Reproduction of the Bank Vole (Evotomys glareolus, Schreber). I. The Oestrous Cycle of the Female

F. W. Rogers Brambell and I. W. Rowlands

Phil. Trans. R. Soc. Lond. B 1936 **226**, 71-97
doi: 10.1098/rstb.1936.0003

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

I—The Oestrous Cycle of the Female

By F. W. ROGERS BRAMBELL and I. W. ROWLANDS,
From the Department of Zoology, University College of North Wales, Bangor

(Communicated by A. S. PARKES, F.R.S.—Received July 26, Read November 14, 1935)

[PLATES 10 and 11]

CONTENTS

I—INTRODUCTION

The Bank Vole is one of the commonest and most widely distributed of British mammals, sometimes increasing in numbers to such an extent as to constitute a serious agricultural pest. The details of its reproductive processes therefore are of some economic importance to agriculture and forestry.

---

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

VOL. CCXXVI.—B 531 (Price 11*s.*) M [Published March 18, 1936.

Remarkably little information is available regarding the reproductive processes of the species. MARSHALL (1922) states that it " is almost certainly polyoestrous, since it can become pregnant immediately after parturition at certain times of the year " ; a conclusion which is fully substantiated. The results of the earlier observations on the breeding habits are summarized by BARRETT-HAMILTON (1911). Recently BAKER (1930) has provided some further information on this species, and SVIHLA (1929) has recorded some interesting observations on the breeding in captivity of the allied American species *Evotomys gapperi*.

The oestrous cycle of the Bank Vole described in this paper is that of a wild species, uninfluenced by captivity or domestication. Comparison with the oestrous cycle of the white mouse which is essentially similar in its main features should throw some light on the modifications resulting from domestication.

II—TECHNIQUE

The account of the reproductive processes of the Bank Vole contained in this and the succeeding paper is based on wild specimens none of which wsa kept in captivity. All the material was obtained by trapping, chiefly dead in break-back traps but part of it alive in box-traps. The greater part was obtained in North Wales but some of the animals were trapped in the Home Counties. It was collected at the same time and in exactly the same way as the Common Shrews recently described by one of us (BRAMBELL, 1935). *Evotomys* was caught slightly more frequently than *Sorex araneus* on the mainland of North Wales but was decidedly less plentiful in Anglesey where the ratio was approximately 3 Shrews to 1 Bank Vole. The technique of dissection and the histological treatment employed were similar to those described in the paper referred to on the Shrew. Complete serial sections were made of the ovaries of all animals that were not obviously immature obtained from March to October inclusive, except for some animals trapped in September and October, 1932, after the collection for these months was already completed. Since the reproductive organs of these were not preserved they are only included in this series for body-weight and sex-ratio purposes. The ovaries of some of the animals obtained during the months of November, December, January, and February were also sectioned. Complete serial sections were made of both uteri of all animals with recent corpora lutea in the ovaries that were not otherwise known to be pregnant. Counts were made of all sets of corpora lutea that could be distinguished with certainty.

III—MATERIAL AND CLASSIFICATION

The total material consisted of 1036 Bank Voles of which 443 were females. It was obtained between March, 1931, and May, 1933, in North Wales and the Home Counties. Collecting was continued systematically from March, 1931, to June, 1932. The numbers obtained each month from each county are given in Table I.

TABLE I

	Anglesey	Caernarvon-shire	Denbigh-shire	Middlesex	Kent	Essex	Total
1931							
March		4					4
April	1	3					4
June		2					2
July	2	64					66
August		37			91		128
September		30					30
October		15					15
November		11					11
December		18				1	19
1932							
January		34		1	10		45
February		59		3			62
March	13	38	10	1		2	64
April	12	66	15				93
May	5	175	4				184
June		146					146
September		46					46
October		67					67
November		30					30
December		18					18
1933							
May		2					2
	33	865	29	5	101	3	1036

The number of each sex obtained each month is given in Table II.

TABLE II

Month	♂♂	♀♀	%♂
January	28	17	62
February	29	33	47
March	34	34	50
April	60	37	62
May	104	82	56
June	87	61	59
July	37	29	56
August	77	51	60
September	41	35	54
October	45	37	55
November	27	14	66
December	24	13	65
Total	593	443	57·24

The sex-ratio, if the whole material is to be taken as a random sample, is 57·24 ± 1·04. Baker (1930) records from the neighbourhood of Oxford 359 ♂♂ : 250 ♀♀, a ratio of 58·95 ± 1·34 which obviously does not differ significantly.

Classification of the material according to the stage of the oestrous cycle was based on the macroscopic condition and the histology of the reproductive organs. It was found that the oestrous cycle resembled that of the white mouse sufficiently closely to render classification relatively easy. Anoestrous animals during the autumn, winter, and early spring were identified by the inactive condition of the reproductive organs. It was usually possible to distinguish parous from non-parous anoestrous animals macroscopically by the presence of placental sites in the uterus. These retrogressed maternal placental tissues, especially the giant cells, remain for a very long time as conspicuous nodules in the mesometrial wall of the uterus. In some animals histological examination of the uterus was necessary to detect them. In a few anoestrous animals, which had no signs of placental sites, corpora albicantes, or patches of pigment in the ovarian stroma, indicated that they were parous.

During the breeding season the immature animals were readily distinguished by weight and the condition of the reproductive organs. The mature animals were divided into those with and without corpora lutea. The latter were either approaching or in their first oestrus. The former were classified as pregnant or non-pregnant animals. This involved cutting complete serial sections of the uteri and Fallopian tubes of all animals which were not obviously pregnant and searching systematically for embryos. Animals with tubal ova or unimplanted uterine blastocysts could usually be identified as parous or non-parous according to the condition of the uteri or mammary glands. In many animals, but not for all, it was possible to determine whether or not they were lactating. Late stages of pregnancy presented more difficulty in this respect and it was only possible in a few cases to be sure that they were parous and lactating. Non-pregnant animals with corpora lutea in the ovaries were found to belong to one of the following groups: (*a*) animals in the dioestrous cycle the stage of which was readily identified histologically, (*b*) parous animals in post-partum or post-lactation oestrus, and (*c*) animals in lactation anoestrus.

IV—Structure of the Reproductive Organs

The reproductive organs resemble those of the mouse in their general plan, fig. 10, Plate 10. The ovaries are surrounded by closed ovarian capsules into which the Fallopian tubes open. The uterine cornua are separate and there are two distinct cervical canals opening into the vagina. The urethra runs in the ventral wall of the vagina but does not open into the vaginal lumen. The urinary opening is situated on the clitoris, thus permitting of the closure of the vaginal opening in immature and anoestrous animals. There are two pairs of thoracic and two pairs of abdominal mammae, whereas the mouse has three thoracic and two abdominal pairs.

V—GROWTH, DURATION OF LIFE, AND BREEDING SEASON

The oldest foetus obtained which, from its condition, was approximately full-term, weighed 2·37 gm when preserved. This foetus was, however, the only one in the litter and probably, therefore, was unusually large. The foetuses of another litter of four had a mean weight of 1·64 gm. Since the mean weight of these embryos in their membranes was 1·87 gm it is probable that they were also approaching full-term. The estimated weight at birth is therefore approximately 2·0 gm. This figure corresponds well with those observed by SVIHLA (1929) for *E. gapperi;* he records 1·7 to 2·3 gm with a mean weight of 1·9 gm at birth.

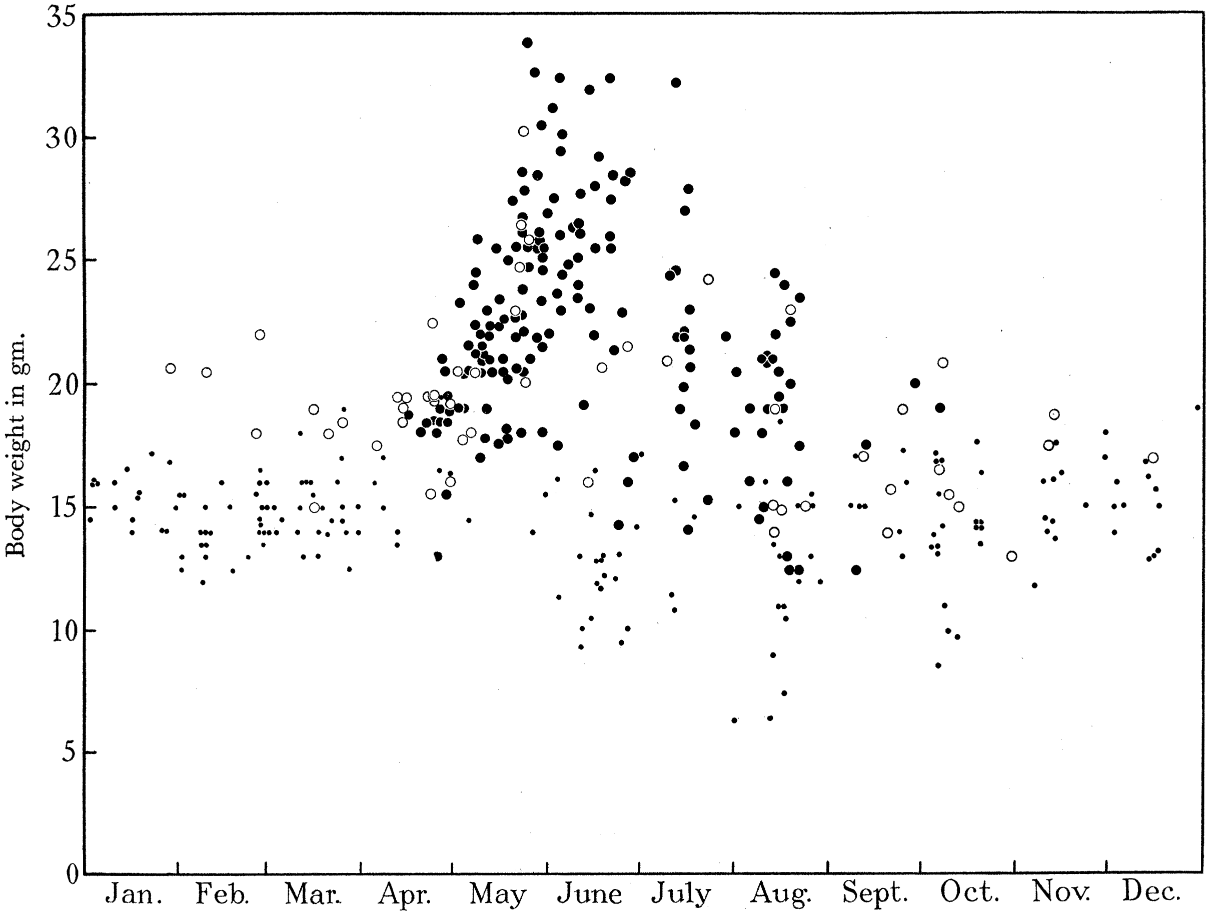

FIG. 1—Scatter diagram of the body-weights of females according to the days of the year. • non-parous non-pregnant animals ; ○ parous non-pregnant animals ; ● pregnant animals.

The body-weights of 394 females are shown against the day of the year on which they were trapped in fig. 1.

It can be seen that the lightest animal weighed 6·4 gm, but that only four under 9·0 gm were obtained. Ten animals were over 30·0 gm, the heaviest being 33·8 gm, but if these weights are corrected for the foetuses and membranes of late pregnancies only five remain over 30·0 gm, the heaviest being 32·0 gm. The lightest parous or pregnant animal was 12·5 gm, and only six were obtained under 14·0 gm. All except four of the non-parous non-pregnant animals weighed under 18 gm, and the only one of these over 19 gm was in oestrus and had mated.

All animals except four obtained between the middle of October and the middle of April weighed between 12 and 19 gm. Three of the four exceptions were parous animals weighing 20–22 gm, and one was a non-parous animal just under 12·0 gm. During the second half of April and May there is a rapid and steady rise in body-weight to the summer level and pregnancies appear simultaneously with its beginning. During July and August there is a steady decrease in the maximum body-weights observed. It may be accounted for, in part by heavy mortality among the larger and presumably older females and partly by a failure of young animals to reach a large body-size in their first season. It is also possible that an actual loss of weight by parous animals occurs.

It is clear that young females born early in the season become mature and breed before its close. *Evotomys* differs in this respect from the Common Shrew which does not breed in the season in which it is born (Brambell, 1935). It is equally obvious that parous animals frequently survive the winter and participate in a second breeding season. It is not possible to decide with certainty, owing to lack of means of distinguishing between parous animals that have bred in one or two seasons, whether any animals survive a second winter and breed in yet a third season but the body-weights would appear to indicate that this is exceptional.

The breeding season begins abruptly in the middle of April, the first pregnancy having been obtained on the 15th but 16 of the 26 animals trapped during the second half of the month were pregnant.

The total number of females examined each month, the number that are adult, and the number pregnant are given in Table III. Only animals with corpora lutea or traces of them in the ovary, with old placental sites in the uterus, or with

Table III

Month	Total number	Adults	Pregnant
January	17	1	—
February	33	3	—
March	34	4	—
April	37	28	16
May	82	79	69
June	61	40	38
July	29	24	22
August	57	36	30
September	15	7	3
October	26	6	1
November	14	2	—
December	13	1	—
Total	418	231	179

both, and which therefore have ovulated at some time, are included as adults. Since these structures are so persistent during anoestrus it is improbable that any adult animals have been excluded owing to failure to detect them.

The percentage of adult animals that are pregnant each month, extracted from this table, is represented graphically in fig. 2.

It can be seen that the points fall on a remarkably smooth curve rising steeply from zero in March to a maximum of 95% in June and then declining again to zero in November. It is clear therefore that the breeding season extended, in the years in which the material was obtained, from April to October reaching a peak in June. The latest pregnancy was obtained on October 6. Barrett-Hamilton (1911) states that the breeding season in the south of England lasts regularly from March to December inclusive, and may include January and February. Baker (1930) records that in Oxfordshire the peak of the breeding season is reached in June and that there was complete cessation of breeding, as determined by the occurrence of pregnant females, during the period October to February inclusive in the winters 1925–26 and 1926–27, but not in 1927–28. The results presented in this paper confirm Baker's statement that breeding reaches a maximum in June. Since most of the winter material was obtained in North Wales in 1931–32 and 1932–33 it is clear that breeding stopped during those years, at least in Caernarvonshire and Anglesey.

