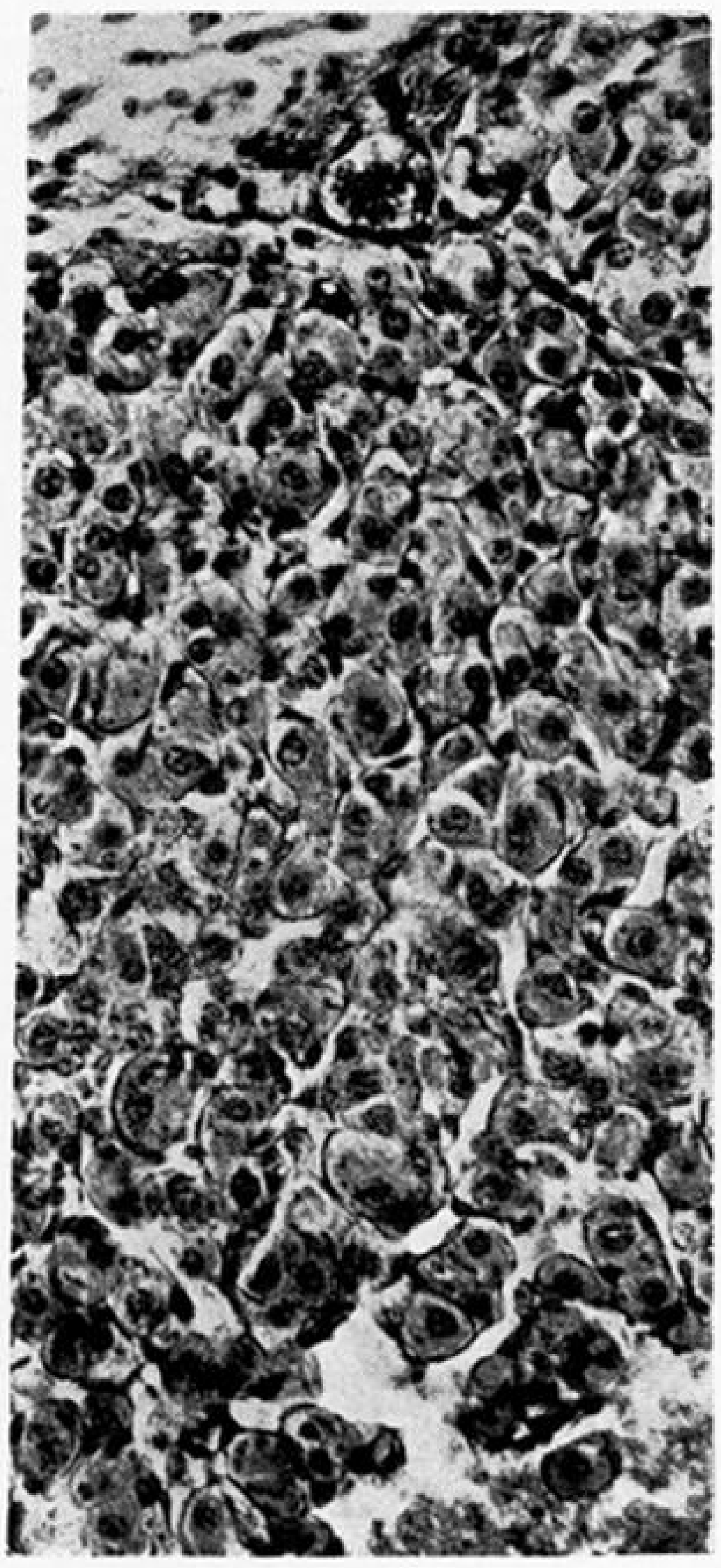

Fig. 20.

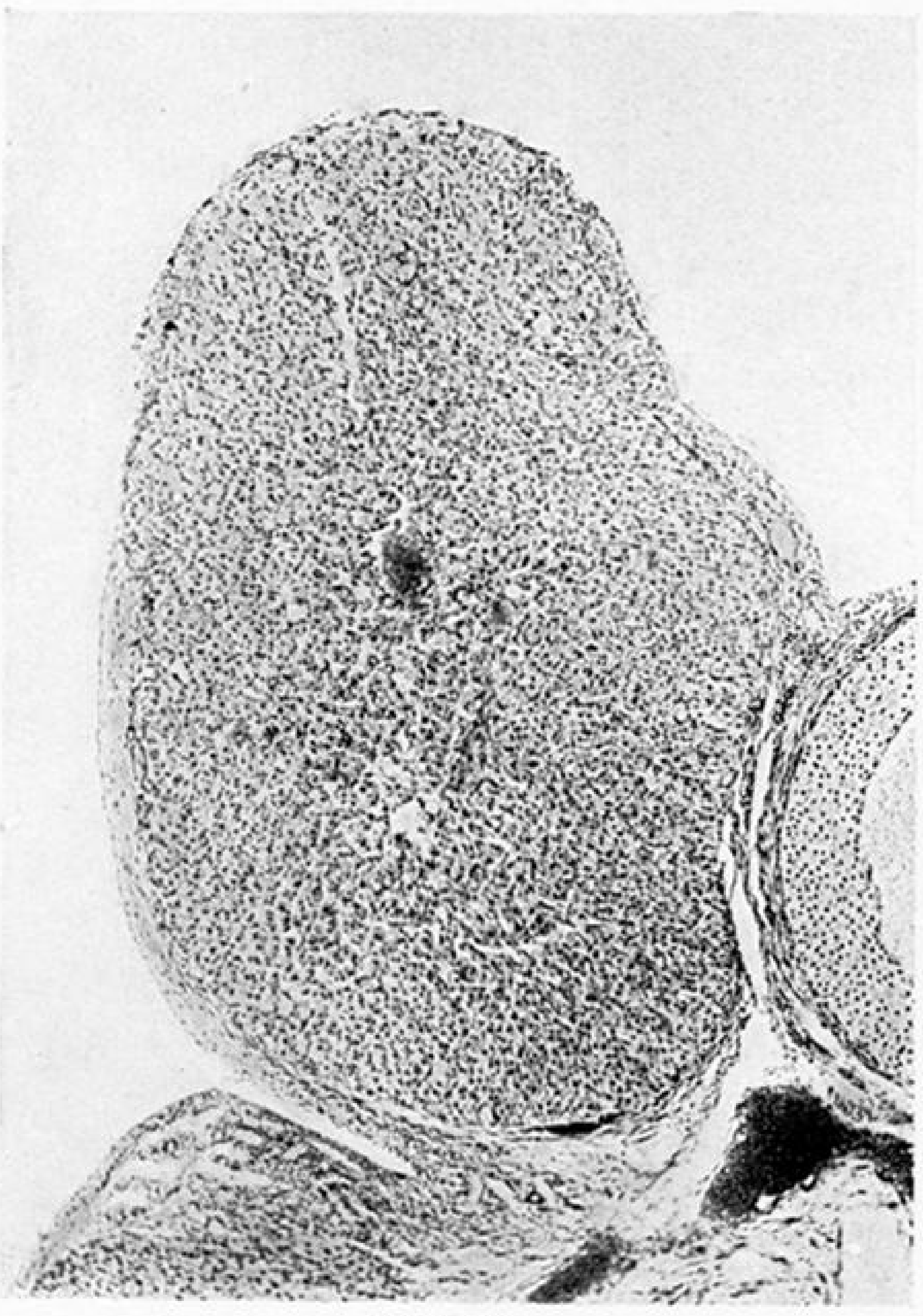

Fig. 16.

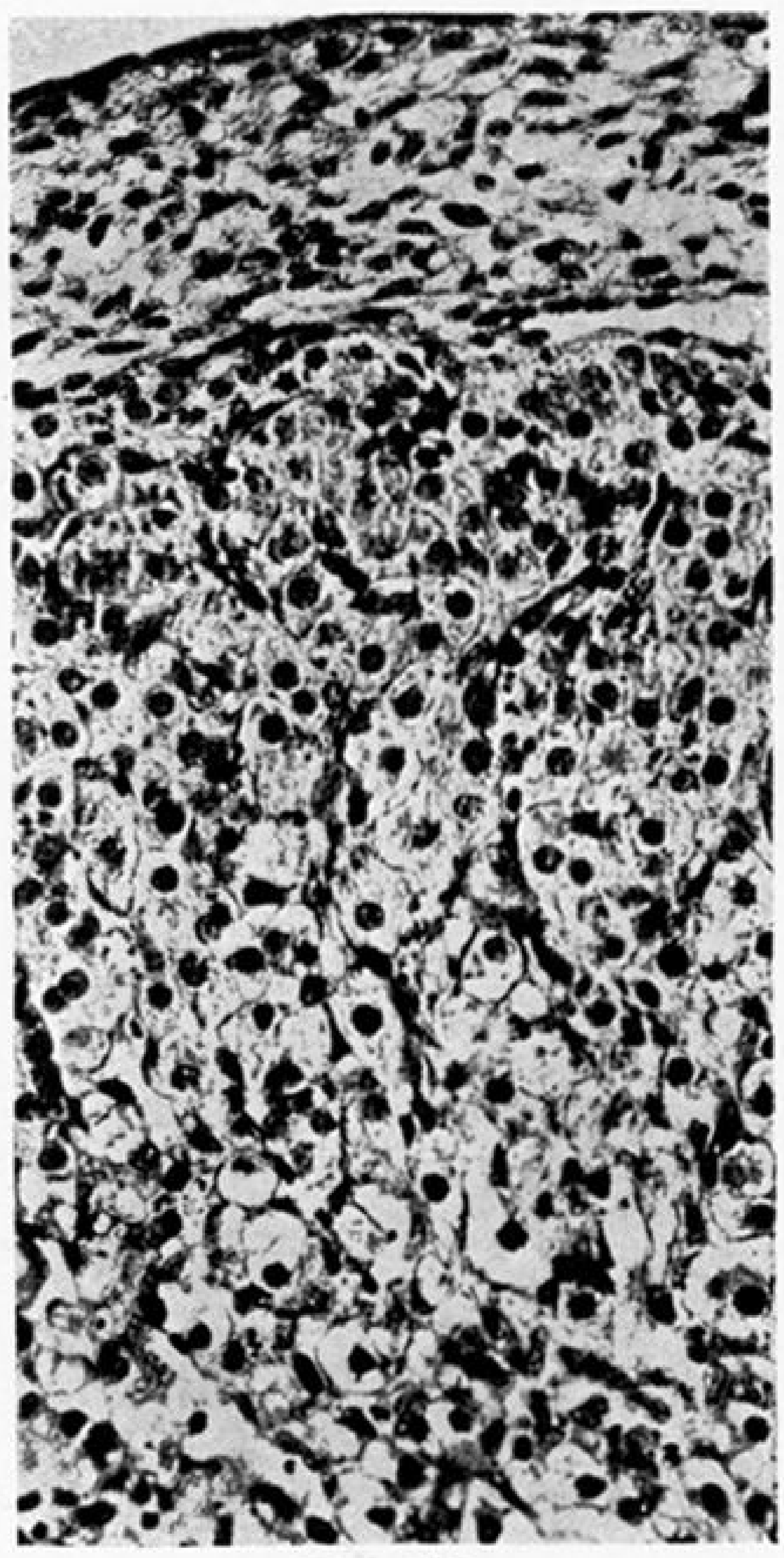

Fig. 19.

PLATE 29.

Follicles and corpora lutea.

FIG. 13.—No. 159. Œstrous follicle. × 45.

FIG. 14.—No. 152. Just ruptured follicle. × 45.

FIG. 15.—No. 126. Corpus luteum of ovulation with central blood clot. × 45.

FIG. 16.—No. 104. Corpus luteum of pregnancy. × 45.

FIG. 17.—No. 114. Part of a 0·74 mm. diameter follicle, showing enlargement of epithelial cells. × 183.

FIG. 18.—No. 159. Part of the œstrous follicle in fig. 13, showing theca and follicular epithelium. × 183.

FIG. 19.—No. 331. Part of a corpus luteum of ovulation. × 183.