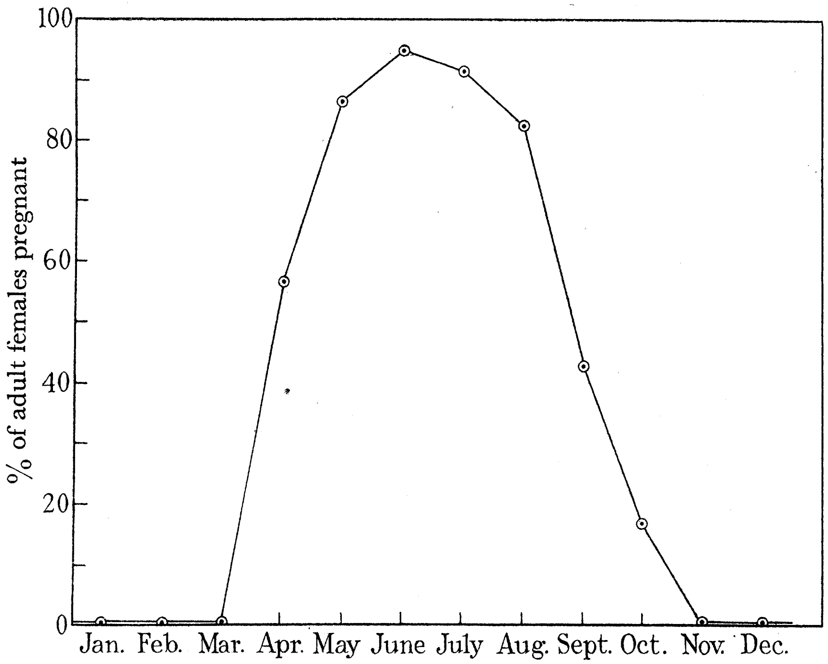

Fig. 2—Graphical representation of percentage of adult animals that are pregnant according to the month. The points are derived from the data in Table III.

Assuming that gestation and suckling together take about six weeks, as in *E. gapperi* (SVIHLA, 1929) or in the white mouse, and that breeding begins in mid-April then young animals of the season might be expected to occur in the traps in the 4th week of May. Actually the first young animal was obtained on May 26, which supports these assumptions.

Examination of fig. 1 leaves little doubt that young animals born at the beginning breed later in the same season. This is borne out by examination of fig. 3 in which the percentages of all females that are adult each month, extracted from Table III, are shown. The first peak is reached in May and is followed by a drop in June, presumably owing to the appearance of immature animals. The second and lesser peak in July is probably due to some of the young animals having become mature.

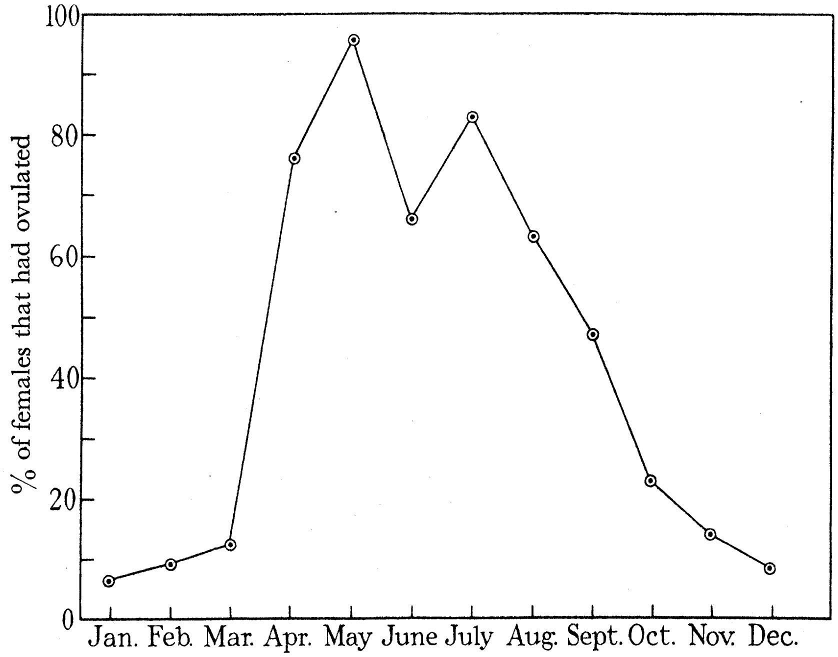

FIG. 3—Graphical representation of the percentage of females that are adult (*i.e.*, have ovulated previously) according to the month. The points are extracted from the data in Table III.

More direct evidence of breeding in the season in which they were born is provided by the occurrence in the latter part of the season of pregnant animals of light weight which do not appear to be parous.

VI—FERTILITY

It can be seen from fig. 2 that during May, June, July, and August over 80% of all adults are pregnant. Since it may be assumed that the period of gestation is short, as in the white mouse, and since many of the adults during these months are known to be parous it is clear that many animals must be pregnant while suckling previous litters. It is probable, in fact, that the majority of animals become pregnant again at the post-partum oestrus. Thus, those which start to breed at the beginning of the season and continue until the end of July or beginning of August may rear as many as four or even five litters in succession. The frequent occurrence of pregnant animals that were also lactating confirms these deductions. In some of the early stages of pregnancy the condition of the uterus as well as that of the mammary glands showed that the pregnancy dated from an oestrous period occurring immediately after parturition.

The mean number of young in a litter can be estimated from the mean number of ova ovulated at each oestrus as shown by the number of corpora lutea in each set, from the mean number of embryos *in utero* in the later stages of pregnancy and from the mean number of placental sites visible in parous uteri.

Analysis of the number of corpora lutea in each set and their distribution yields interesting information. The total number of complete sets of corpora lutea available was 277. These were distributed as in Table IV. It can be seen that the most frequent number of ova ovulated at one oestrus was 4, that the largest number observed was 12, and the mean number 4·43. The percentage frequency of each class is represented graphically in fig. 4.

TABLE IV

No. in set or litter	Observed			Compiled from ADAMS and BAKER.
	Corpora lutea	Placental sites	Embryos	Embryos
1	1	—	1	1
2	8	1	1	4
3	43	11	16	29
4	108	20	27	35
5	82	13	21	14
6	22	11	4	5
7	7	2	—	—
8	2	—	—	—
9	2	—	—	—
10	—	—	—	—
11	1	—	—	—
12	1	—	—	—
Total . . .	277	58	70	88

The distribution of the corpora lutea in each set between the two ovaries of each pair, represented as the difference between the numbers in each ovary, is shown in the third column of Table V. The expected values, on the assumption that the distribution between the two ovaries is random, are given in the second column and the divergences of the observed from the expected values in the fourth column.

Testing by means of χ^2 (FISHER, 1930) the divergence of the observed from the expected values is found to be without significance, and therefore the distribution of the corpora lutea of each set between the two ovaries of a pair may be assumed to be random.

TABLE V

Difference between the number of corpora lutea in each of a pair of ovaries	Expected	Observed	Divergence of observed from expected values	x^2/m
5+	7·5	5	− 2·5	0·833
4	18·3	22	+ 3·7	0·748
3	39·7	25	−14·7	5·443
2	69·6	70	+ 0·4	0·002
1	89·8	106	+16·2	2·922
0	52·1	49	− 3·1	0·184
Total	277·0	277	0·0	$\chi^2 = 10{\cdot}132$

The number of embryos in each of 70 late pregnancies and the number of placental sites in each of 58 parous uteri are given in the third and fourth columns of Table IV. It will be seen that the largest number in a uterus was 6 for the embryos and 7 for the placental sites. The mean number of embryos was 4·11 which is rather greater than 3·82 recorded independently by both ADAMS (quoted by BARRETT-HAMILTON, 1911) and BAKER (1930) whose data are given in the fifth column. The mean number of placental sites is 4·48. The numbers of embryos and placental sites in the litters observed are represented as percentage frequencies in figs. 5 and 6, which are therefore comparable to fig. 4.

The number of ova ovulated at each oestrus exhibits considerable seasonal variation, as shown by the data given in Table VI.

TABLE VI

Month	No. of animals	No. of sets of corpora lutea	Total No. of corpora lutea	Mean No. of corpora lutea in a set
April	28	46	180	3·9
May	78	109	519	4·8
June	38	47	235	5·0
July	24	31	132	4·3
August	33	40	146	3·6
September	3	3	10	
October	1	1	4	
Total	205	277	1,226	4·43

The mean numbers of corpora lutea in a set, for each period, as shown in the last column of Table VI, are represented graphically in fig. 7.

The number of ova ovulated at each oestrus varies also according to the body-weight, as is shown by the data presented in Table VII. It can be seen from these data that the number of ova ovulated is proportional to the body-weight.

TABLE VII

Body-weight groups, gm	Mean body-weight, gm	No. of animals	No. of sets of corpora lutea	Total No. of corpora lutea	Mean No. of corpora lutea in a set
26<	28·6	35	44	227	5·2
24–25·9	24·9	25	35	164	4·7
22–23·9	22·8	27	34	158	4·6
20–21·9	20·9	41	60	268	4·5
18–19·9	18·8	38	59	235	4·0
>17·9	15·6	28	32	117	3·7
Total . . .	21·9	194	264	1,169	4·43

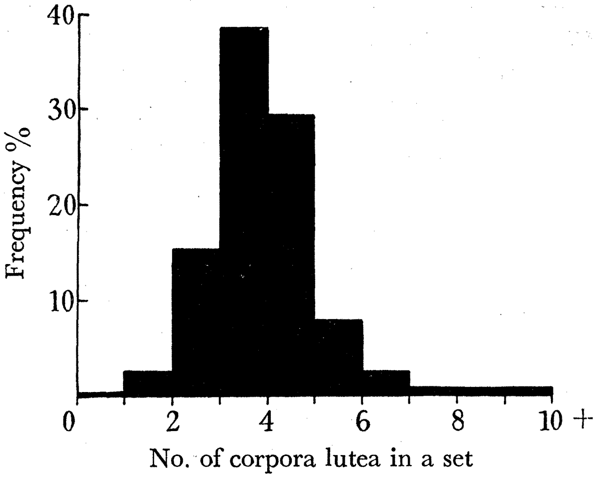

FIG. 4.

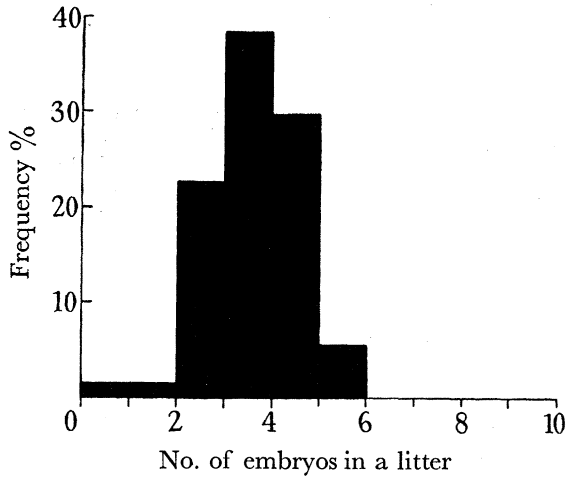

FIG. 5.

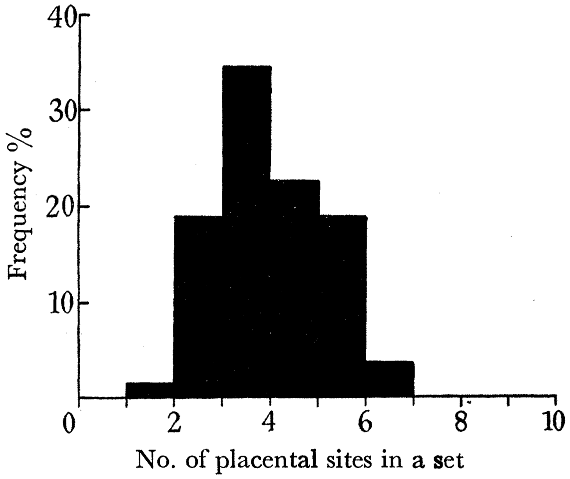

FIG. 6.

FIGS. 4–6—Frequency polygons illustrating size of litter as shown by the number of corpora lutea in a set, fig. 4; by the number of embryos *in utero* in a litter, fig. 5; and by the number of placental sites in a pair of post-partum uteri, fig. 6. The frequency in each case is represented as a percentage of all cases to render the figures more readily comparable.

Statistical examination of the whole of the data given in this table shows that they can be represented in the form of a straight line regression of number of corpora lutea in a set on body-weight of the form :—

$$y = 0\cdot 1144x + 1\cdot 92,$$

where $y =$ the number of corpora lutea in a set, and $x =$ the body-weight. Testing by means of the table of t (Fisher, 1930) this regression is found to be highly significant. The regression line and the means of each group are represented graphically in fig. 8.

Since the body-weight varies seasonally, reaching a maximum in June at the end of the spring rise and falling thereafter, owing to the appearance of young animals and possibly to an actual decrease in weight of the old animals, it is clear that the relations of the number of ova ovulated to month on the one hand and to the body-weight on the other hand cannot be considered as independent. If it is assumed that the seasonal variation is the more fundamental, then the relation to body-weight would follow in consequence to a large extent. Conversely if the relation to body-weight is the more fundamental then it would largely explain the seasonal variation. Unfortunately the data do not permit of deciding which relation is fundamental. It may be significant in this connexion that the pituitary itself is known to exhibit a positive heterogonic relation to body-size in the rabbit (Robb, 1928, 1929, and Allanson, 1932). If the amount of hormone produced by the pituitary is proportional to its size then positive heterogony of the pituitary would account for the number of ova ovulated being proportional to the body-size.

The number of embryos *in utero* in late stages of pregnancy also varies seasonally and with body-weight. The data concerning seasonal variation are given in Table VIII together with those recorded by Baker (1930) for the seasons 1926 and 1927.

TABLE VIII

Month	Observed			Compiled from Baker (1930)		
	No. of litters	No. of embryos	Mean size of litter	No. of litters	No. of embryos	Mean size of litter
Before June	31	134	4·3	22	85	3·9
June and July	27	113	4·2	17	75	4·4
After July	12	41	3·4	11	31	2·8
Total . . .	70	288	4·11	50	191	3·82

The data according to body-weight are given in Table IX.

TABLE IX

Body-weight groups, gm	No. of litters	No. of embryos	Mean size of litter
25<	15	67	4·5
20–24·9	34	142	4·2
>19·9	13	50	3·8
Total	62	259	4·18

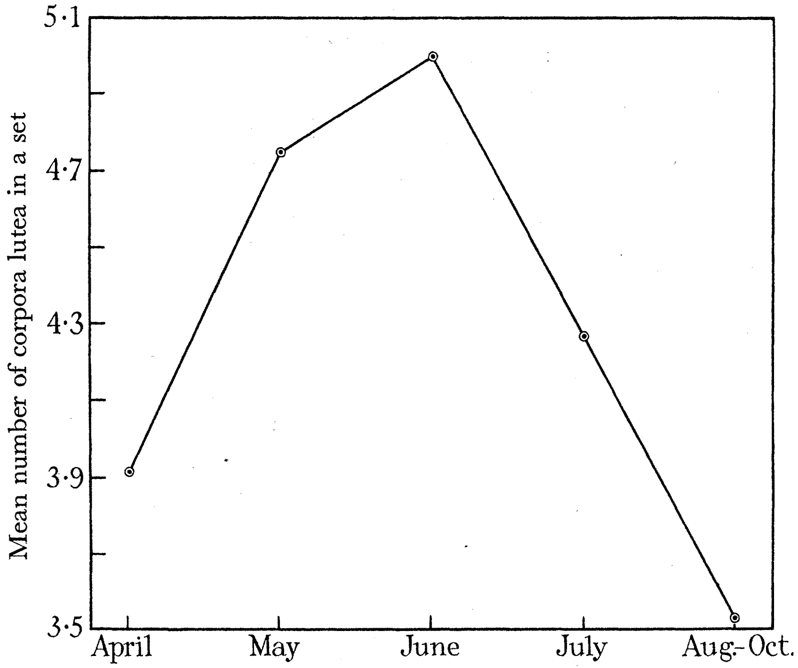

FIG. 7—Graphical representation of the mean number of corpora lutea in a set according to the month. The data are given in Table VI to the nearest first decimal place.

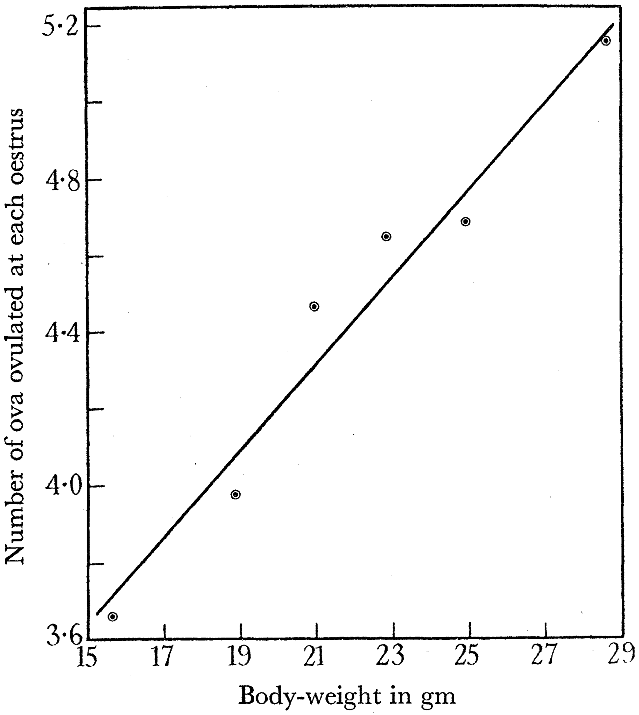

FIG. 8—Graphical representation of the regression of the number of ova ovulated on body-weight. The points represent the mean values for the body-weight groups given in Table VII to the nearest first decimal place, and are plotted for comparison with the calculated regression line.

The body-weights of those animals which were in late stages of pregnancy were corrected by subtraction of the weights of the uteri and contained embryos for the purposes of this table.

The observations show that the number of embryos *in utero* falls off as the season advances, although BAKER's somewhat less extensive data show a maximum in June and July. The number of embryos *in utero* increases with body-weight.

Information regarding the incidence of intra-uterine mortality is provided by comparison of the number of embryos with the number of ova ovulated as shown by the corpora lutea in late uterine pregnancies. The data, grouped according to the number of ova ovulated, are given in Table X. It can be seen that there is a much heavier mortality, as judged both by the percentage of litters affected and the percentage of ova lost, when 6 or more, than when 5 or less, ova are ovulated. Moreover, in no case have more than 6 survived (*see also* fig. 5). It is reasonable to assume that this mortality is not due to genetical causes, since these would not explain the differential incidence observed.

TABLE X

No. of ova ovulated	No. of examples	No. of animals showing mortality	No. of ova lost	% of animals showing mortality	% of ova lost
2	1	0	0	20·7	6·6
3	8	1	2		
4	28	7	8		
5	21	4	6		
6	9	6	10	75·0	24·5
7	1	1	2		
8	1	1	4		
9	1	1	3		
Total . . .	70	21	35	30·0	10·9

The increased mortality when 6 or more ova are ovulated might be due either to deficiency of nutritive and other substances necessary for the maintenance of the embryos or to the mechanical effects of overcrowding in one or both of the uterine cornua. If the latter alternative were true the mortality, falling most heavily on the cornu with the larger numbers of embryos would result in a tendency towards equality in the distribution of the healthy embryos between the two cornua. This tendency should be detected by comparing the observed distribution of embryos in late pregnancies and of old placental sites in parous animals with the expected random distribution as given in Table XI. The agreement of observed and expected values is very close, and when tested by means of χ^2 (FISHER, 1930) there is obviously no significant departure from the random distribution.

Examination of the mortality in each uterine cornu according to the number of ova ovulated in the corresponding ovary without reference to the other side, that is

TABLE XI

Difference between No. in right and left uterine cornua	Expected	Observed		Divergence of sum of the observed from expected values	x^2/m
		Embryos	Placental sites		
5+	2·7	2	1	+0·3	0·225
4	8·7	5	5	+1·3	
3	18·1	10	5	−3·1	0·531
2	31·6	14	16	−1·6	0·081
1	43·6	26	20	+2·4	0·132
0	23·3	13	11	+0·7	0·021
Total . . .	128·0	70	58	0·0	$\chi^2 = 0{\cdot}990$

without taking account of the total number of ova ovulated in the two ovaries, supports this conclusion. The data are given in Table XII.

TABLE XII

No. of ova ovulated in each ovary	No. of ovaries	Total No. of ova ovulated	No. of ova lost	% of ova lost
1 or 2	73	125	13	10·4
3 or more	52	183	15	8·2

It is apparent that the mortality is actually higher, though not significantly, when 1 or 2 than it is when 3 or more ova are ovulated in one ovary. It is concluded that the increased mortality when the total number of ova ovulated from both ovaries is large, is due to deficiency of nutritive or other substances required for development and not to mechanical effects of overcrowding or failure of the uterus to contain the embryos.

VII—OESTROUS CYCLE

a. Dioestrous Cycle

The histological changes in the reproductive organs during the oestrous cycle are so similar to those of the white mouse and the rat that they do not require detailed description. It will be sufficient for the purposes of this paper to refer to, and figure, the more characteristic phases for comparison with those of the mouse. The oestrous cycle does differ, however, from that of the white mouse in several ways, probably all connected with the fact that *Evotomys* is a wild species with a restricted breeding season, whereas the white mouse is semi-domesticated and has a continuous breeding season.

The majority of females undergo, at the beginning of the breeding season in April and May, a number of sterile cycles, accompanied by ovulation, before they become pregnant. They resemble in this respect the Hedgehog in which DEANESLY

(1934) has recorded the occurrence of a number of sterile dioestrous cycles accompanied by ovulation. This is shown by the presence in the ovaries of several distinct sets of corpora lutea, sometimes as many as four, fig. 11, Plate 10. Since it is very doubtful whether corpora lutea would persist long enough to be recognizable after more than four dioestrous cycles it is quite possible that some of the animals undergo more than four cycles before becoming pregnant. The number of non-pregnant and pregnant animals with tubal ova that had 1, 2, 3, or 4 sets of corpora lutea in the ovaries are shown in Table XIII. Pregnant animals with uterine stages are excluded because an increasing number of the earlier sets of corpora lutea would be indistinguishable as pregnancy advanced. All animals that could be in an immediately post-partum or post-lactation oestrus are omitted also, since they would show the corpora lutea of pregnancy or lactation respectively, as well as those of the subsequent oestrus.

TABLE XIII

No. of distinct sets of corpora lutea in the ovaries	April and May		June to October	
	Non-pregnant	Pregnant	Non-pregnant	Pregnant
1	2	1	1	5
2	7	10	1	1
3	5	17	—	1
4	1	6	—	1

It will be seen that only one of the 34 tubal pregnancies obtained in April and May which are recorded in Table XIII became pregnant at the first oestrus. One animal (E 520, *see* Table XV, and fig. 12, Plate 10), in addition, was obtained which was in its first oestrus but had not yet ovulated. The ova in the large follicles about to ovulate contained 1st polar spindles, and the animal had mated as shown by the vaginal plug still *in situ*. It may be concluded that although pregnancy begins most frequently at the third oestrus it may do so even at the first or not until the fifth.

There is no evidence that any of these sterile cycles were accompanied by copulation. Spermatozoa were not found in any non-pregnant animals except in those in oestrus which had obviously just mated. No animals were found which were pseudo-pregnant. It seems probable, therefore, that these sterile cycles are not accompanied by copulation and that the latter, when it does occur, is usually fertile. The cause of this failure to copulate at these early oestrous periods is obscure, but it lies, presumably, in the state of the female since the males are all in full breeding condition at this time.

Young animals which attain puberty in the latter part of the season appear to become pregnant at the first oestrus much more frequently, as is shown by the data in the fourth and fifth columns of Table XIII. This difference between animals passing from winter anoestrus into the breeding condition and animals attaining puberty during the breeding season is remarkable.

It seems probable that the sterile dioestrous cycle is of very short duration because of the sudden appearance of animals with several sets of corpora lutea at the onset of the breeding season in April. This can be seen from the records for the month (excluding uterine pregnancies) given in Table XIV. The evident short duration of these cycles also suggests that copulation does not occur, since the sterile mated cycle in the white mouse is 12 days, twice as long as the unmated cycle.

Table XIV

Date	No. of sets of corpora lutea	Condition
May 4	None	Non-pregnant
,, 5	,,	,,
,, 7	,,	,,
,, 7	,,	,,
,, 12	,,	,,
,, 12	,,	,,
,, 13	3	,,
,, 13	2	,,
,, 14	3	,,
,, 14	2	,,
,, 18	2	,,
,, 19	3	Pregnant (ova in tubes)
,, 22	4	,, ,,
,, 22	3	Non-pregnant
,, 23	3	,,
,, 23	1	,,
,, 24	2	,,
,, 24	3	Pregnant (ova in tubes)
,, 24	4	Non-pregnant
,, 25	None	,,
,, 25	,,	1st oestrus with vaginal plug
,, 25	1	Pregnant (ova in tubes)
,, 25	3	,, ,,
,, 26	3	,, ,,
,, 26	3	,, ,,
,, 27	3	,, ,,
,, 27	2	,, ,,
,, 27	3	,, ,,
,, 28	3	,, ,,
,, 29	2	Oestrus with vaginal plug
,, 29	1	Non-pregnant
,, 29	None	,,
,, 30	4	Pregnant (ova in tubes)
,, 30	4	,, ,,

b. Oestrus

The primordial follicles in the ovarian cortex measure approximately 15 μ and the contained oocytes approximately 9 μ in diameter. The subsequent growth of the ovum relative to the follicle can be divided into two phases, each of which can be expressed as a straight line regression (BRAMBELL, 1928), as in other mammals. The regression formulae for the two phases are :—

(*a*) $y = 2{\cdot}56 + 0{\cdot}455x$, where $x = 10$ to 124,
(*b*) $y = 56{\cdot}84 + 0{\cdot}018x$, where $x = 125$ to 800,

where y = diameter of oocyte in μ, and x = diameter of the follicle in μ. The fully-grown ovum thus measures approximately 70 μ in diameter. The largest follicle measured 820 μ in diameter but it is probable that there is a good deal of variation in the size of the follicle when it ruptures. At oestrus the follicle appears to reach its full size, fig. 15, Plate 11, about the time that the spindles of the heterotypic division are formed in the oocytes. Six animals with oocytes in this stage were obtained, as shown in Table XV.

TABLE XV

Ref. No.	Stage of oocytes	Mean diameter of mature follicles μ	Mean diameter of corpora lutea of previous oestrus mm	Whether copulation has occurred
E 241	Metaphase of heterotypic division . . .	568	1·15	—
E 501	,, ,, ,, . . .	636	1·10	+
E 548	,, ,, ,, . . .	686	0·79	+
E 588	,, ,, ,, . . .	650	1·01	+
E 189	,, ,, ,, . . .	793	1·01	—
E 520	Late anaphase of heterotypic division .	556	None	+

The corpora lutea of the previous oestrus measure 0·8 to 1·2 mm. Copulation occurs at this time, four of the six animals with heterotypic spindles in the oocytes having spermatozoa in the vagina and uterus, while none of those in oestrus, with the large follicles but with vesicular nuclei in the oocytes, contained spermatozoa. One animal, E 241, Table XV, contained one follicle which had just ruptured although the other follicles had not done so. It would appear, therefore, that the heterotypic division is completed after ovulation. Ovulation takes place spontaneously in the absence of copulation.

Three animals with tubal ova containing homotypic spindles were obtained, only two of which had copulated. In one of these, sperm-heads could be distinguished in the cytoplasm of some of the ova. It is apparent, therefore, that fertilization occurs either in the ovarian capsule or in the upper part of the tube and before the separation of the second polar body.

The two animals with ova in the metaphase of the heterotypic division and the other with tubal ova in the homotypic division, which had not copulated support the suggestion (p. 86) that the sterile dioestrous cycles noted, especially at the beginning of the breeding season, are due to failure to copulate rather than to sterile mating.

The condition of the uterus and vagina of *Evotomys* during oestrus closely resembles that of the rat and mouse. The uterus becomes distended with fluid, fig. 16, Plate 11, in a characteristic manner and the vaginal epithelium is intensely cornified, fig. 12, Plate 10. Copulation results in the formation of a hard vaginal plug as in many other small rodents. This plug remains in position for a short time and was found in seven of the ten animals with fertilized but unsegmented tubal ova containing two pronuclei. It was not present, however, in animals with tubal ova undergoing the first cleavage or in the two-cell stage.

c. Pregnancy

The total number of pregnant animals obtained was 179, which were divided between the various stages as in Table XVI.