FIG. 20.—No. 104. Part of a corpus luteum of pregnancy, fig. 16. × 183.

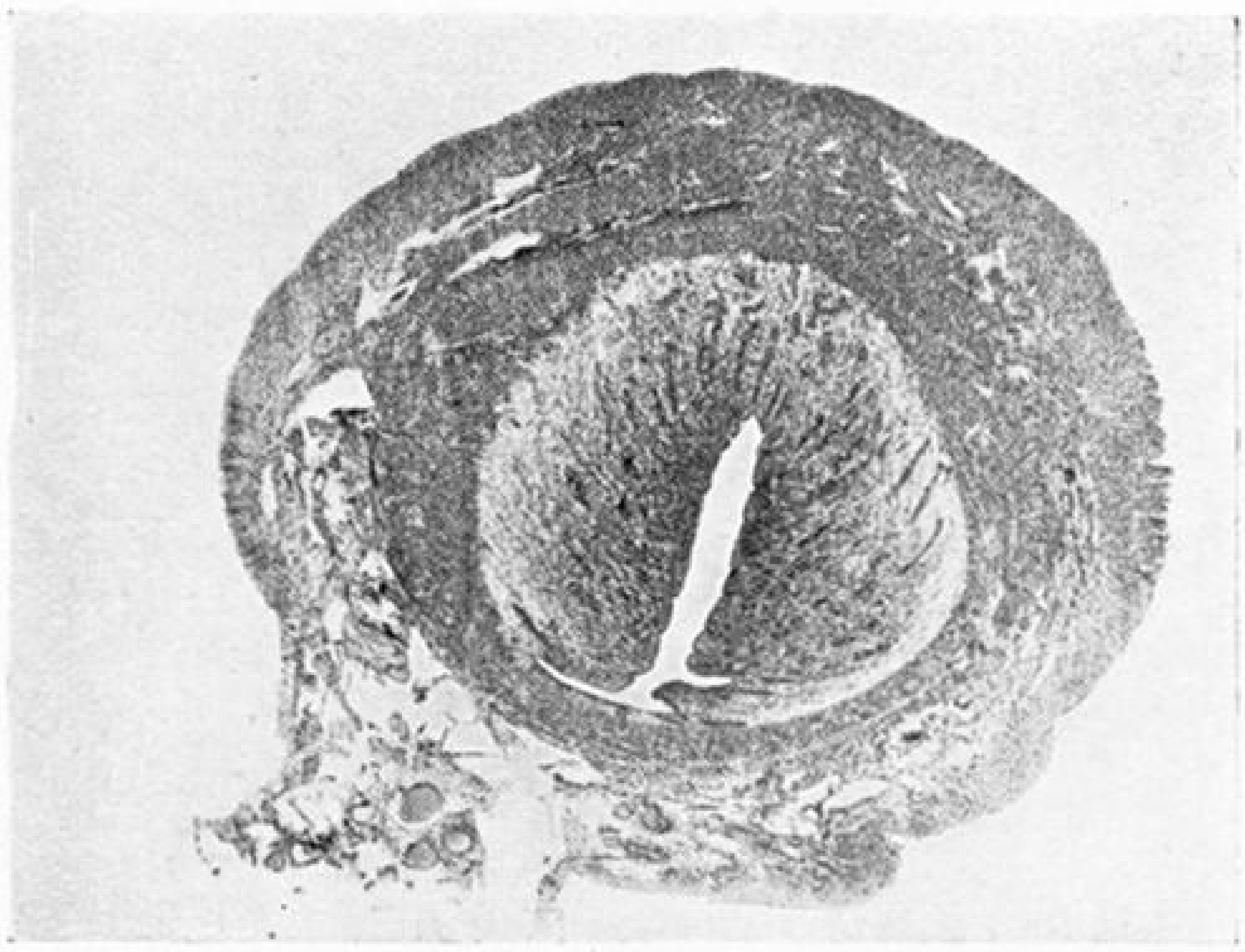

Fig. 21.

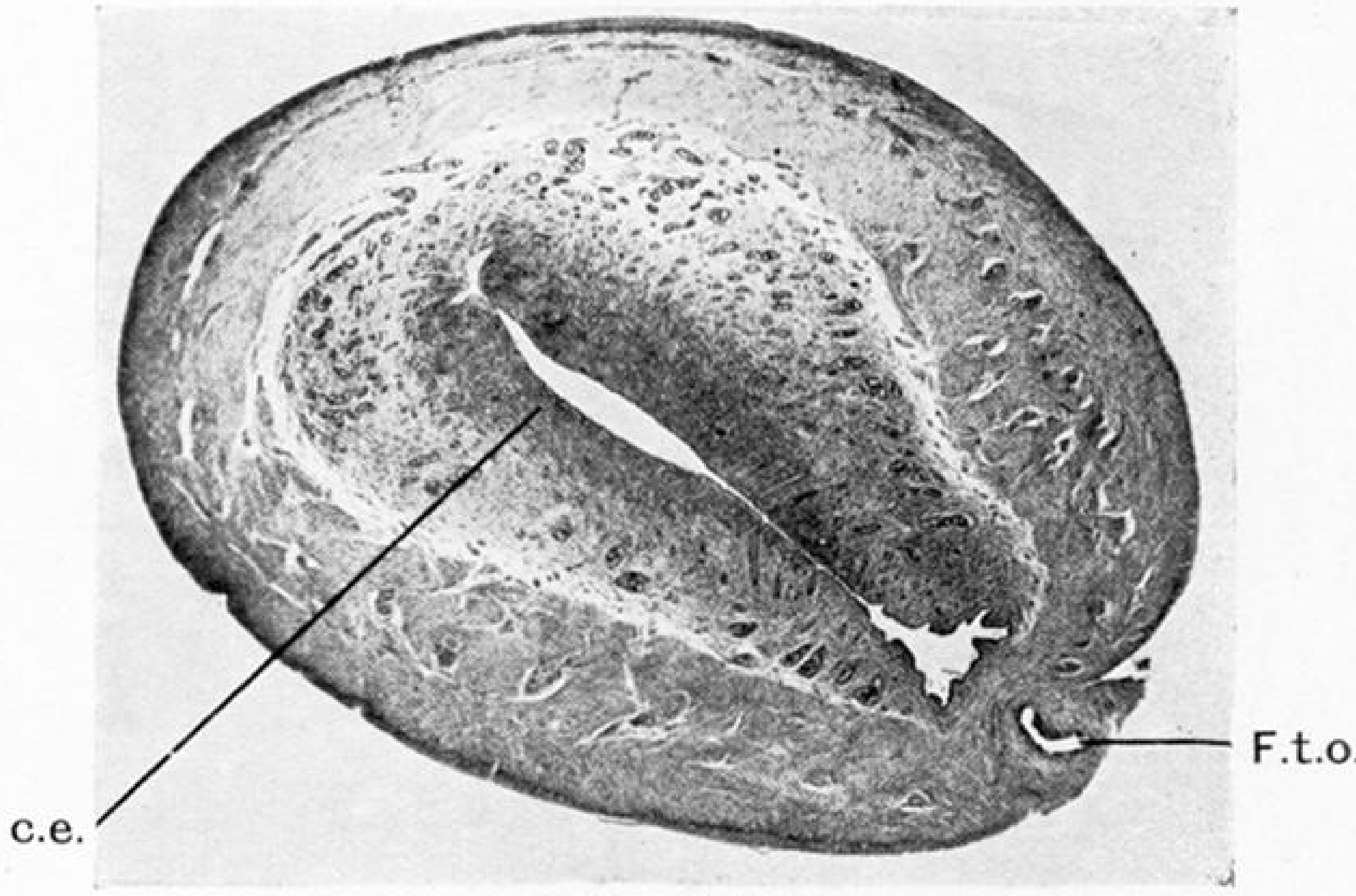

Fig. 24.

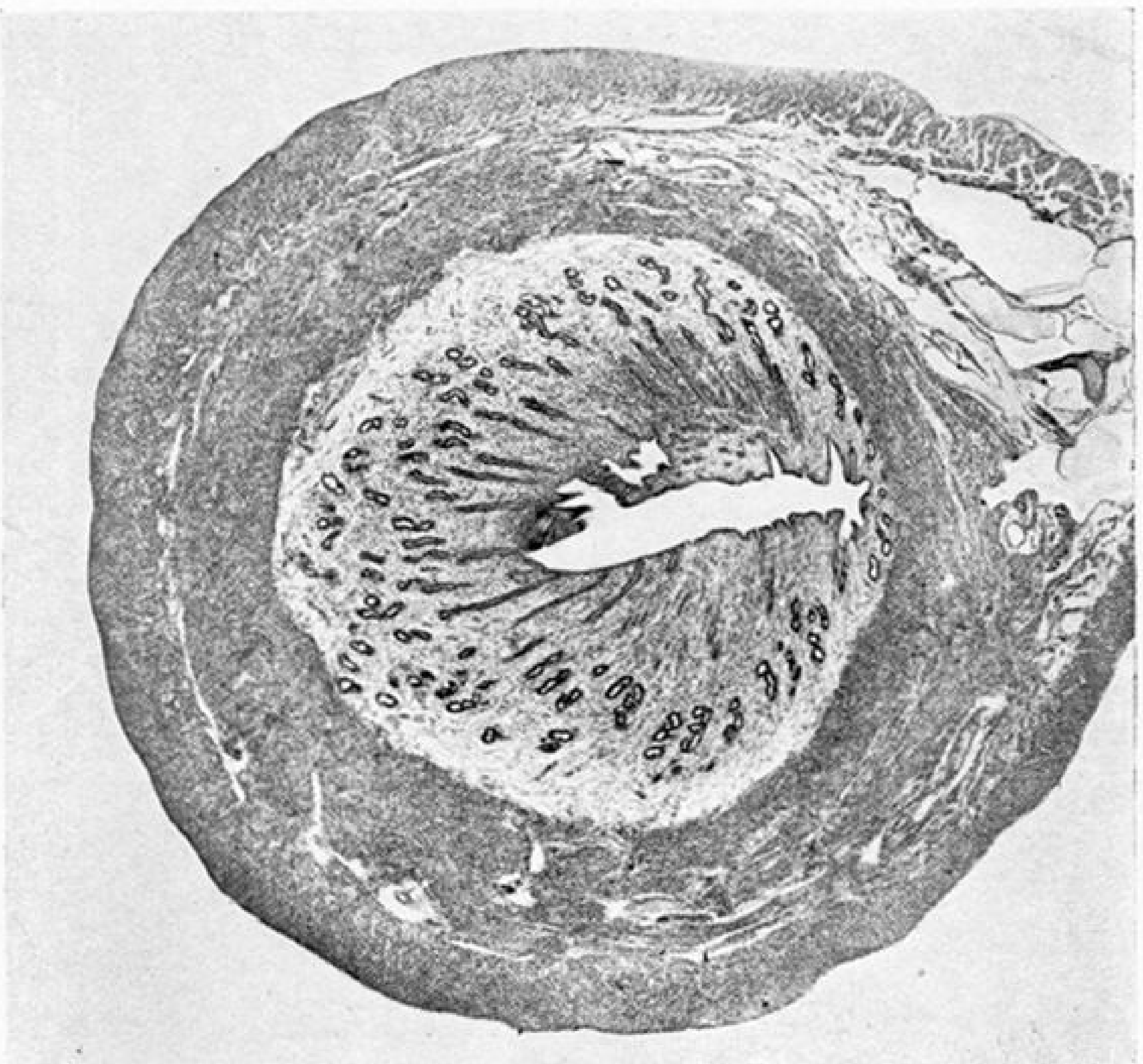

Fig. 22.

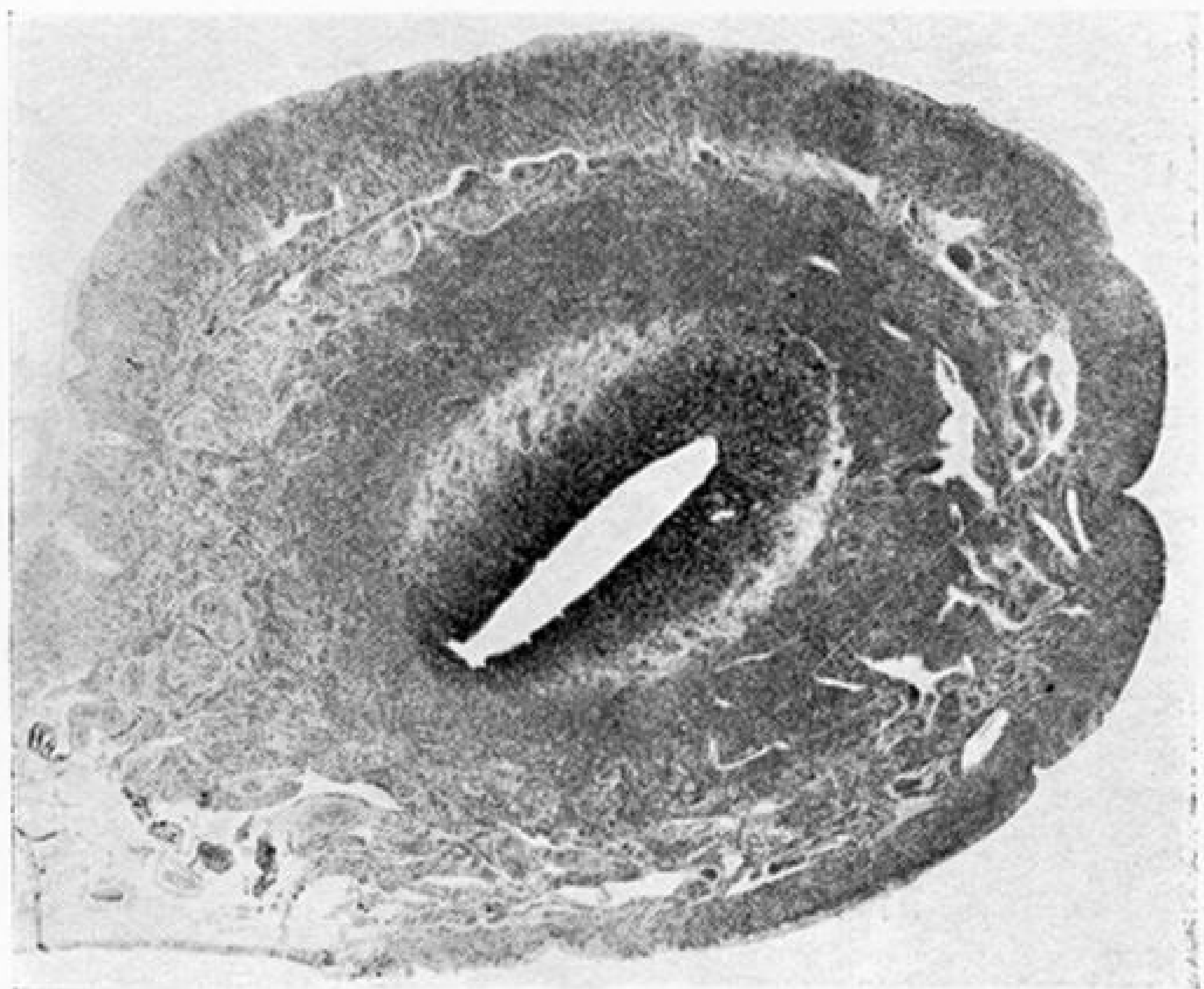

Fig. 26.

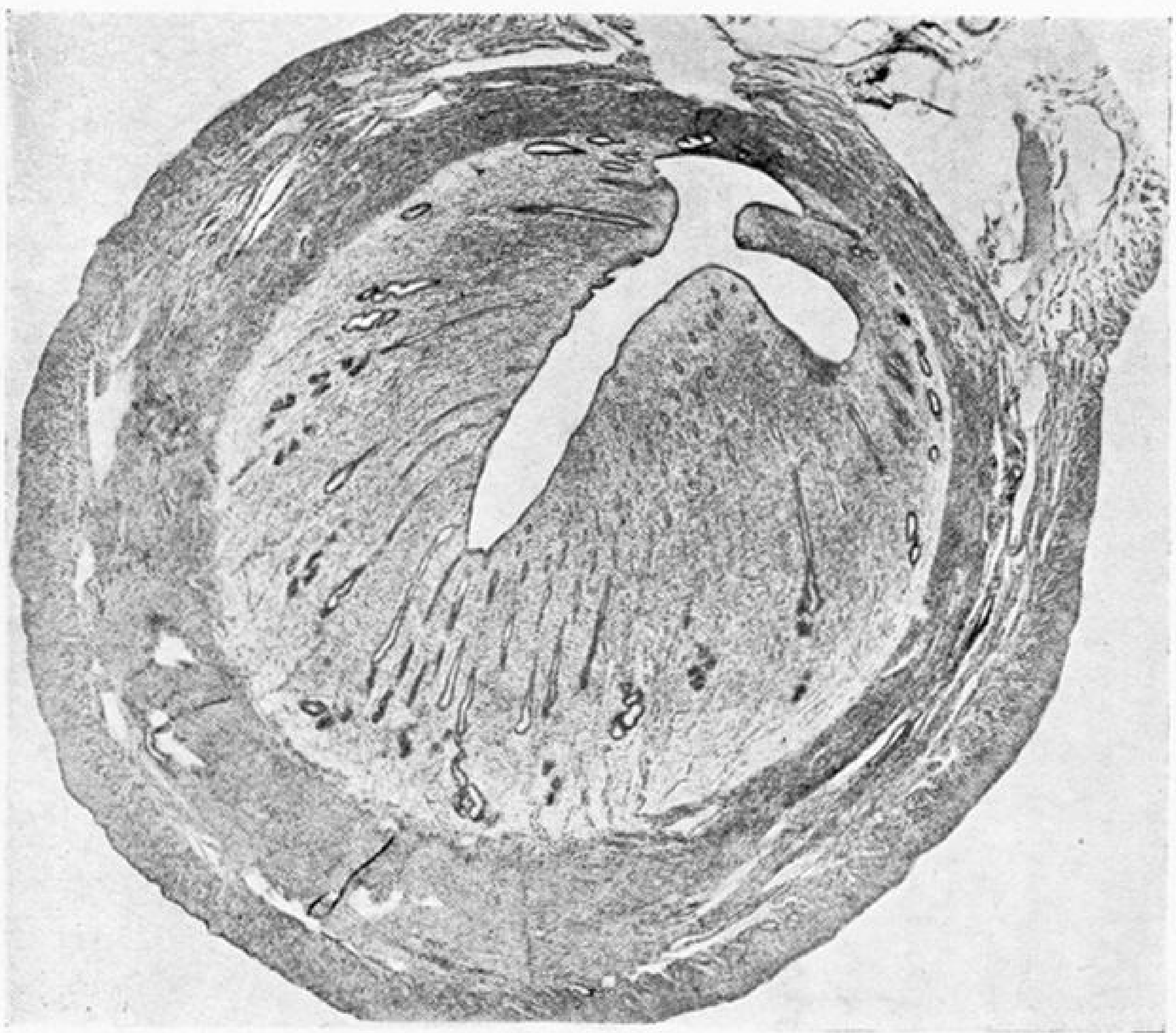

Fig. 23.

Fig. 25.

PLATE 30.

Uterus × 16 (except fig. 24 × 12).

FIG. 21.—No. 169. Prepubertal uterus (0·14 gm.) in September.

FIG. 22.—No. 153. Prepubertal uterus in May (0·35 gm.), fresh glands fully developed.

FIG. 23.—No. 163. Non-parous uterus (0·53 gm.) in first pseudo-pregnancy cycle. Spermatozoa in the glands. Sub-epithelial tissue slightly œdematous.

FIG. 24.—No. 264. Section showing the tubal opening and progestational congestion, fig. 36.

FIG. 25.—No. 136. Lactation uterus (0·71 gm.).

FIG. 26.—No. 272. Anœstrous parous uterus (0·42 gm.) in January.

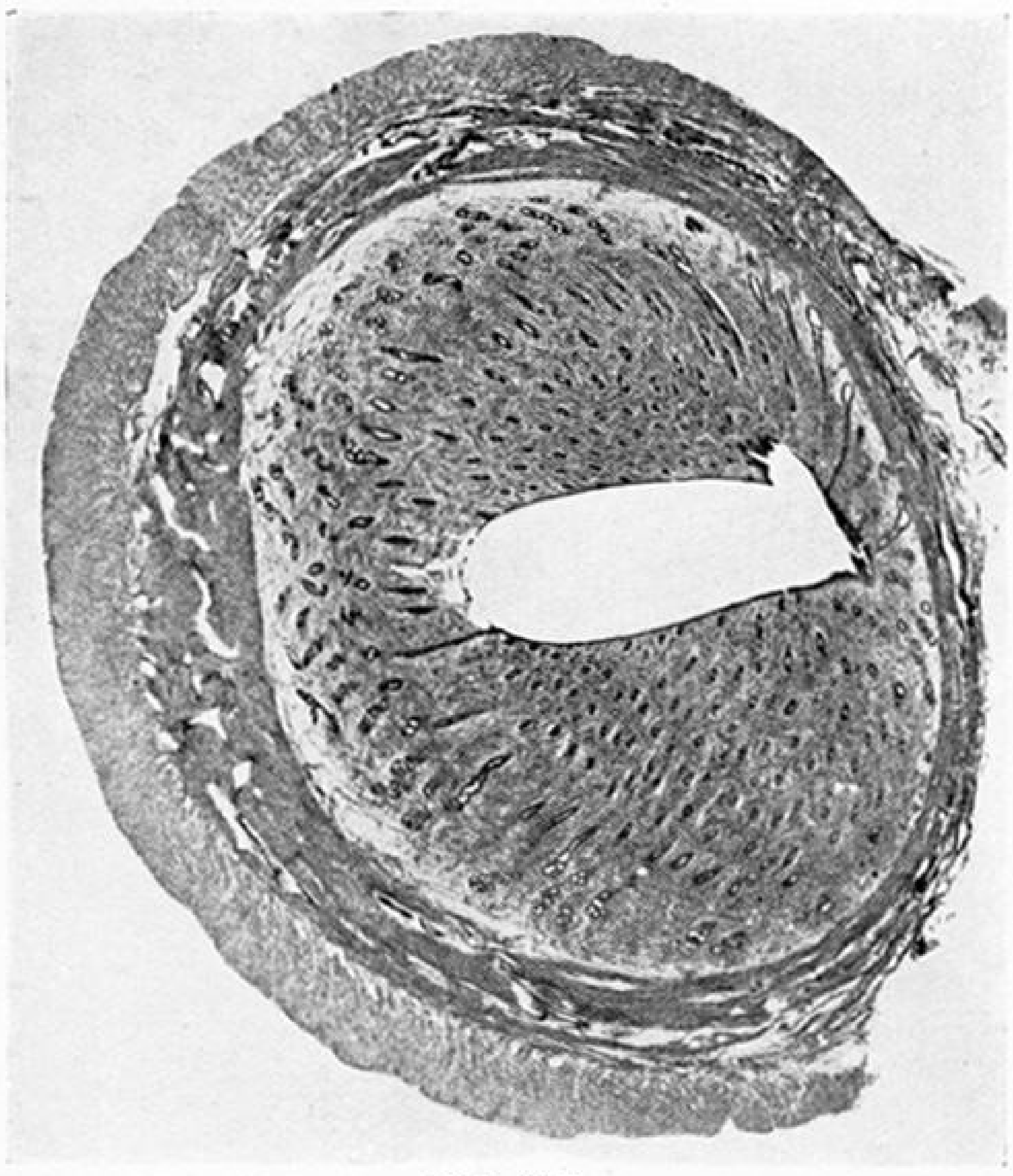

Fig. 27.