Table XVI

Stage	No. of examples
Tubal stages—	
Ova containing homotypic spindles and sperm-heads	2
Ova with ♂ and ♀ pronuclei	10
Ova with first cleavage spindles	2
2-cell stages	8
2-cell to 4-cell stages	3
4-cell stages	5
4-cell to 8-cell stages	2
8-cell stages	6
16-cell stages	5
Morulae in Fallopian tubes	6
Total	49
Uterine morulae or blastocysts prior to implantation	50
Post-implantation uterine stages	80

The relative frequency of the various tubal stages provides a rough indication of their relative duration. The eggs pass from the Fallopian tube into the uterus as solid morulae in which the primitive yolk-sac cavity appears soon afterwards. Implantation closely resembles that of the mouse and rat. According to Kirkham (1916) pregnancy lasted 20 days in the strain of mice he used, the ova were found in the tubes for the first four days ; on the fifth day the blastocysts were free in the lumen of the uterus, and implantation then occurred. It is probable that the duration of pregnancy in *Evotomys* is approximately the same as it is in the mouse, but even if it differs considerably, it may still be assumed that the relative duration of the various stages is similar. It follows that a random sample of pregnant animals would tend to the ratio of 4 tubal stages : 1 free uterine stage : 15 post-implantation stages. The observed ratio of 49 : 50 : 80 does not conform to this expectation. The relatively small number of late uterine stages obtained may be due to their being less easily trapped, since probably they are less active at the end of pregnancy. This explanation can hardly apply to animals with tubal and early uterine stages. If it is assumed that the numbers of these two stages do represent a random sample some other explanation must be sought. To explain a similar ratio observed in trapped material of the Common Shrew, BRAMBELL (1935) suggested that the relatively large number of early uterine stages was due to prolongation of pregnancy in lactating animals. LATASTE (1887) first showed that the period of gestation is considerably prolonged during lactation, and KIRKHAM (1916) demonstrated that this prolongation is due to delay in implantation, the ova remaining free in the uterus without apparently developing further, for a much longer time than in animals which are not suckling. MIRSKAIA and CREW (1931) record the duration of 15 pregnancies in lactating mice which showed a prolongation beyond the normal for non-lactating animals of from 8 to 16 days with a mean of 11·8 days. It is known from the condition of the mammary glands that some of the pregnant animals recorded herein were lactating, and it appears probable, from the high percentage of adults pregnant in June, July, and August, that many were also lactating at the same time.

Since animals in the early part of the season, during April and the first half of May, cannot have been lactating, comparison of the ratio of tubal to early uterine stages obtained with that of those obtained subsequently should show a difference. This can be seen to be so from Table XVII.

TABLE XVII

	Tubal stages	Unimplanted uterine stages
Beginning of season to May 15	23	8
May 16 to end of season	26	42
Total	49	50

It is apparent that the unexpected preponderance of early uterine stages is almost entirely confined to the later part of the season, thus strongly supporting the theory that it is due to delayed implantation in lactating animals. If it is assumed that the delay in implantation bears the same time relation to the period of gestation that it does in the mouse then, on the basis of the data of MIRSKAIA and CREW (1931), the percentage of animals exhibiting delay (*i.e.*, lactating) in the later part of the season can be calculated as in Table XVIII.

TABLE XVIII

Prolongation of pregnancy	% of pregnant animals lactating
Minimum (8 days in mouse)	68
Mean (11·8 days in mouse)	46
Maximum (16 days in mouse)	34

Since some of the pregnant animals will be young non-parous animals and others will be adults which are not suckling owing to accidental loss of the litter it is clear that pregnancy must follow the post-partum oestrus in a large percentage of parous animals and must accompany lactation.

The correspondence of the number of embryos in each of the uterine cornua with the number of corpora lutea in the ovary belonging to it shows that no transference of embryos from one side to the other, such as was observed in the Common Shrew (Brambell, 1935), occurs in this species.

The newly ruptured follicle immediately after ovulation measures approximately

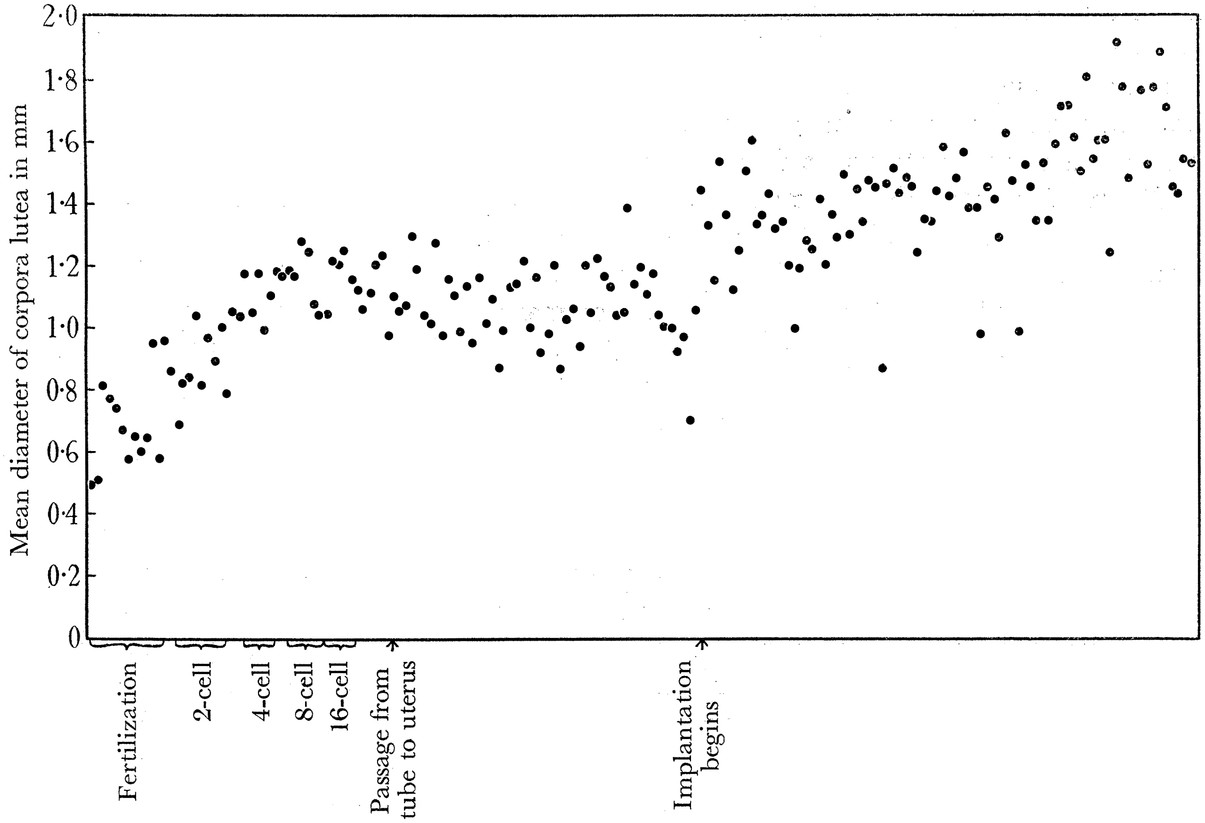

Fig. 9—Graphical representation of the mean diameters of the corpora lutea of pregnancy present in the ovaries of each pregnant animal. The successive stages of pregnancy are arranged in order on the abscissa beginning with fertilization at the origin and ending at approximately full-term on the right. It can be seen that there is an initial period of rapid growth ending, before the ova pass from the Fallopian tube into the uterus, and a second period of growth which begins when implantation occurs and continues until parturition.

0·5 mm in diameter. The subsequent growth of the corpus luteum during pregnancy is represented in fig. 9, in which the mean diameters of the corpora lutea of pregnancy of each animal are plotted. The animals are arranged in order on the abscissa, the earliest stage on the left and the latest on the right. The tubal stages were seriated with accuracy, microscopically, and the post-implantation stages approximately, by weight. The early uterine stages, prior to implantation, cannot be seriated with any certainty since they develop so little while free in the uterine lumen. It is apparent that the corpus luteum grows rapidly at first, attaining a diameter of 1·0 to 1·3 mm by the time the tubal ova are in the 8-cell stage. Thereafter there is no growth and there may even be a slight decrease in diameter until implantation occurs, when a second less rapid growth phase begins and continues until parturition. It is remarkable that there is no definite decrease in the size of the corpus luteum until after parturition, since in many animals it has been found that retrogression sets in before parturition and is marked by a very rapid decrease in size toward the end of pregnancy.

Since it has been deduced that many of these pregnant animals were lactating, with a prolonged gestation period in consequence, these data provide, for the first time, information as to the growth of the corpus luteum during the prolonged period when the blastocyst is free in the uterine lumen and is consequently in a condition of arrested development. It would be expected, from analogy with the rat and the mouse (p. 89), that without delay due to lactation, free uterine stages should be one-fourth as numerous as tubal stages. Since 49 tubal stages are included it follows that about 38 of the 50, or approximately 75% of early uterine stages, must be accounted for by prolongation of gestation due to lactation. Examination of fig. 9 therefore strongly suggests that, when the development of the blastocysts is arrested and their sojourn free in the uterine lumen is prolonged by lactation, the growth of the corpus luteum is also arrested. This conclusion is of considerable interest. The work of Long and Evans (1922) on the rat, and of Deanesly (1930) on the mouse has shown that after oestrus, accompanied by copulation, the corpus luteum undergoes an initial period of growth which is completed about the sixth or seventh day in the latter species. During this initial period the secretion of the corpus luteum prepares the uterus for implantation, as is shown by the production of placentomata following suitable experimental stimulation of the uterus. Following this initial period, if the copulation was sterile (*i.e.*, was not followed by implantation of the embryos), the corpus luteum regresses ; if fertile the corpus luteum enters upon a second growth phase immediately after the time when implantation occurs. It is therefore reasonable to suppose that implantation stimulates directly or indirectly the corpus luteum to enter upon this second growth stage. If this is so, the prolonged resting stage between the two growth phases of the corpus luteum, accompanying the delay in implantation, is easily understood.

Corpora lutea atretica frequently, though not invariably, are formed during pregnancy. They vary in number, as many as six or seven having been found in a pair of ovaries. They do not grow as large as the corpora lutea of pregnancy and they can be distinguished from them by size, as well as by the inclusion of the remains of the ovum and the histological character.

The only pregnant animal (E 968) obtained in October, calls for special consideration. It was 19 gm in weight and was obtained on the 6th. The uterus contained two unmistakable blastocysts free in the lumen. The condition of the corpora lutea in the ovaries and of the placental sites in the uterus indicate that it had probably become pregnant during a post-lactation oestrus but, since the mammary glands were not preserved, it is just possible that it did so at the post-partum oestrus and that implantation had been postponed by lactation for some days prior to its being trapped. The uterus of this animal, fig. 18, Plate 11, though parous, is exceedingly small and histologically resembles that of an animal in anoestrus, figs. 17 and 19, Plate 11. It is quite unlike the large and active uterus usually associated with uterine blastocysts and in which the mucosa is preparing for implantation. It is almost impossible to believe that the blastocysts could become implanted with the uterus in this condition and it seems more probable that it was entering into anoestrus and that pregnancy would not have been maintained. If this interpretation is correct, then not only can an animal pass into anoestrus during the early stages of pregnancy but the blastocysts can persist in the uterus while it is retrogressing and until it is in an inactive condition characteristic of anoestrus.

Remarkable giant cells were found in the uterus of one animal in which the uterine blastocysts were in process of implantation. The uterine epithelium was disappearing in the immediate vicinity of the blastocysts and they were passing from the uterine lumen into the sub-epithelial tissues. The giant cells, fig. 20, Plate 11, of which there were several, were confined to one cornu and were scattered along its length. They were situated in the mucosa, between the epithelium and the circular muscle and were of enormous size, measuring as much as 0·4 mm in diameter, although the whole cornu was less than 1·0 mm in diameter. They resembled the normal placental giant cells in appearance and probably had a similar origin. In comparison their size was great, even for the placental giant cells at their maximum development, and their occurrence in the uterus prior to the establishment of the placenta is obviously abnormal. It follows that either they have arisen from the uterine tissues or else, if of embryonic origin, they have persisted from a previous pregnancy. The condition of the uterus indicated that the animal was probably non-parous so that the latter alternative is improbable. The former alternative is in accord with the views of many (*see* SANSOM, 1927), but not all, embryologists who have investigated the origin of the placental giant cells in rodents.

The changes in the reproductive organs typical of pregnancy closely resemble those of the mouse. The uterine and vaginal changes and the development of the mammary glands are similar. At the end of pregnancy the vaginal epithelium becomes greatly thickened and undergoes intense mucification, fig. 13, Plate 10, and fig. 21, Plate 11, as in the mouse and the rat.

d. Lactation Anoestrus

There is an immediate post-partum oestrus in *Evotomys*, as in many other animals, This oestrus is easily identified by the condition of the uterus and by vaginal cornification as in the mouse. The material provides no evidence of oestrus occurring during lactation in animals which do not become pregnant at the post-partum oestrus. The inactive condition of the reproductive organs in non-pregnant lactating animals indicates that there is a lactation anoestrus which probably extends throughout lactation. There is probably a post-lactation oestrus but at the end of the season some animals may pass directly from lactation to winter anoestrus. The condition of the corpora lutea and mammary glands of some early pregnancies suggests that they became pregnant at a post-lactation oestrus period (*see* E 968, p. 92). Two oestrous animals, obtained in June and August respectively, had only very old corpora lutea in the ovaries. The oestrous period, therefore, could not have followed a dioestrous cycle and the condition of the uterus shows that it was not post-partum. It must therefore have followed a period of anoestrus, presumably lactation anoestrus, since both were obtained during the height of the breeding season. The uteri, however, contained no visible placental sites so that, if the animals had just finished lactating, these must have retrogressed much more rapidly than they do during winter anoestrus.

e. Winter Anoestrus

Animals in winter anoestrus are easily identified by the atrophy of the reproductive organs and their inactive appearance on histological examination. The ovaries contain neither large follicles nor recent corpora lutea. Throughout the greater part of the winter the ovaries, in mature animals, contain small fibrosed remnants of the old corpora lutea, and even in the spring, just before the beginning of the breeding season, patches of pigment in the stroma indicate their former presence. The uteri are very small, figs. 17 and 19, Plate 11, but the remnants of placental sites in parous animals persist in the base of the mesometrium throughout the winter. The vaginal epithelium is thin and inactive, fig. 14, Plate 10, and the lumen is reduced in size. The vaginal orifice during anoestrus becomes closed by epithelial fusion. This does not occur in the shrew (BRAMBELL, 1935), which has a single urino-genital orifice in the female, but is possible in *Evotomys*, in which the urethra opens on the clitoris and is thus entirely separate from the vagina.

The authors' thanks are due to Dr. A. S. PARKES, F.R.S., and to Mrs. PARKES for their advice and for collecting part of the material from the Home Counties, to Professor J. P. HILL, F.R.S., for advice, and to Messrs. L. H. JACKSON, H. A. COLE, and W. H. EDWARDS for much assistance in collecting the material.

The authors are indebted to the Rt. Hon. Lord PENRHYN for permission to trap on his estates, where many of the animals were obtained.

The expenses of this research were defrayed in part by grants from the Government Grant Committee of the Royal Society to one of us (F. W. R. B.), for which we wish to express our thanks.

VIII—Summary

The material consisted of 1036 Bank Voles obtained between March, 1931, and May, 1933, chiefly in North Wales, of which 443 were females.

The sex-ratio of the whole of the material trapped was 57·24 ± 1·04 males per cent.

The anatomy of the reproductive organs is similar to that of the mouse. There are closed ovarian capsules and separate cervical canals. The urethral orifice is distinct from that of the vagina. There are two pairs of thoracic and two pairs of abdominal mammae.