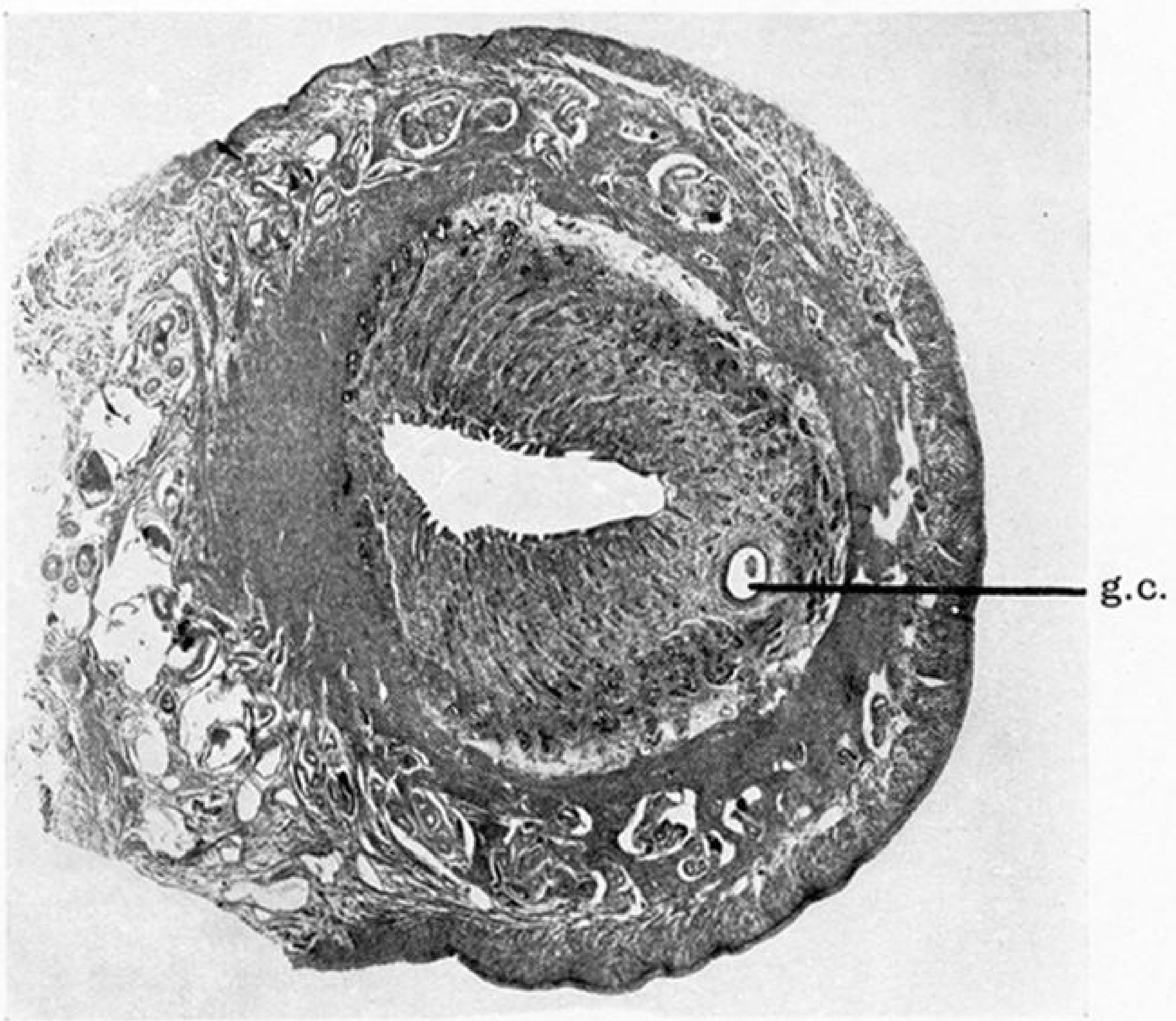

Fig. 30.

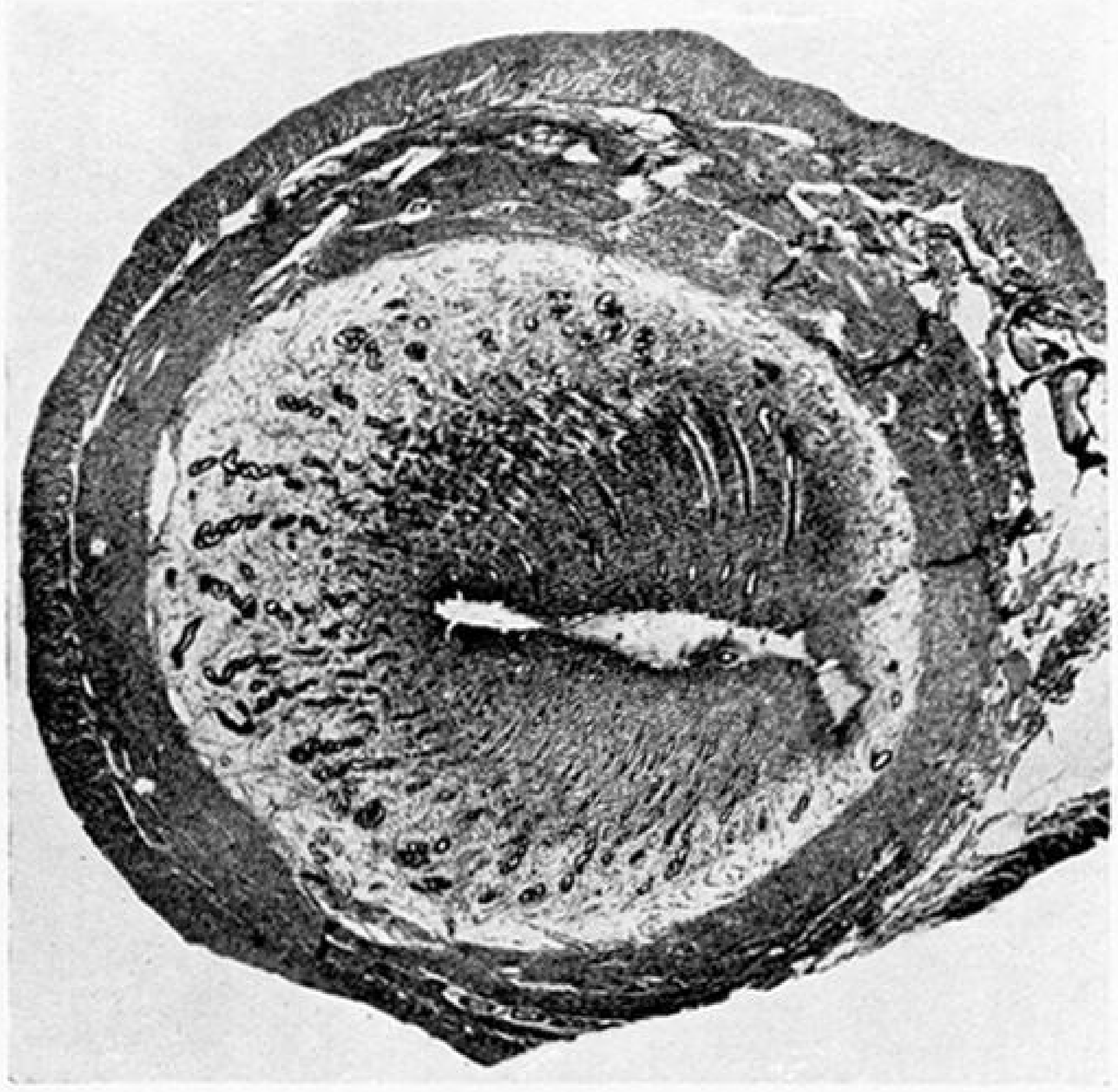

Fig. 28.

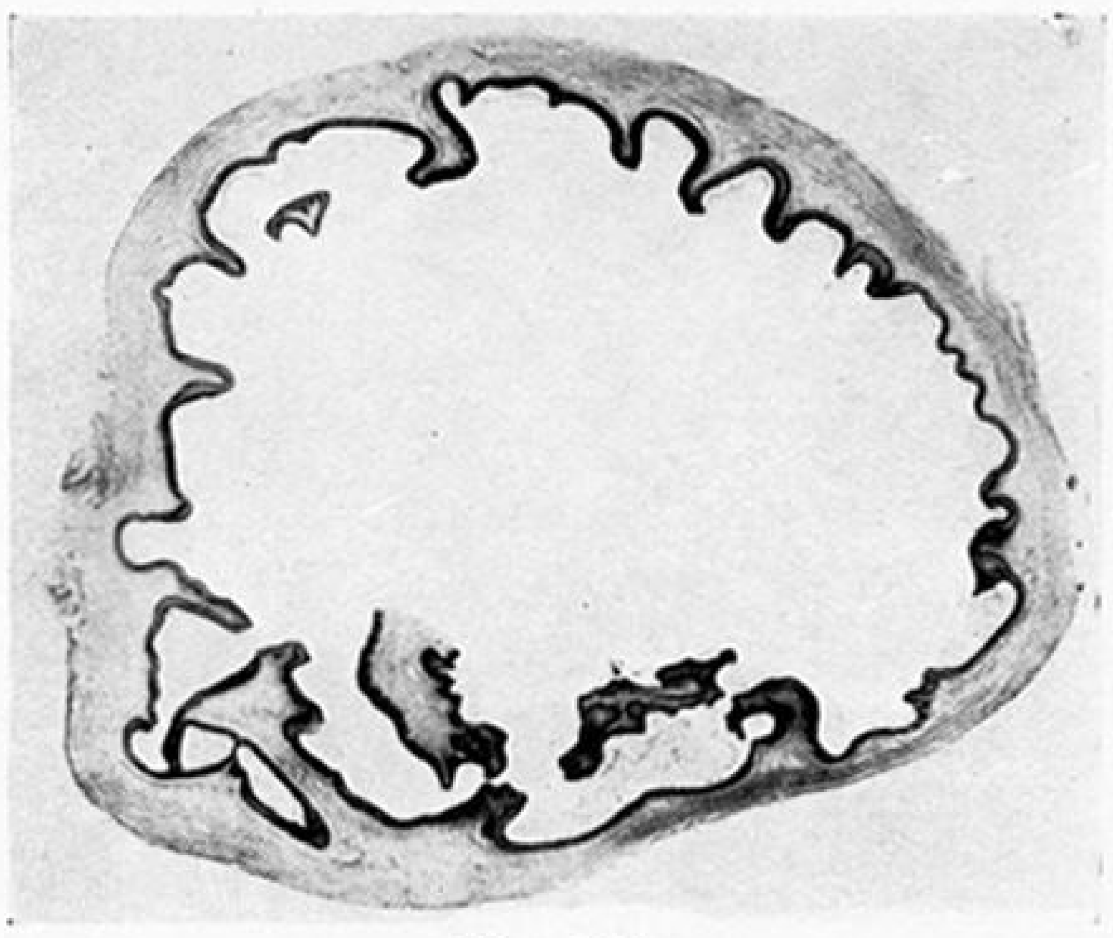

Fig. 31.

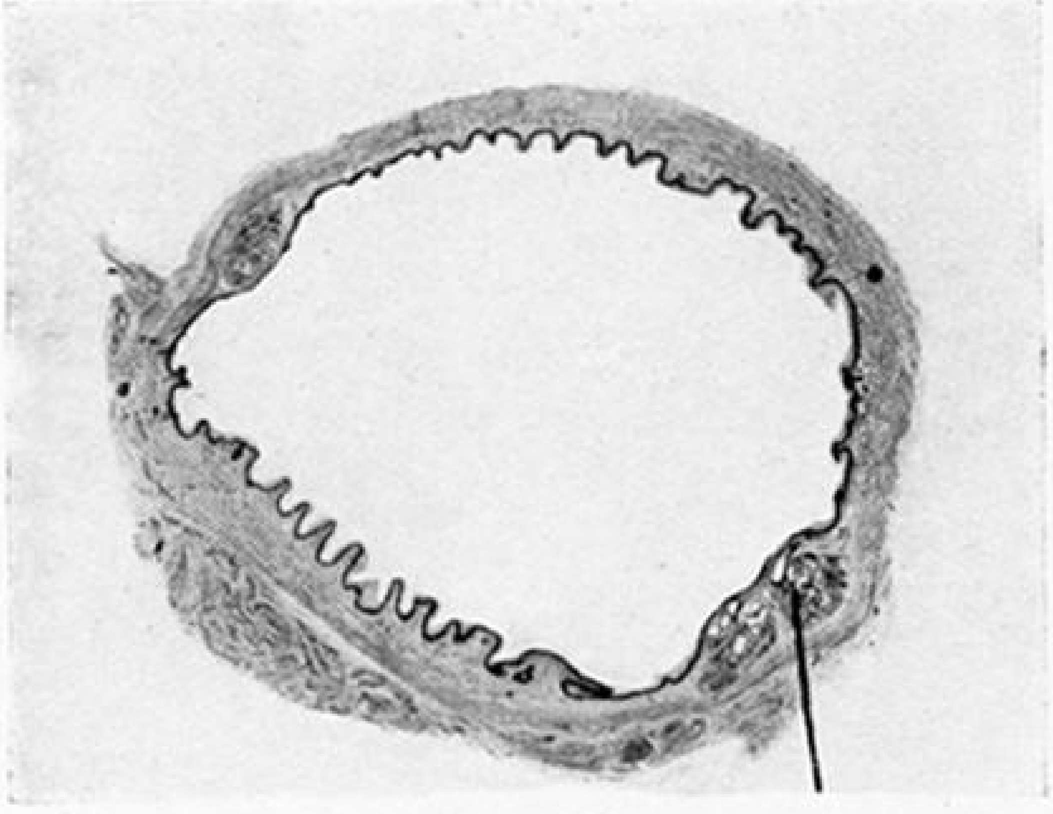

Fig. 32. uv.g.

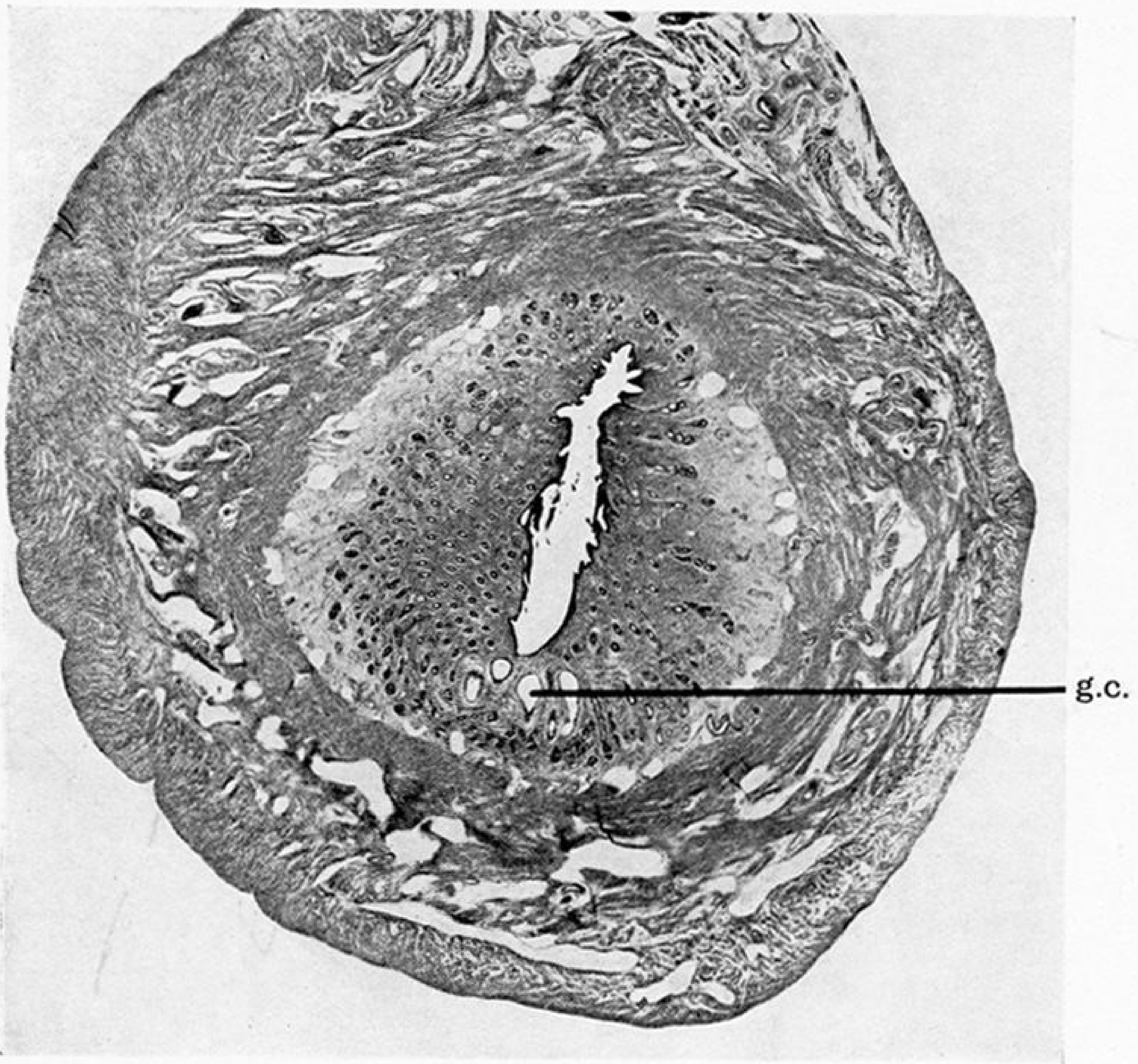

Fig. 29.

Fig. 33.

PLATE 31.

Uterus × 11. Vagina × 2·8.

FIG. 27.—No. 99. Non-parous uterus of hedgehog which has just mated and ovulated at the end of pseudo-pregnancy.

FIG. 28.—No. 104. Early implantation stage in non-parous uterus, *cf.*, fig. 37.

FIG. 29.—No. 125. Uterus (2·1 gm.) which has not involuted after parturition. No. 125 had ruptured follicles and uterine spermatozoa, like No. 99 (fig. 27).

FIG. 30.—No. 129. Pseudo-pregnant uterus (1·65 gm.) which has recovered from lactation involution. The uterine mucosa is "notched."

FIG. 31.—No. 162. Upper vagina just after ovulation in an unmated animal.

FIG. 32.—No. 132. Upper vagina in pseudo-pregnancy, following lactation, showing upper vaginal glands.

FIG. 33.—No. 192. Upper vagina in lactation anœstrus.

Fig. 34.

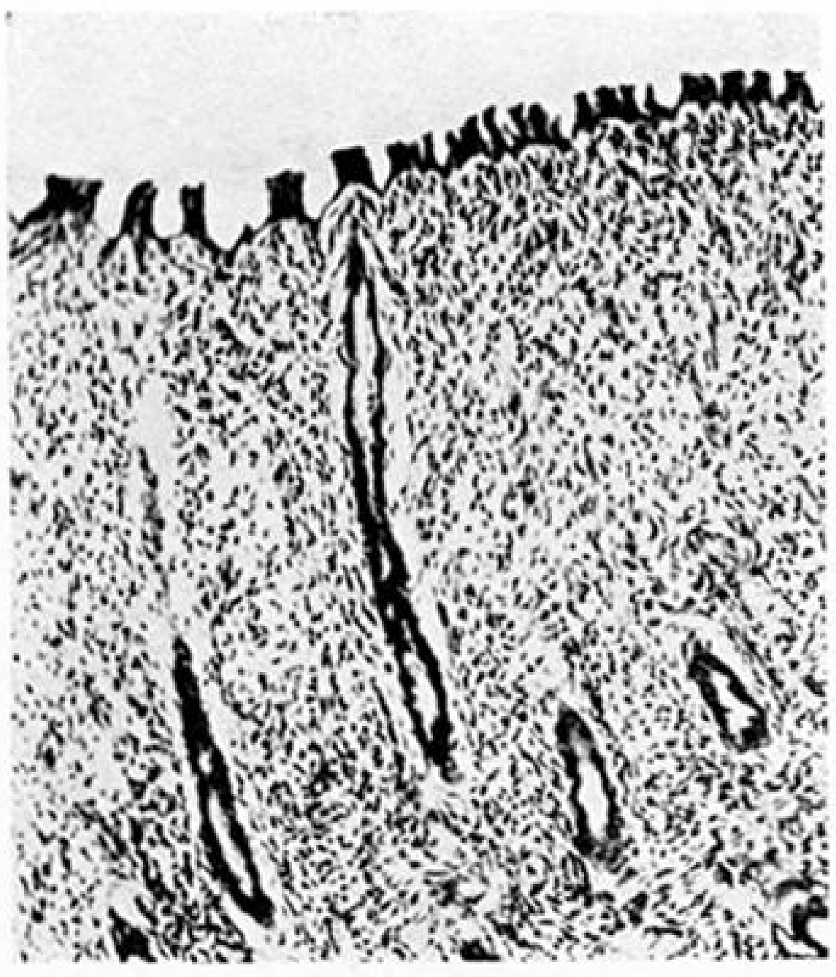

Fig. 35.

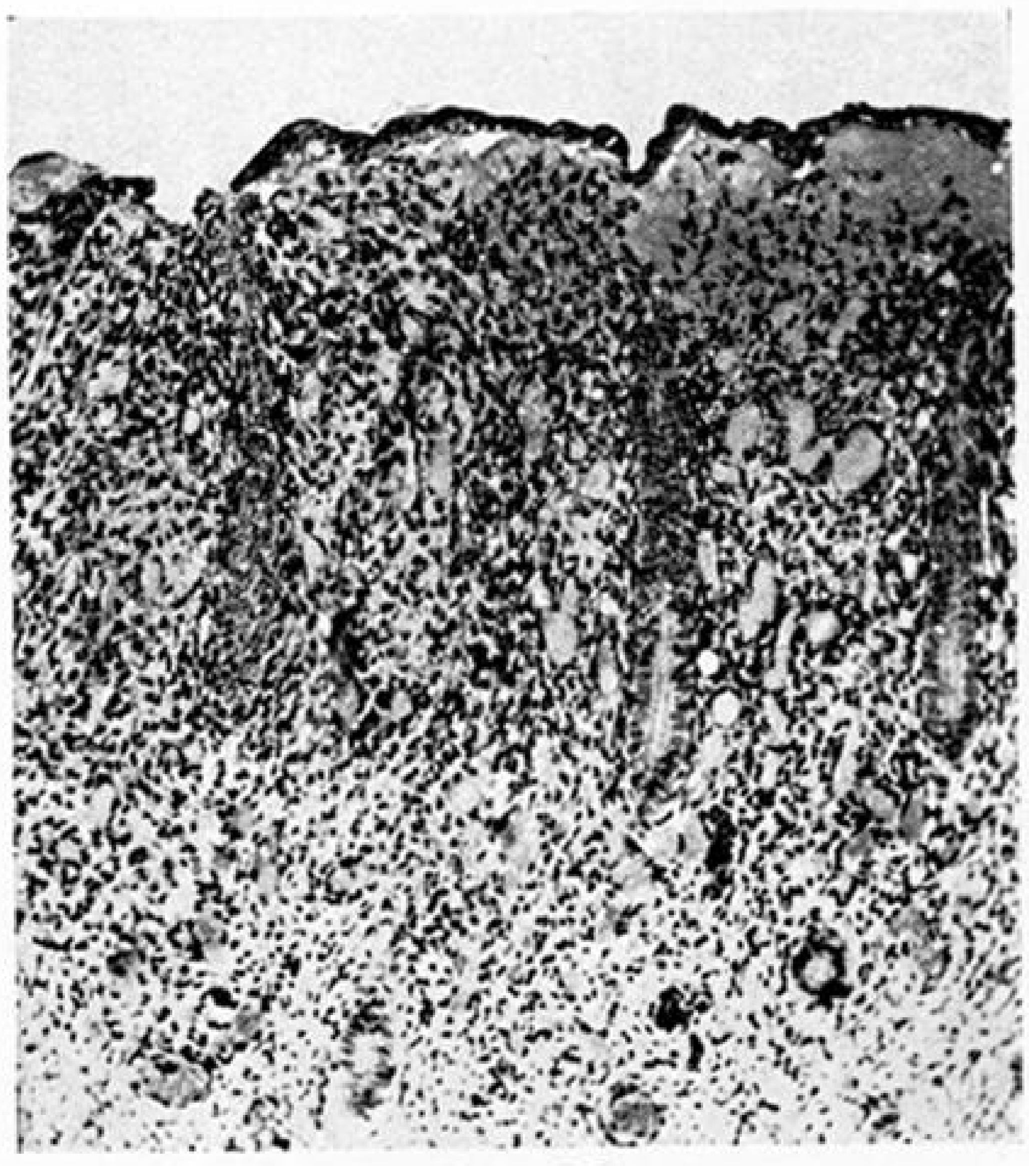

Fig. 36.