The weight of the young at birth is estimated at 1·5 to 2·5 gm. The lightest animal trapped was 6·4 gm, and the heaviest 33·8 gm. The lightest parous or pregnant animal was 12·5 gm. During the winter the weights range from 12 to 19 gm with few exceptions. The body-weights rise rapidly during the second half of April and May.

Females born early in the breeding season breed before its close. Such parous animals frequently survive the winter and breed again the following year.

The breeding season extends from the middle of April until the beginning of October and reaches a maximum in June.

It is estimated that one female may rear four or even five litters in a season.

The mean number of ova ovulated at each oestrus is 4·43 as estimated from a sample of 277 sets of corpora lutea ; the largest number observed was 12. The corpora lutea are distributed at random between the two ovaries of a pair. It is deduced that the number of ova ovulated at each oestrus is not limited by the capacity of the ovaries to produce a sufficient number of mature follicles.

The mean number of foetuses *in utero* in 70 late pregnancies was 4·11 and the largest number observed was 6. Similarly the mean number of placental sites in 58 pairs of parous uteri was 4·48 and the largest was 7.

The mean number of ova ovulated at each oestrus rises during April and May to a maximum in June and falls off thereafter. It is also directly related to the body-weight. This relation is expressed as a straight line regression on body-weight. The seasonal variation and the relation to body-weight cannot be considered independent but the data do not permit a decision as to which is the more fundamental. The mean number of foetuses *in utero* in late pregnancies also varies seasonally and with body-weight.

The incidence of intra-uterine mortality is much heavier when 6 or more, than it is when 5 or less, ova are ovulated. It is concluded that this increased mortality is due to deficiency of materials required for development and not to mechanical overcrowding of the uterus.

At the beginning of the breeding season the majority of females go through a variable number of dioestrous cycles, most frequently 3 but sometimes more, before becoming pregnant. A few become pregnant at the first oestrus. These sterile cycles are probably not accompanied by copulation. Since the males at this time are in full breeding condition the failure to copulate must be due to the females.

Animals attaining puberty during the latter part of the breeding season become pregnant at the first oestrus much more frequently.

The growth of the ovum and follicle is described. The follicles have a mean diameter of 550 to 800 μ at the time of ovulation. The heterotypic spindle is formed before ovulation and the division completed subsequently. Copulation normally occurs shortly before ovulation but after the formation of the heterotypic spindles in the ova. Ovulation occurs spontaneously in the absence of copulation. The spermatozoon enters the ovum before the completion of the homotypic division and the separation of the second polar body. During oestrus the uterus is distended with fluid and the vaginal epithelium is intensely cornified, as in the mouse. Copulation results in the formation of a hard vaginal plug which remains in position until the ova are in the stage with two pro-nuclei.

The total number of pregnant animals obtained was 179, of which 49 had tubal ova, 50 uterine blastocysts free in the lumen and 80 implanted embryos. The ovum passes from the Fallopian tube into the uterus as a morula.

There is evidence that many parous animals are pregnant and lactating simultaneously and that, in these, pregnancy is prolonged by lactation causing a delay in implantation. This delay results in the blastocysts remaining in a resting stage in the uterine lumen for a considerable period.

The newly ruptured follicle measures 0·5 mm in diameter. During pregnancy the corpus luteum grows rapidly until the tubal ova are in the 8-cell stage approximately, when it is 1·0 to 1·3 mm in diameter. It remains at this size until implantation occurs, even when this is delayed by lactation, and then enters upon a second growth phase which continues until the end of gestation.

One animal obtained in October had blastocysts free in the uterine lumen but the uterus was atrophied and in the anoestrous condition.

At the end of gestation the vaginal epithelium becomes very thick and undergoes intense mucification as in the mouse.

There is an immediately post-partum oestrous period, and after lactation animals probably come into oestrus again if they did not become pregnant at the post-partum oestrus.

Non-pregnant lactating animals exhibit a lactation anoestrus.

There is a well-marked winter anoestrus during which the vaginal orifice is closed.

IX—REFERENCES

Allanson (1932). 'J. Exp. Biol.,' vol. **9**, p. 117.

Baker (1930). 'Proc. Zool. Soc. Lond.,' p. 113.

Barrett-Hamilton (1911). "A History of British Mammals," London, Pt. 15, p. 410 *et seq.*

Brambell (1928). 'Proc. Roy. Soc.,' B, vol. **103**, p. 258.

—— (1935). 'Phil. Trans.,' B, vol. **225**, p. 1.

DEANESLY (1930). ‘Proc. Roy. Soc.,’ B, vol. **106**, p. 578.
—— (1934). ‘Phil. Trans.,’ B, vol. **223**, p. 239.
FISHER (1930). “Statistical Methods for Research Workers,” Edinburgh.
KIRKHAM (1916). ‘Anatomical Record,’ vol. **11**, No. 2.
LATASTE (1887). ‘Actes Soc. linn. Bordeaux,’ vol. **40**.
LONG and EVANS (1922). “Mem. Univ. California,” vol. **6**, p. 1.
MARSHALL (1922). “The Physiology of Reproduction,” London, p. 37.
MIRSKAIA and CREW (1931). ‘Proc. Roy. Soc. Edinb.,’ vol. **51**, p. 1.
ROBB (1928). ‘Proc. Nat. Acad. Sci. Wash.,’ vol. **14**, p. 394.
—— (1929). ‘J. Exp. Biol.,’ vol. **6**, p. 311.
SANSOM (1927). ‘Proc. Roy. Soc.,’ B, vol. **101**, p. 354.
SVIHLA (1929). ‘Michigan Acad. Sci. Arts and Letters,’ vol. **11**, p. 1.

X—Description of Plates

Plate 10

Fig. 10—Photograph of the ventral aspect of the adult female reproductive organs dissected so as to show them *in situ* in their natural relations. The pubic symphysis has been removed to expose the vagina. × 1·9.

An outline key is provided in fig. 10A.

Abbreviations :—*b*, bladder ; *c*, median portion of uterus containing the separate cervical canals of the two uterine cornua ; *cl*, clitoris ; *f*, Fallopian tubes ; *k*, kidney ; *m*, mesometrium ; *o*, ovaries ; *p*, prepucial glands of clitoris ; *r*, rectum ; *s*, suprarenal glands ; *u*, uterine cornu ; *ur*, ureter ; *v*, vagina ; *vo*, vaginal orifice.

Fig. 11—Photomicrograph of a section of the ovary of an adult (E 570), obtained in May with tubal ova, showing four generations of corpora lutea. The newest are numbered 1 and the oldest 4. × 32.

Fig. 12—Photomicrograph of a section of the vaginal epithelium during the first oestrus (E 520). A vaginal plug was present and the mature follicles contained oocytes in anaphase of the heterotypic division. The epithelium shows intense cornification. × 370.

Fig. 13—Photomicrograph of a section of the vaginal epithelium at the end of pregnancy (E 680). The epithelium is undergoing mucification. A transverse section of the same vagina is shown at a lower magnification in fig. 21, Plate 11. × 370.

Fig. 14—Photomicrograph of a section of the vaginal epithelium of a parous animal (E 1045) during winter anoestrus. The debris in the uterine lumen in the lower part of the figure contains nucleated epithelial cells and leucocytes. The epithelium is very thin. × 370.

FIG. 11.

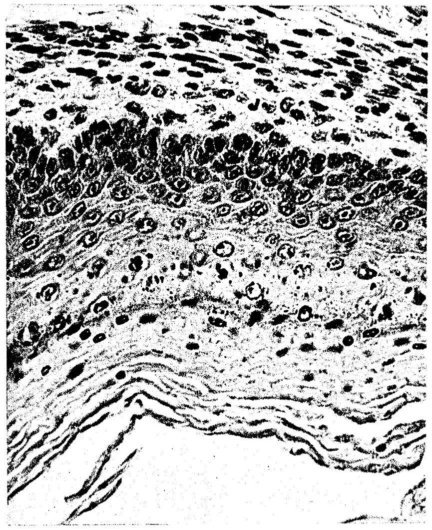

FIG. 12.

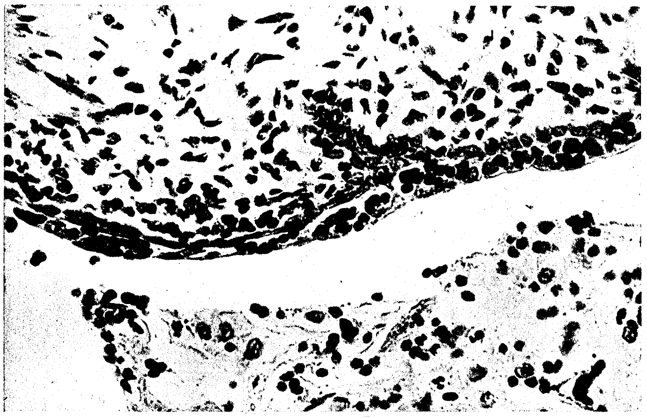

FIG. 14.

FIG. 13.

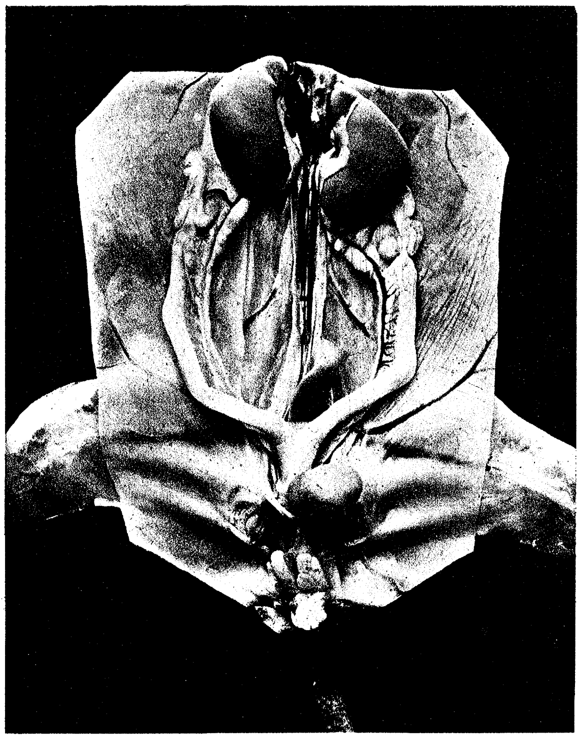

FIG. 10.

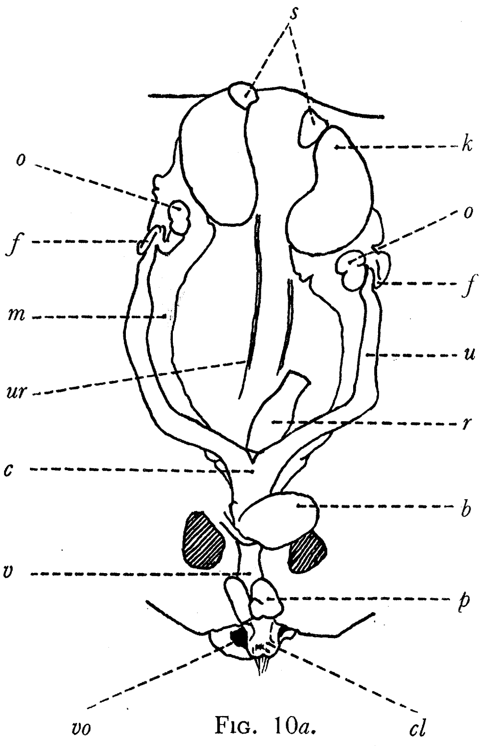

FIG. 10*a*.

PLATE 11

FIG. 15—Photomicrograph of a transverse section of a mature follicle about to ovulate (E 189). The oocyte was in metaphase of the heterotypic division although the chromosomes do not appear in this section. × 87.

FIG. 16—Photomicrograph of a transverse section of the uterine cornu during oestrus (E 501). The extreme distension of the uterus with fluid and the consequent thinning of the uterine wall are apparent. × 24.

FIG. 17—Photomicrograph of a transverse section of the uterine cornu of a non-parous animal (E 402) during winter anoestrus. × 120.

FIG. 18—Photomicrograph of a transverse section of the uterine cornu of a parous animal with unimplanted uterine blastocysts obtained in October (E 968). Comparison with figs. 17 and 19 shows that the uterus is passing into the anoestrous condition and that implantation presumably would not take place. × 120.

FIG. 19—Photomicrograph of a transverse section of the uterine cornu of a parous animal (E 419) during winter anoestrus. Comparison with fig. 17 shows the difference in size and structure of parous and non-parous uteri during anoestrus. × 120.

FIG. 20—Photomicrograph of a transverse section of the uterine cornu of a pregnant animal (E 603), in which the uterine blastocysts were becoming implanted, showing two abnormal giant cells in the mucosa. × 75.

FIG. 21—Photomicrograph of a transverse section of the vagina at the end of pregnancy showing mucification of the epithelium. Part of the epithelium is shown at a higher magnification in fig. 13, Plate 10. × 22.

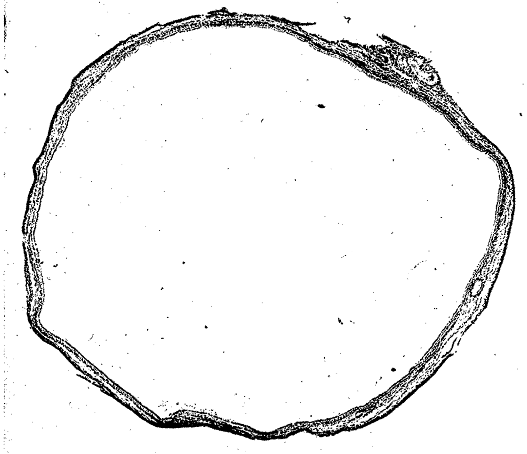

FIG. 16.

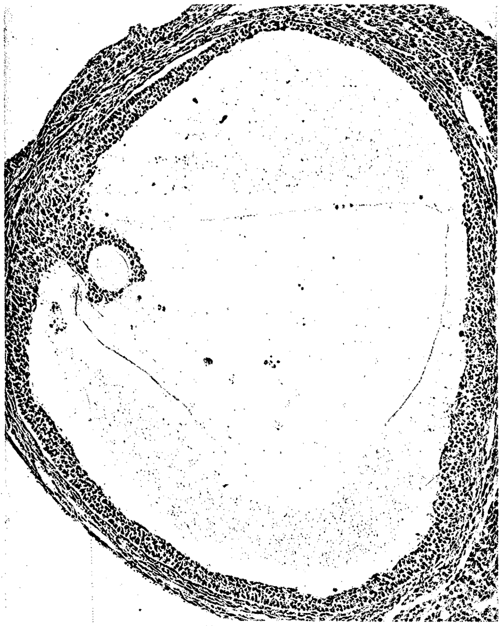

FIG. 15.