Fig. 37.

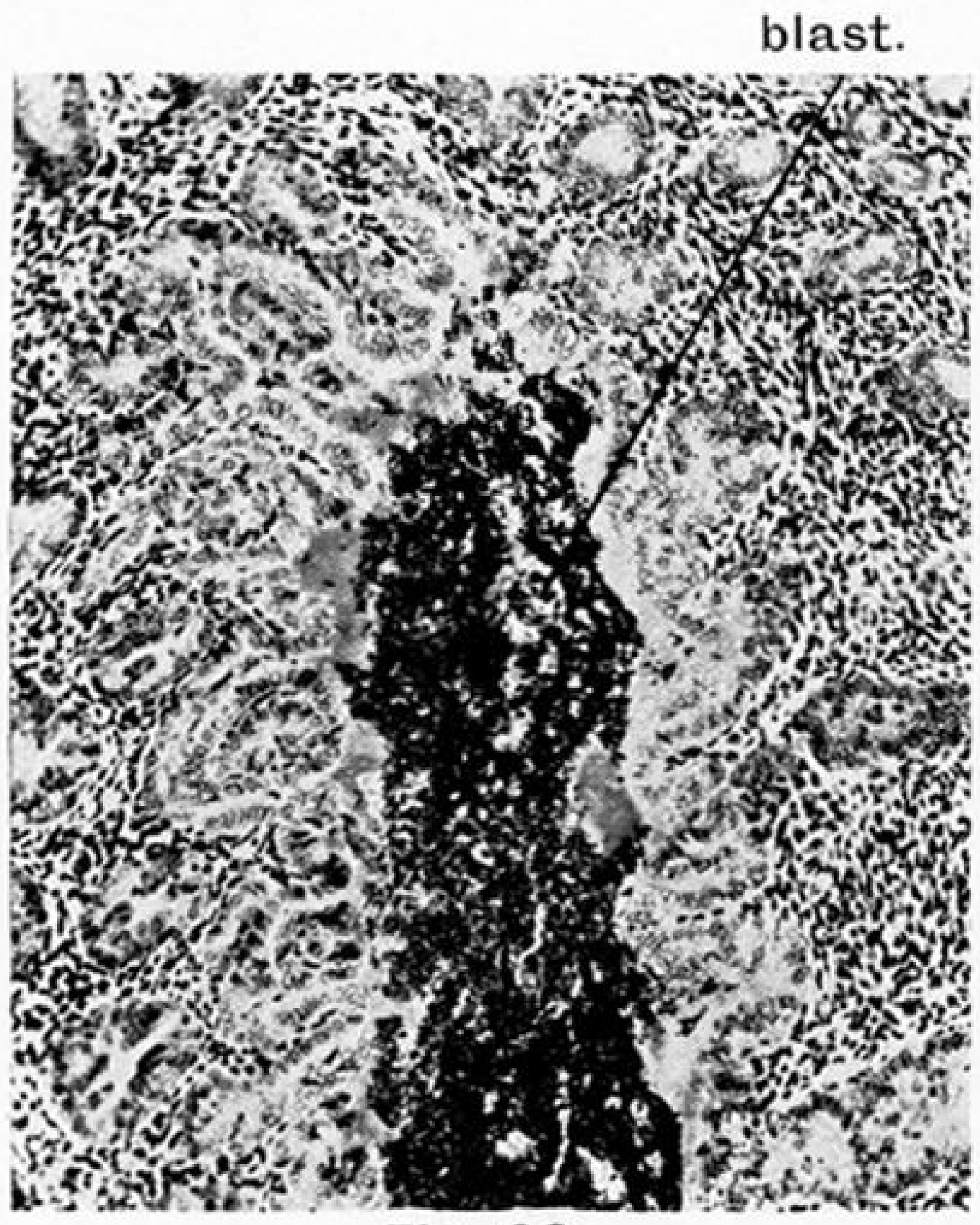

Fig. 38.

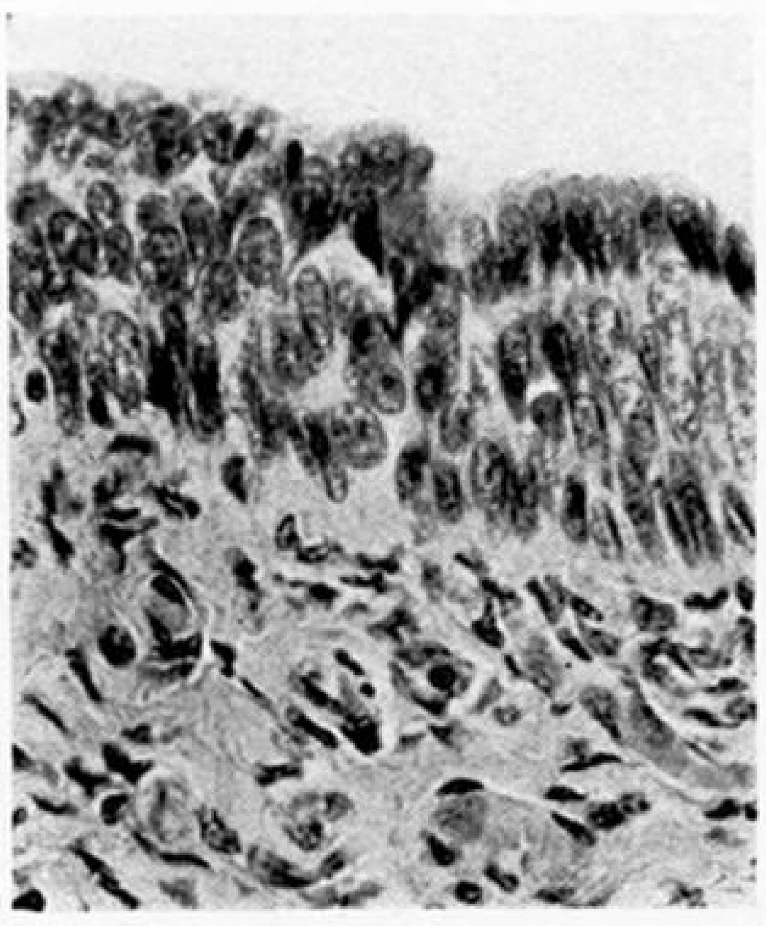

Fig. 39.

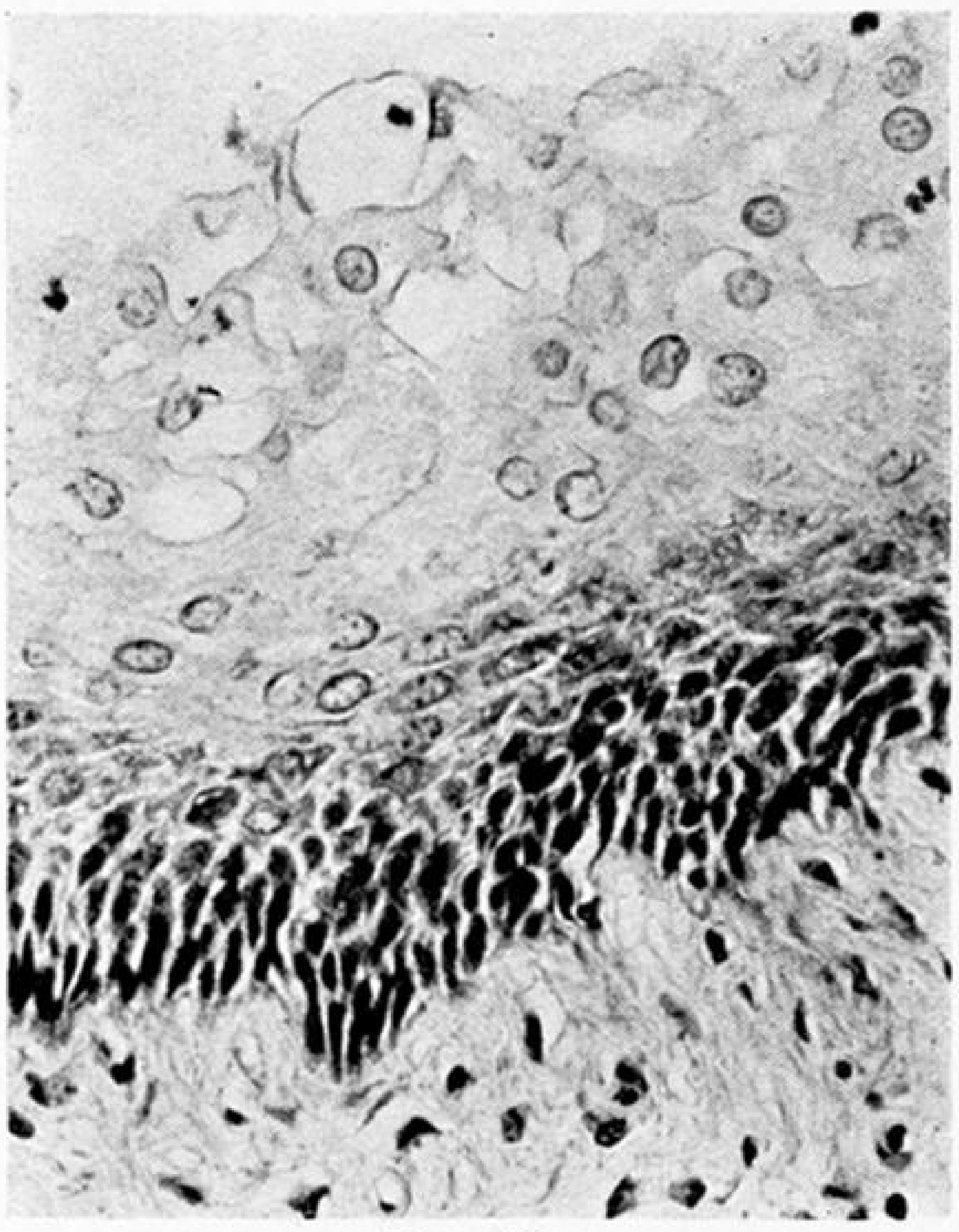

Fig. 42.

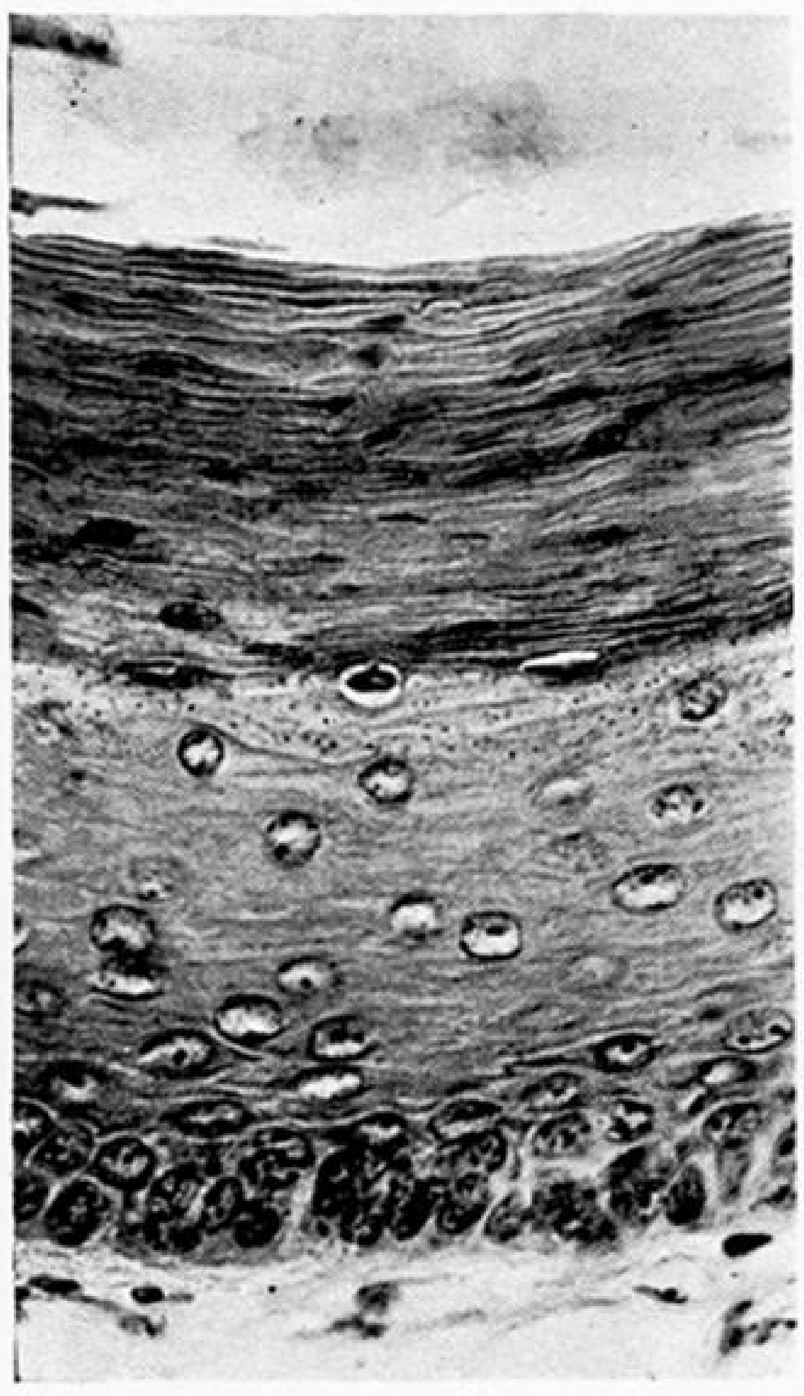

Fig. 40.

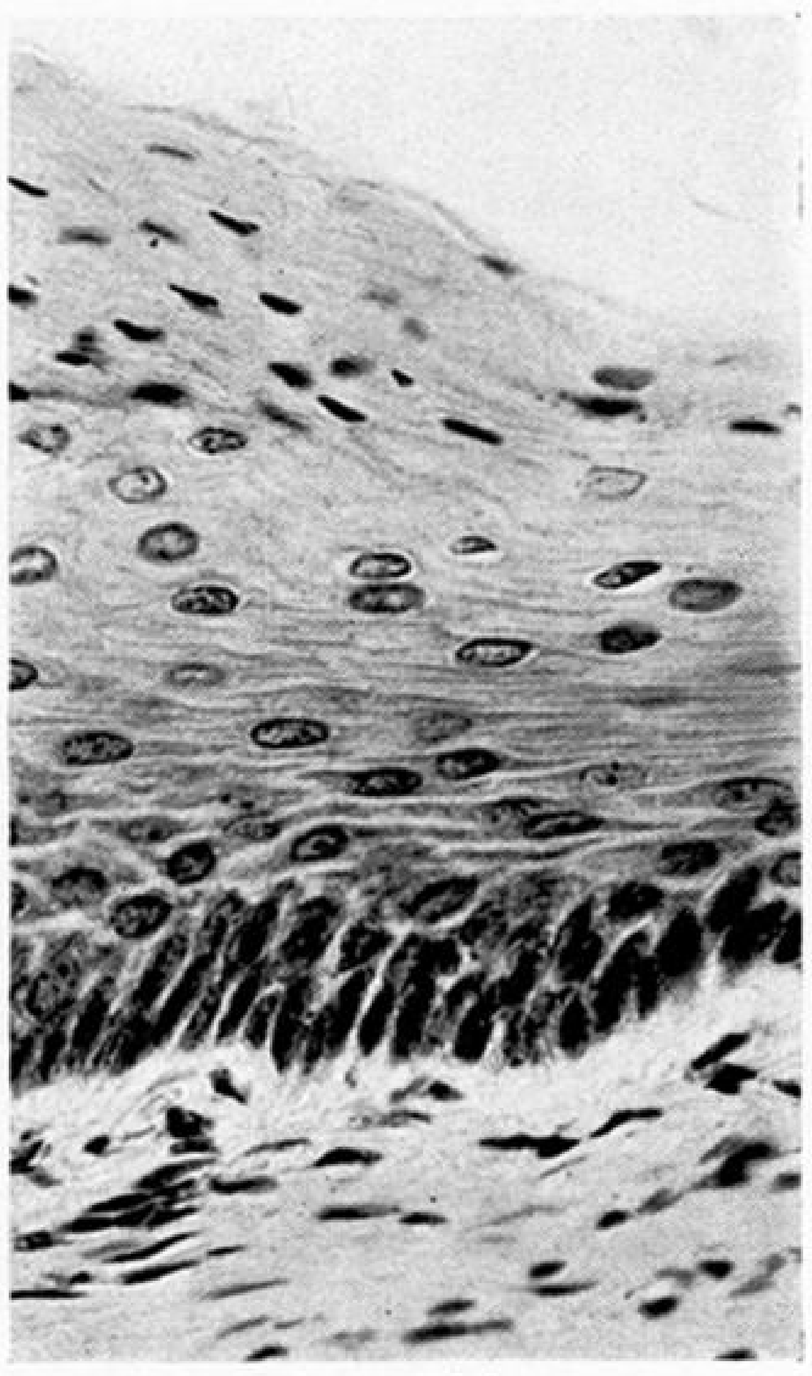

Fig. 41.

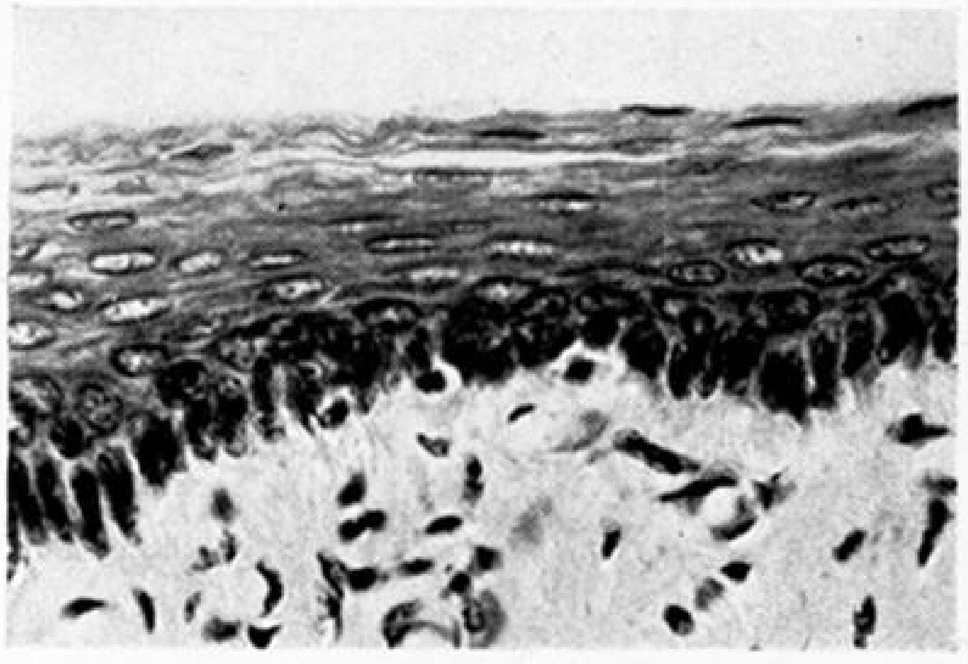

Fig. 43.

Plate 32.

Uterus × 87. Upper vaginal epithelium × 337.

Fig. 34.—No. 264. Accumulation of spermatozoa at tubal opening. × 250.

Fig. 35.—No. 101. Epithelial proliferation in pseudo-pregnancy after repeated infertile matings, *cf.* fig. 38.

Fig. 36.—No. 264. Congestion of uterine stroma in very early pregnancy before the eggs have reached the uterus (*cf.* Hubrecht, 1889, p. 398 : Plate XX, fig. 37).

Fig. 37.—No. 104. Progestational proliferation and secretion in the region of a blastocyst.

Fig. 38.—No. 261. A slightly later stage of progestational proliferation. The blastocyst lies free in the lumen which is filled with blood and pigment.

Fig. 39.—No. 286. Prepubertal October hedgehog. Vaginal epithelium not flattened.

Fig. 40.—No. 156. Hedgehog which has just ovulated but not mated. Vaginal epithelium high and cornified.

Fig. 41.—No. 105. Pseudo-pregnant hedgehog ; vaginal epithelium cornified and sloughing.

Fig. 42.—No. 155. Pregnant hedgehog ; vaginal epithelium low, vacuolated, and infiltrated by leucocytes.

Fig. 43.—No. 192. Lactating hedgehog ; vaginal epithelium low as in anœstrus.

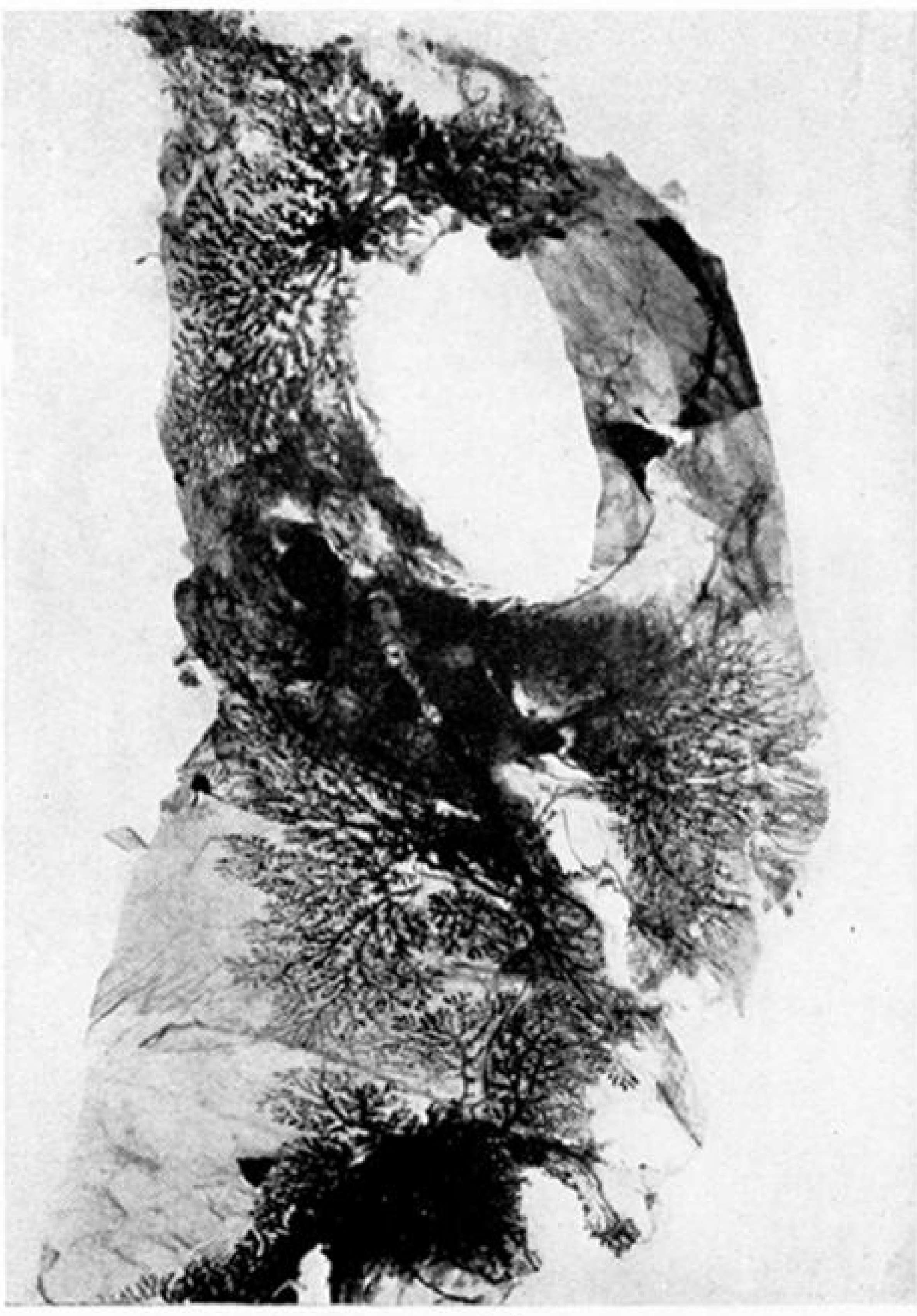

Fig. 44.