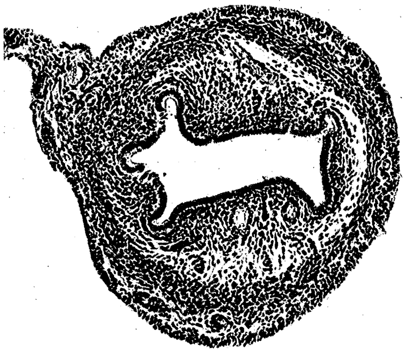

FIG. 17.

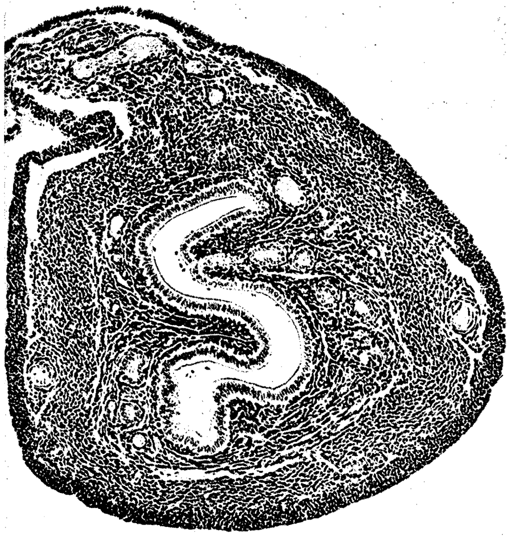

FIG. 18.

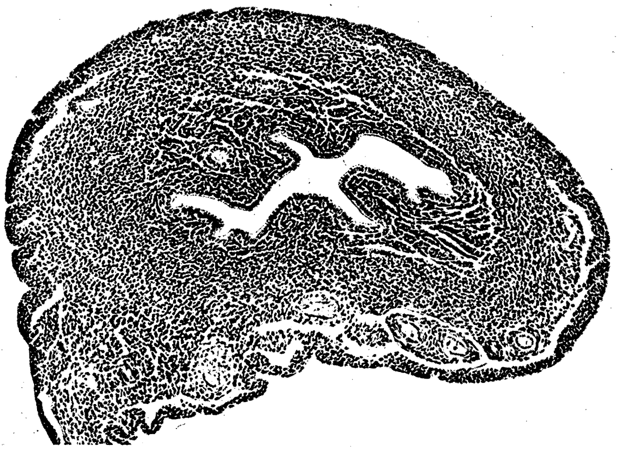

FIG. 19.

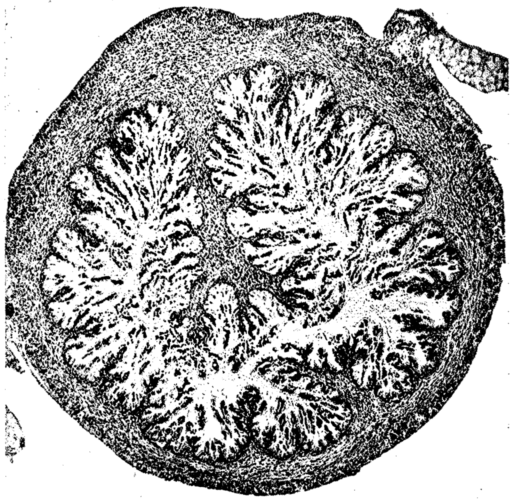

FIG. 21.

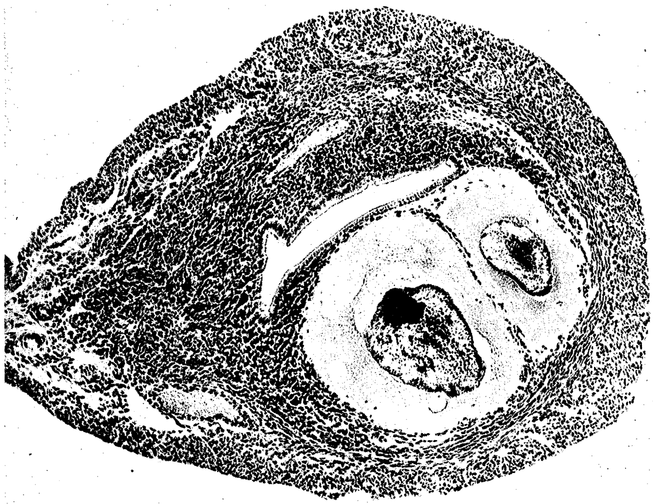

FIG. 20.

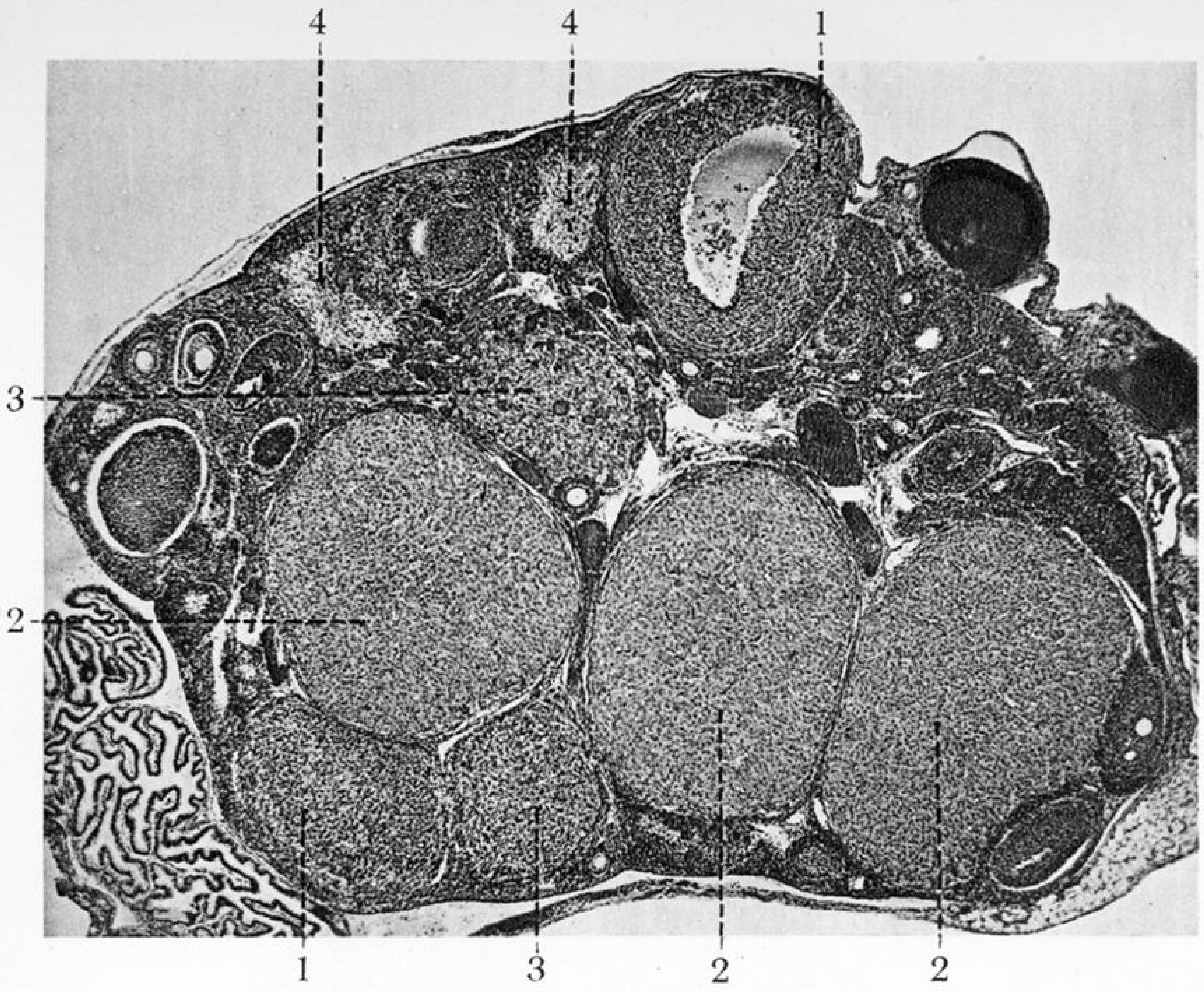

FIG. 11.

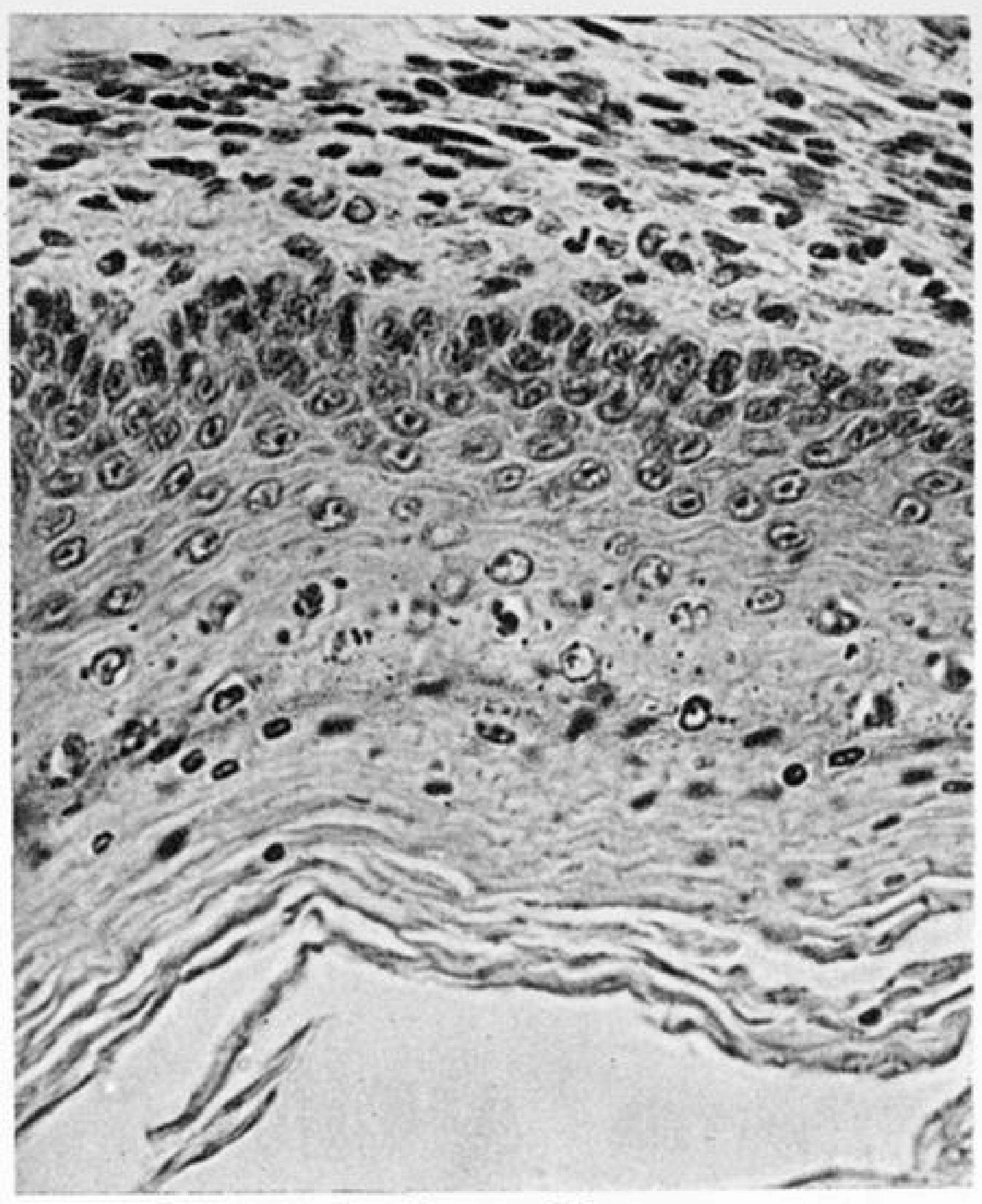

FIG. 12.

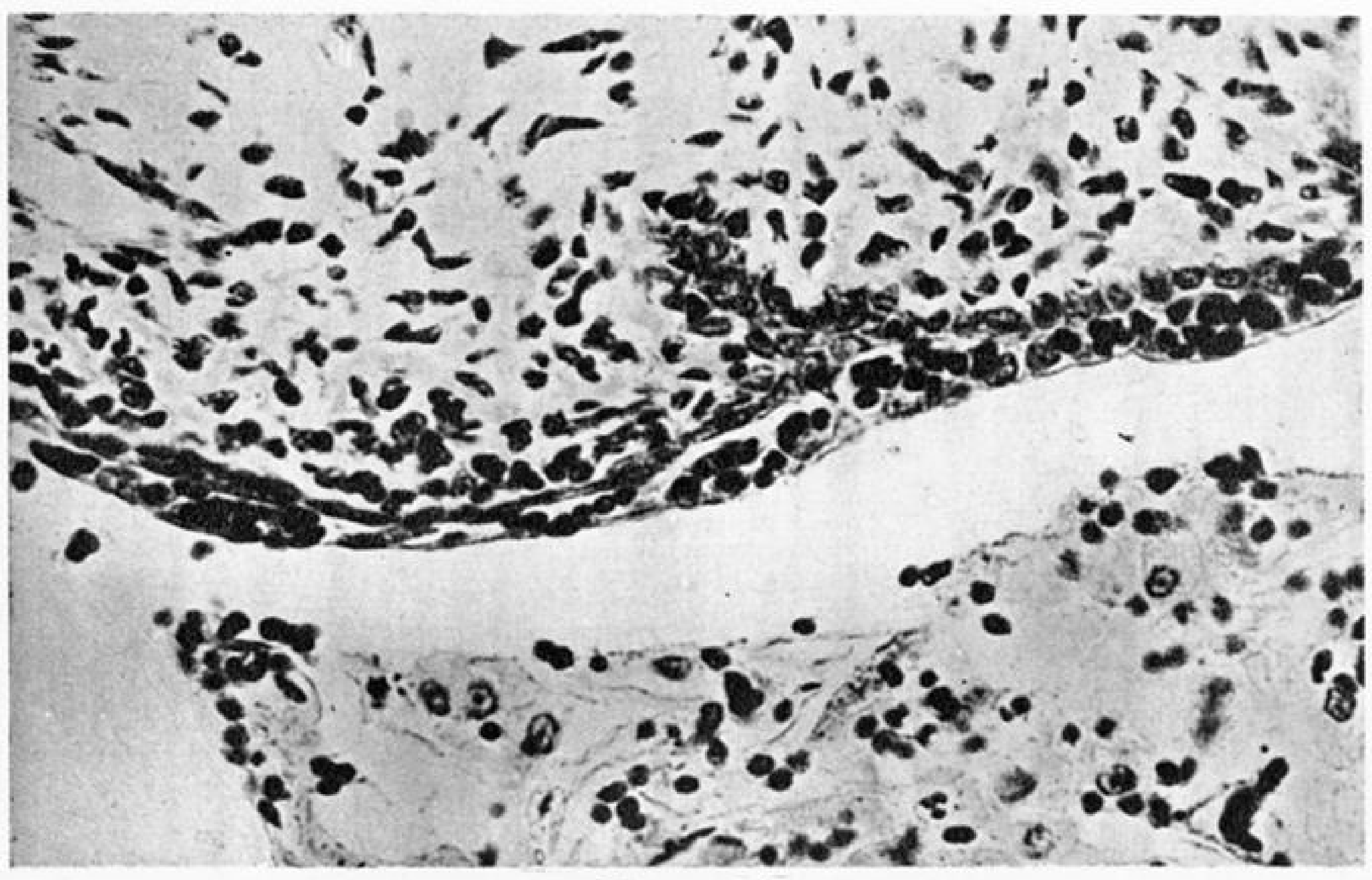

FIG. 14.

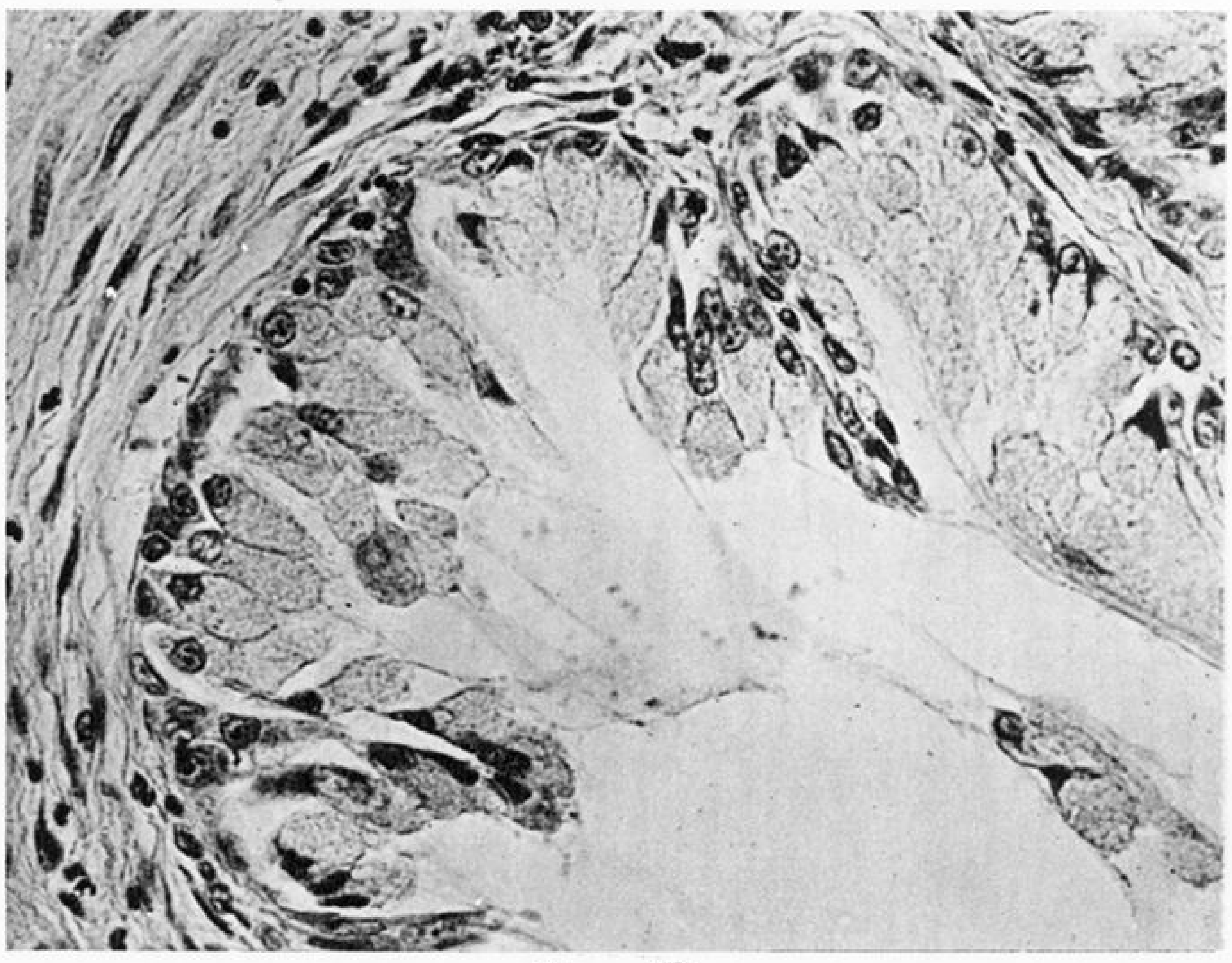

FIG. 13.

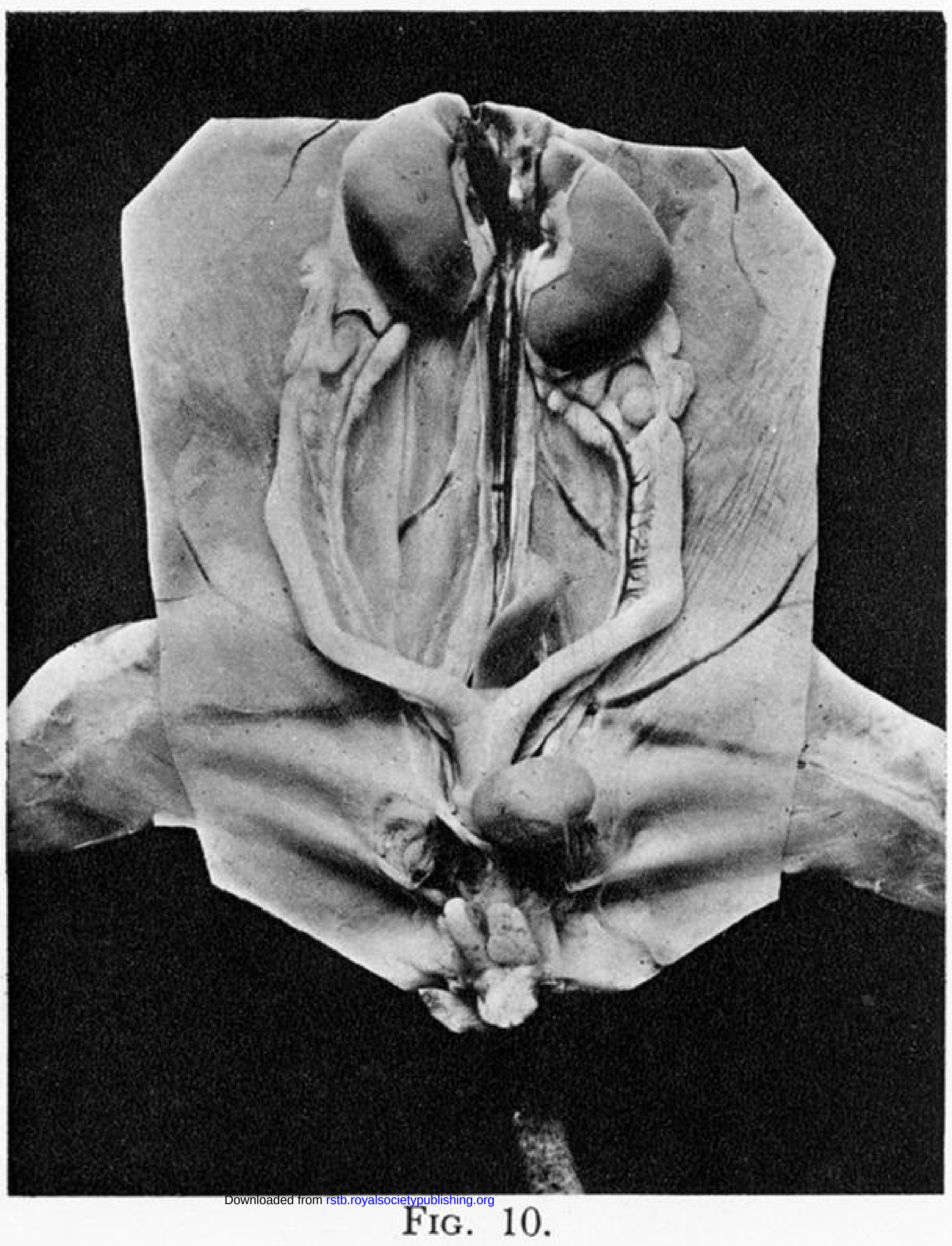

FIG. 10.

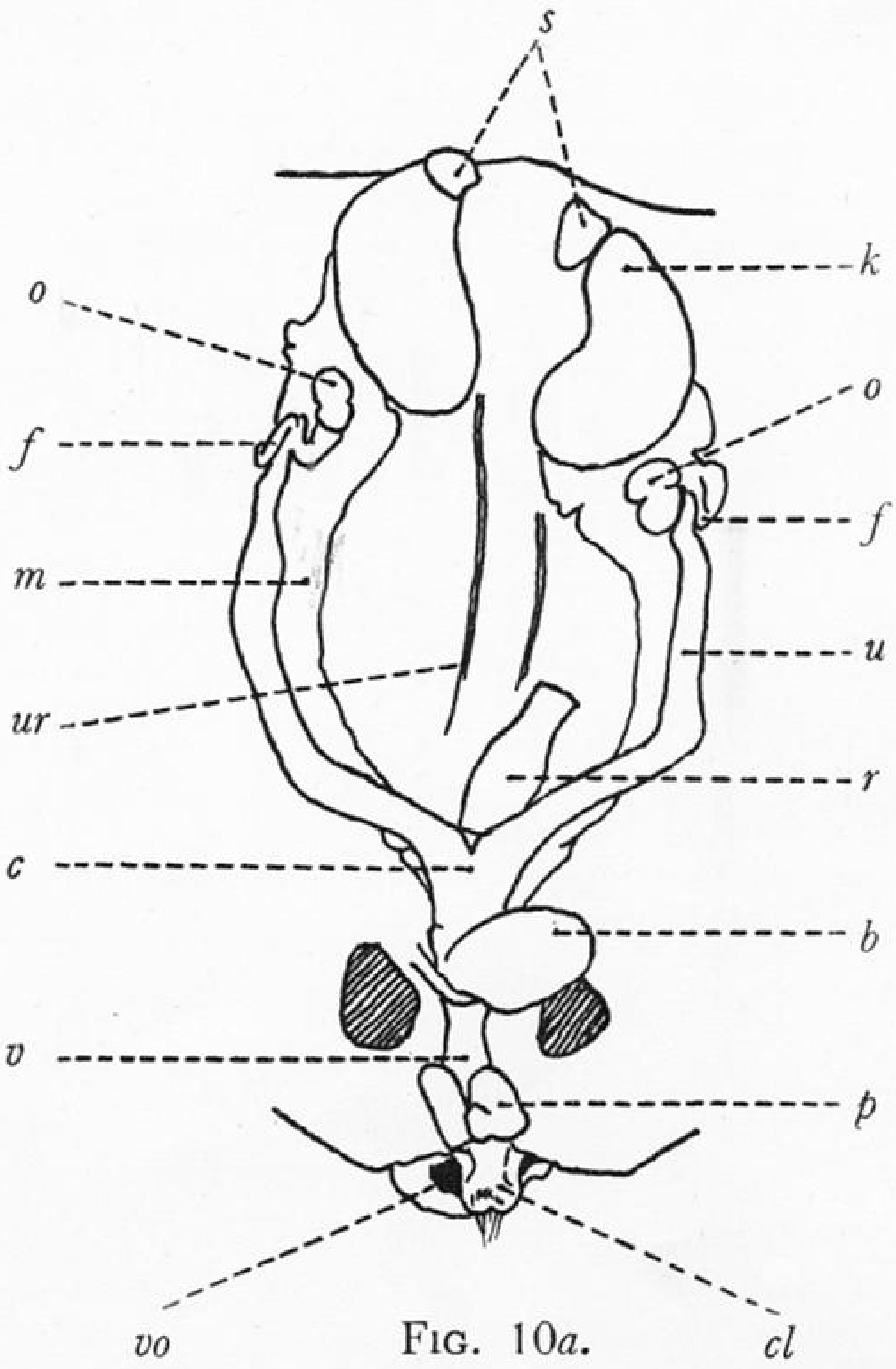

FIG. 10*a*.

PLATE 10

FIG. 10—Photograph of the ventral aspect of the adult female reproductive organs dissected so as to show them *in situ* in their natural relations. The pubic symphysis has been removed to expose the vagina. × 1·9.

An outline key is provided in fig. 10A.

Abbreviations :—*b*, bladder ; *c*, median portion of uterus containing the separate cervical canals of the two uterine cornua ; *cl*, clitoris ; *f*, Fallopian tubes ; *k*, kidney ; *m*, mesometrium ; *o*, ovaries ; *p*, prepucial glands of clitoris ; *r*, rectum ; *s*, suprarenal glands ; *u*, uterine cornu ; *ur*, ureter ; *v*, vagina ; *vo*, vaginal orifice.

FIG. 11—Photomicrograph of a section of the ovary of an adult (E 570), obtained in May with tubal ova, showing four generations of corpora lutea. The newest are numbered 1 and the oldest 4. × 32.

FIG. 12—Photomicrograph of a section of the vaginal epithelium during the first oestrus (E 520). A vaginal plug was present and the mature follicles contained oocytes in anaphase of the heterotypic division. The epithelium shows intense cornification. × 370.

FIG. 13—Photomicrograph of a section of the vaginal epithelium at the end of pregnancy (E 680). The epithelium is undergoing mucification. A transverse section of the same vagina is shown at a lower magnification in fig. 21, Plate 11. × 370.

FIG. 14—Photomicrograph of a section of the vaginal epithelium of a parous animal (E 1045) during winter anoestrus. The debris in the uterine lumen in the lower part of the figure contains nucleated epithelial cells and leucocytes. The epithelium is very thin. × 370.