Fig. 45.

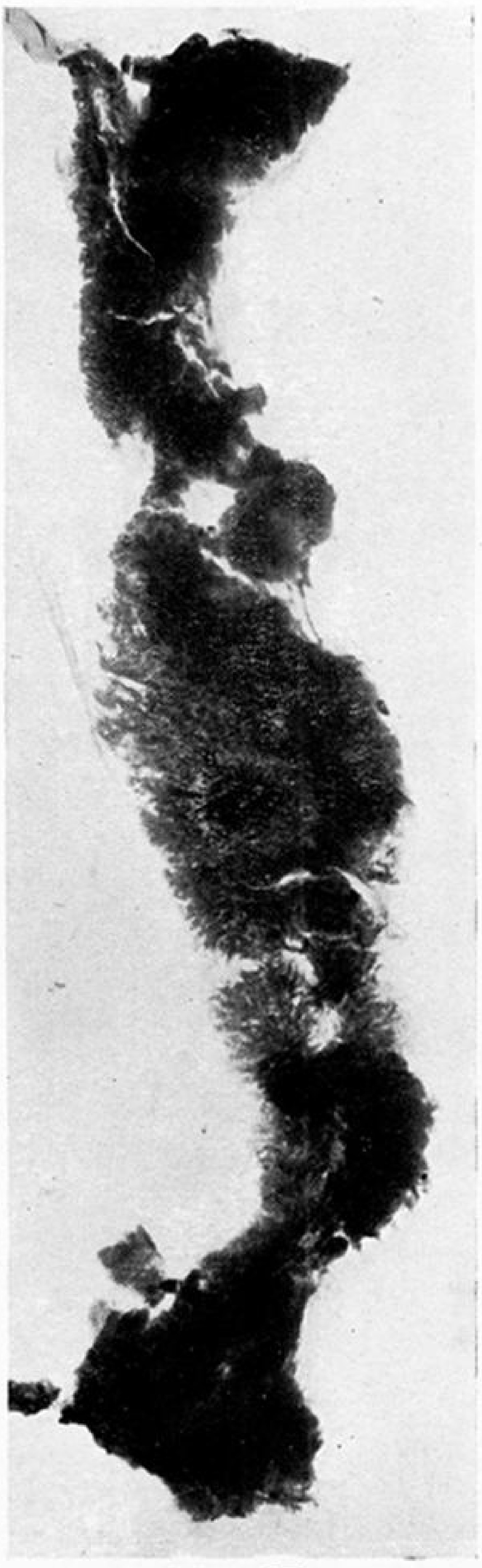

Fig. 47.

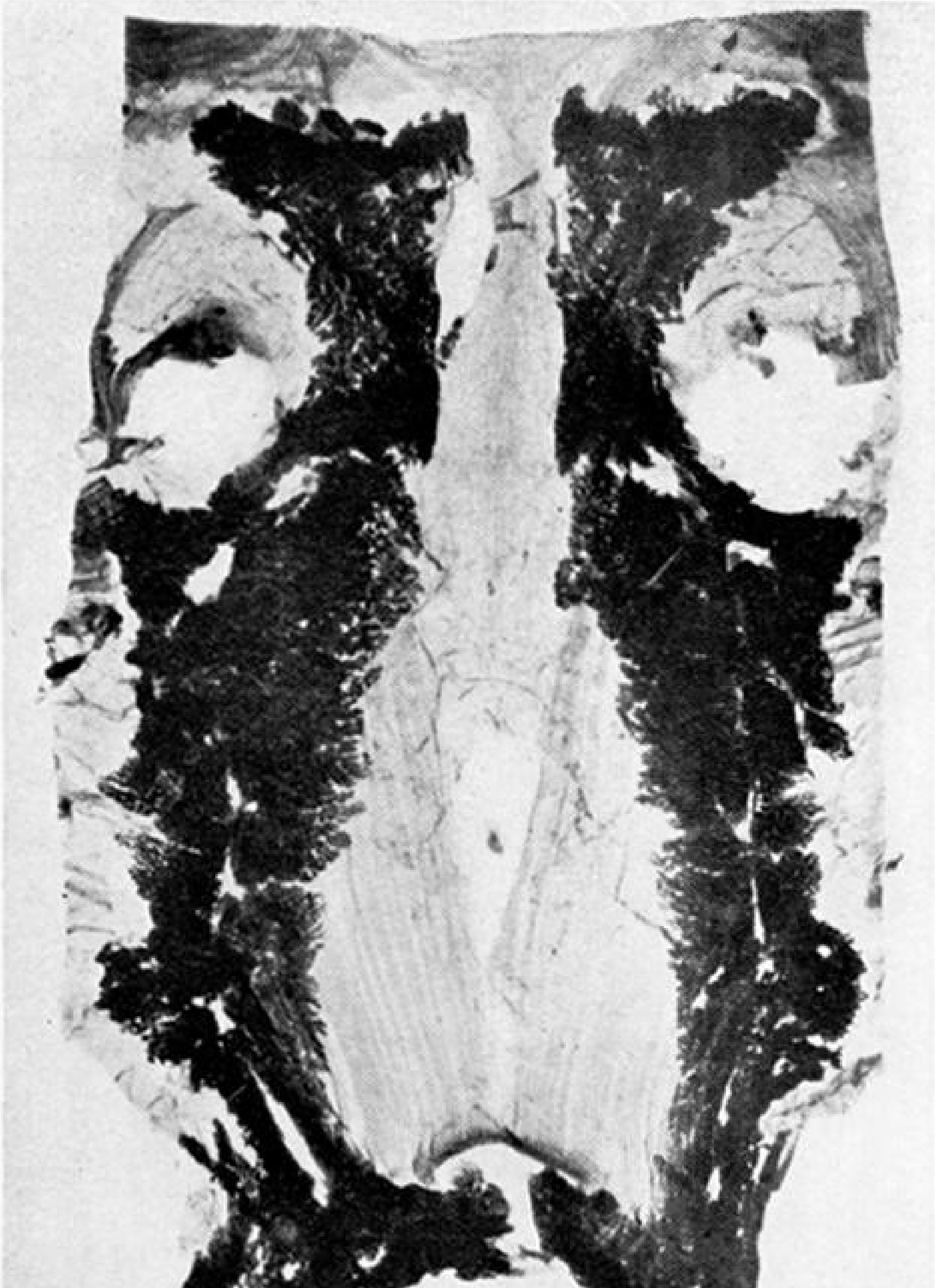

Fig. 46.

Fig. 48.

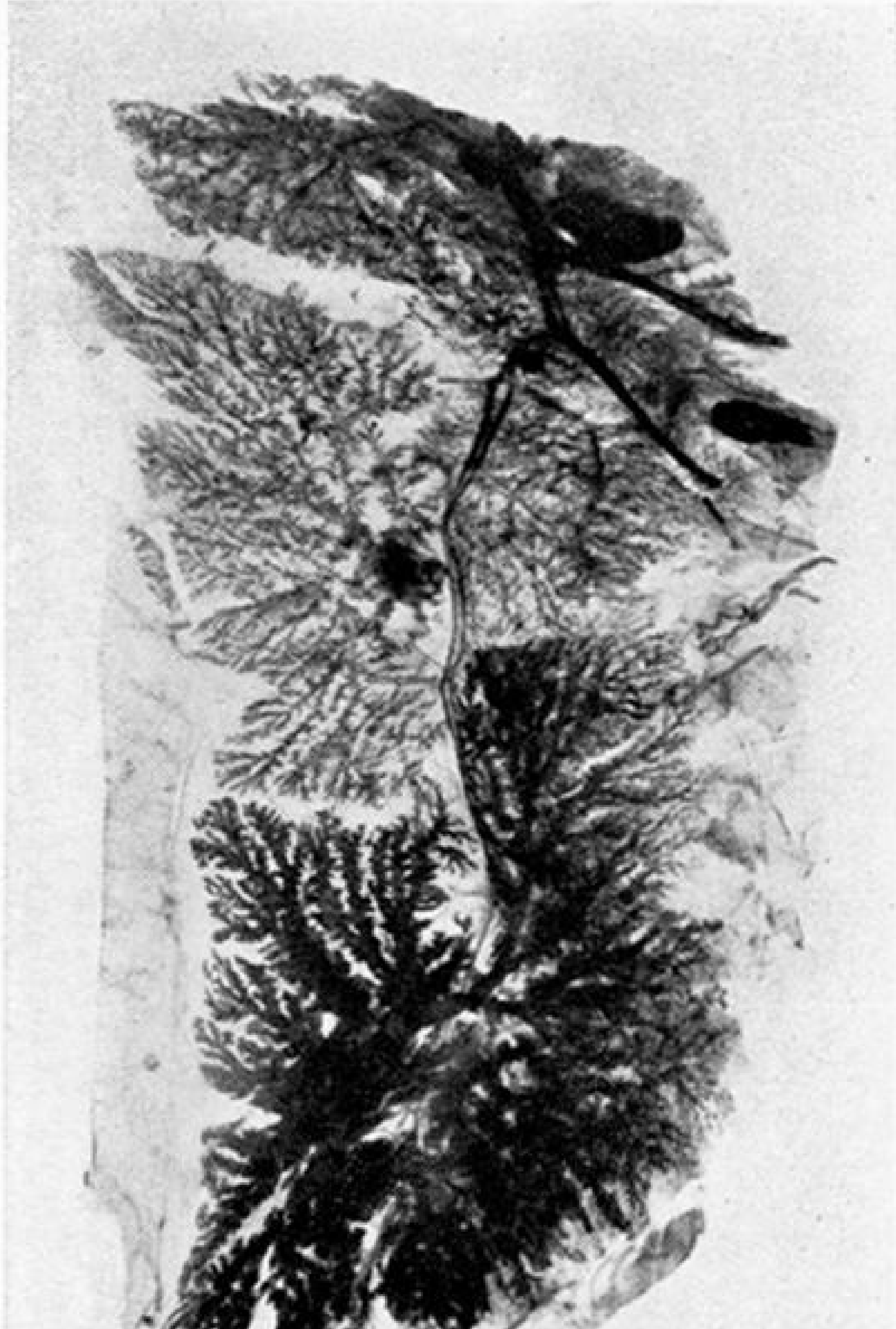

Fig. 49.

PLATE 33.

Mammary glands.

FIG. 44.—No. 317. Part of mammary gland from parous hedgehog in early pregnancy. Natural size.

FIG. 45.—No. 130. Mammary gland in mid-pregnancy. $\times \frac{2}{3}$.

FIG. 46.—No. 262. Mammary gland (both sides) in late pregnancy. $\times \frac{1}{2}$.

FIG. 47.—No. 312. Mammary gland immediately after parturition. $\times \frac{3}{5}$.

FIG. 48.—No. 131. Mammary gland from hedgehog recently lactating and now pregnant. $\times \frac{3}{5}$.

FIG. 49.—No. 271. Part of mammary gland from anœstrous hedgehog in January; not fully regressed. Natural size.