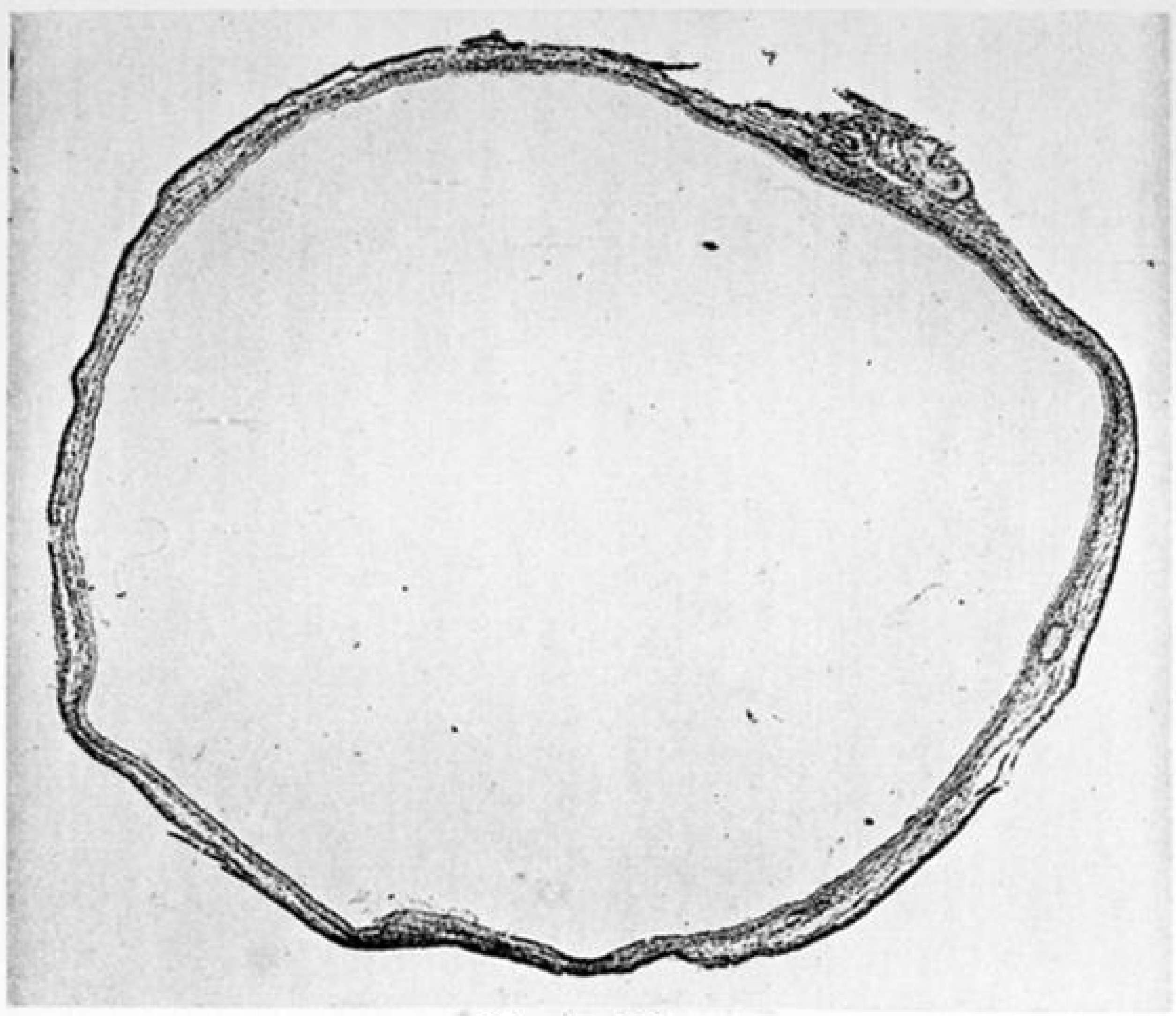

FIG. 16.

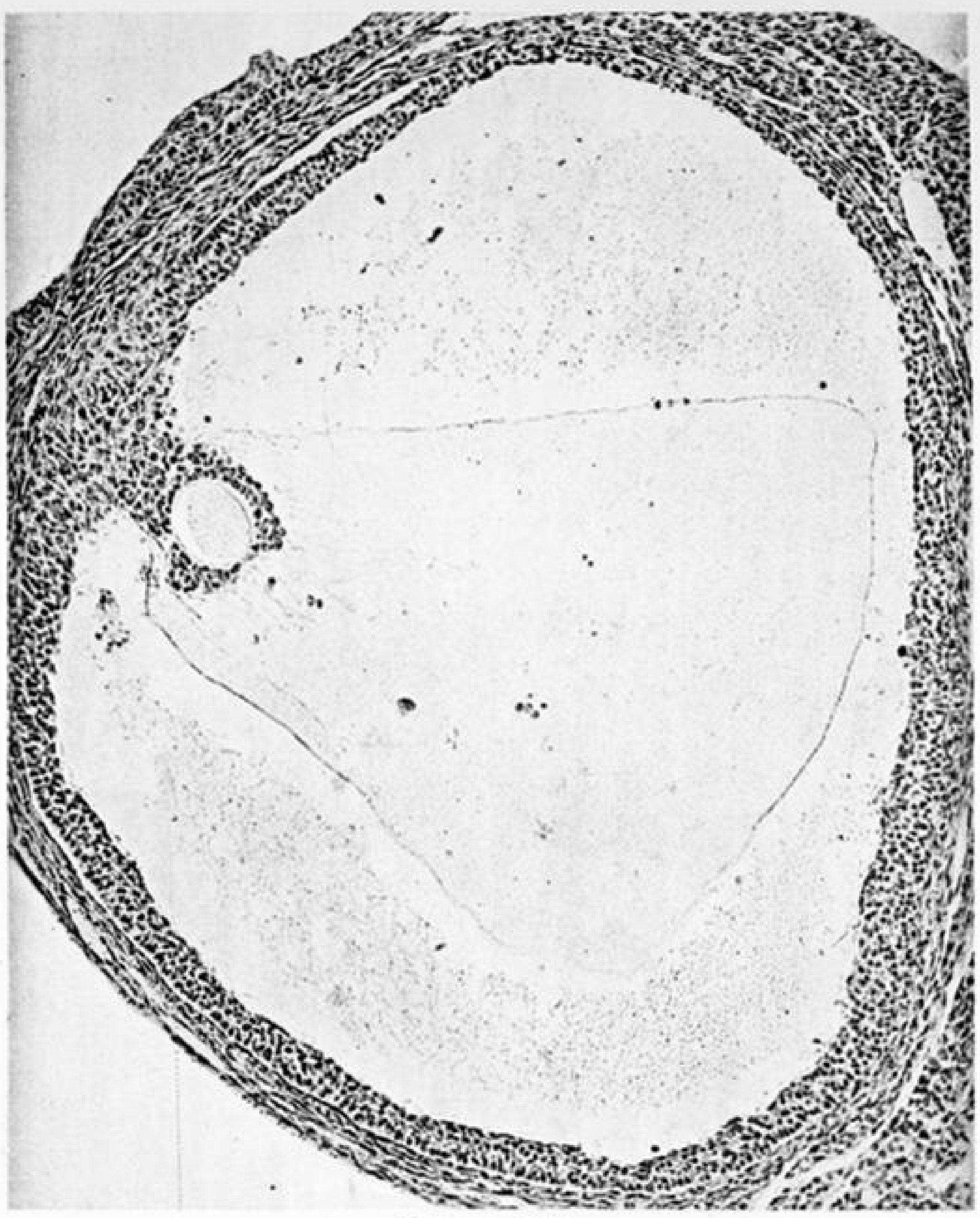

FIG. 15.

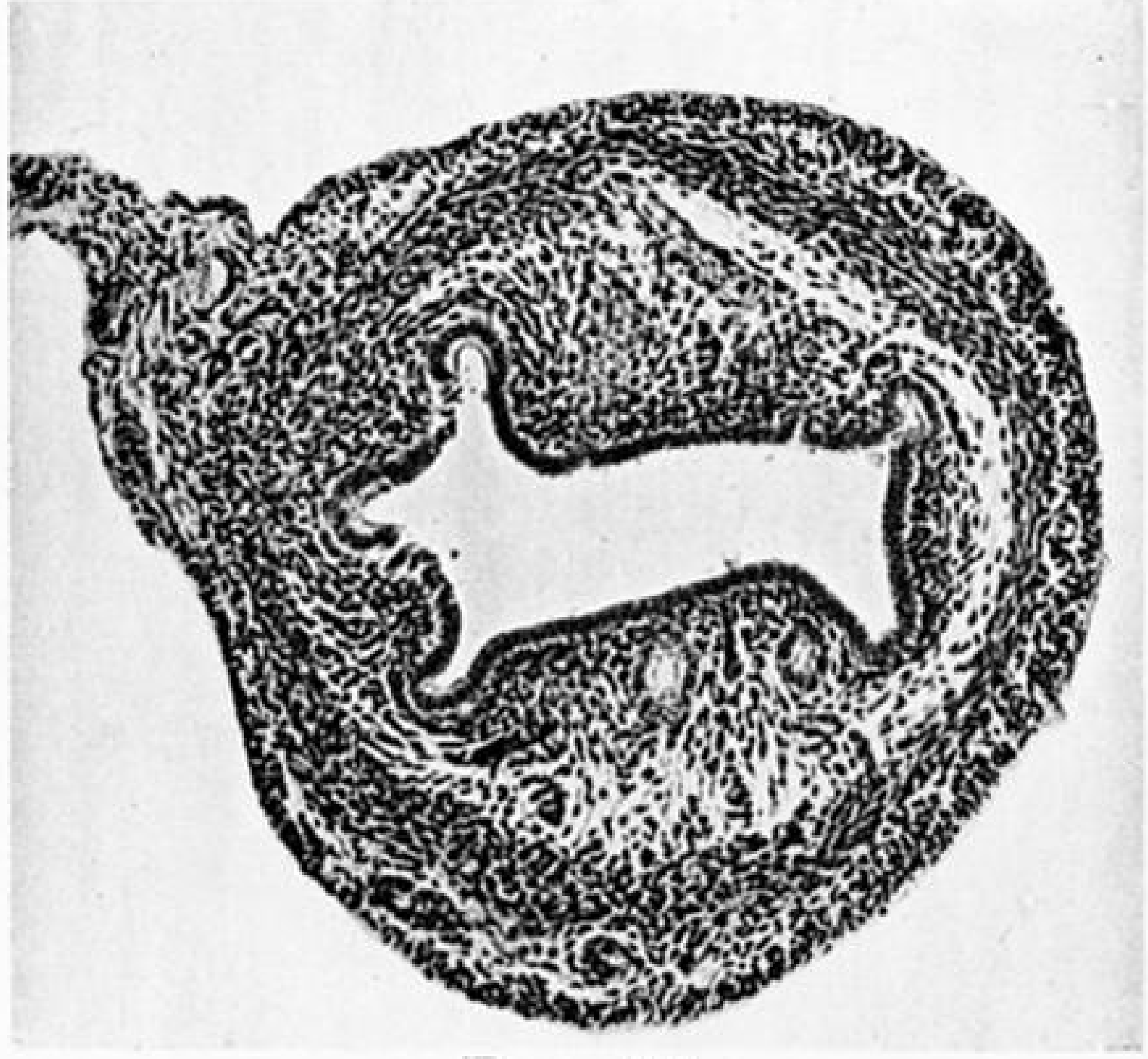

FIG. 17.

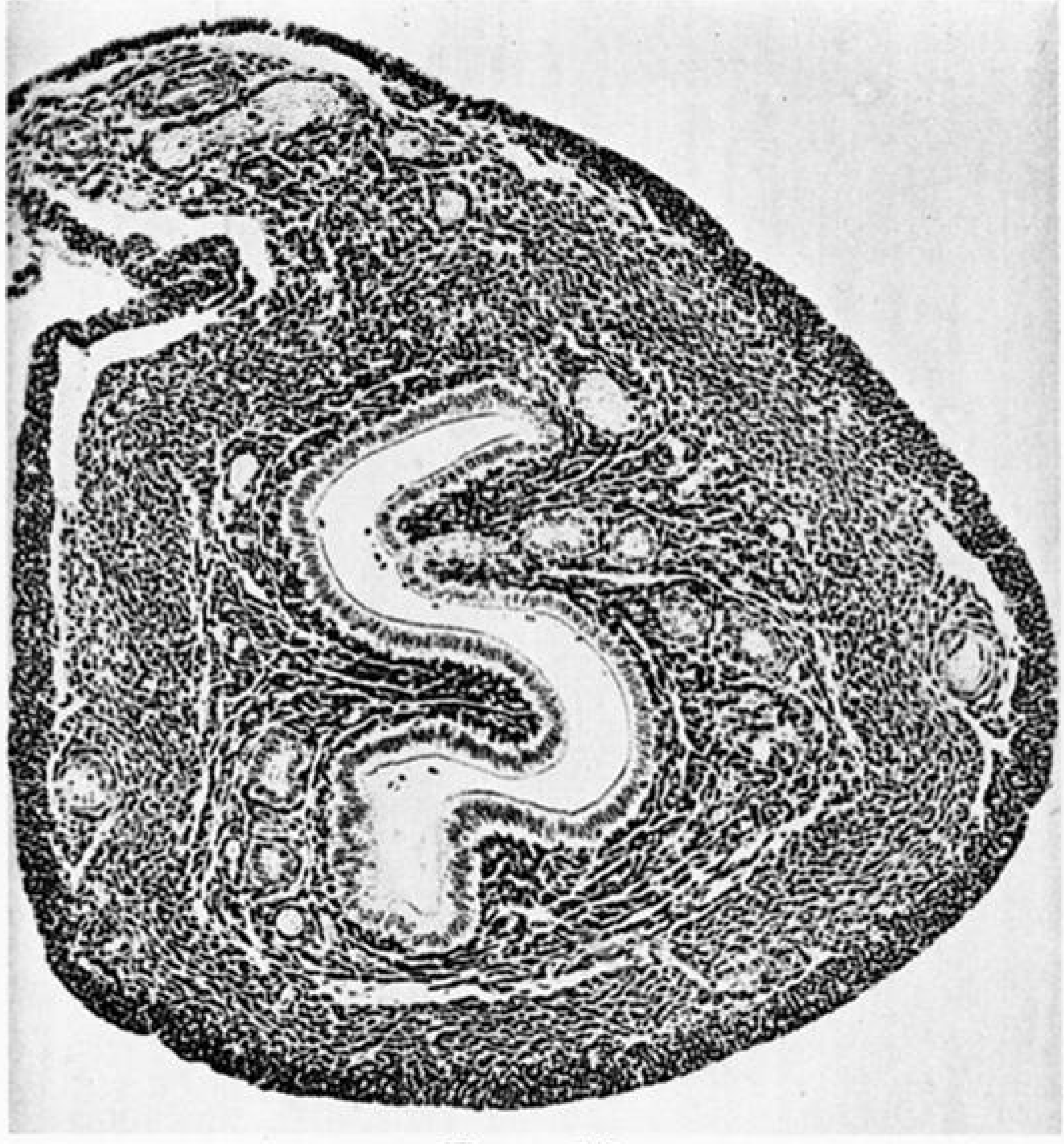

FIG. 18.

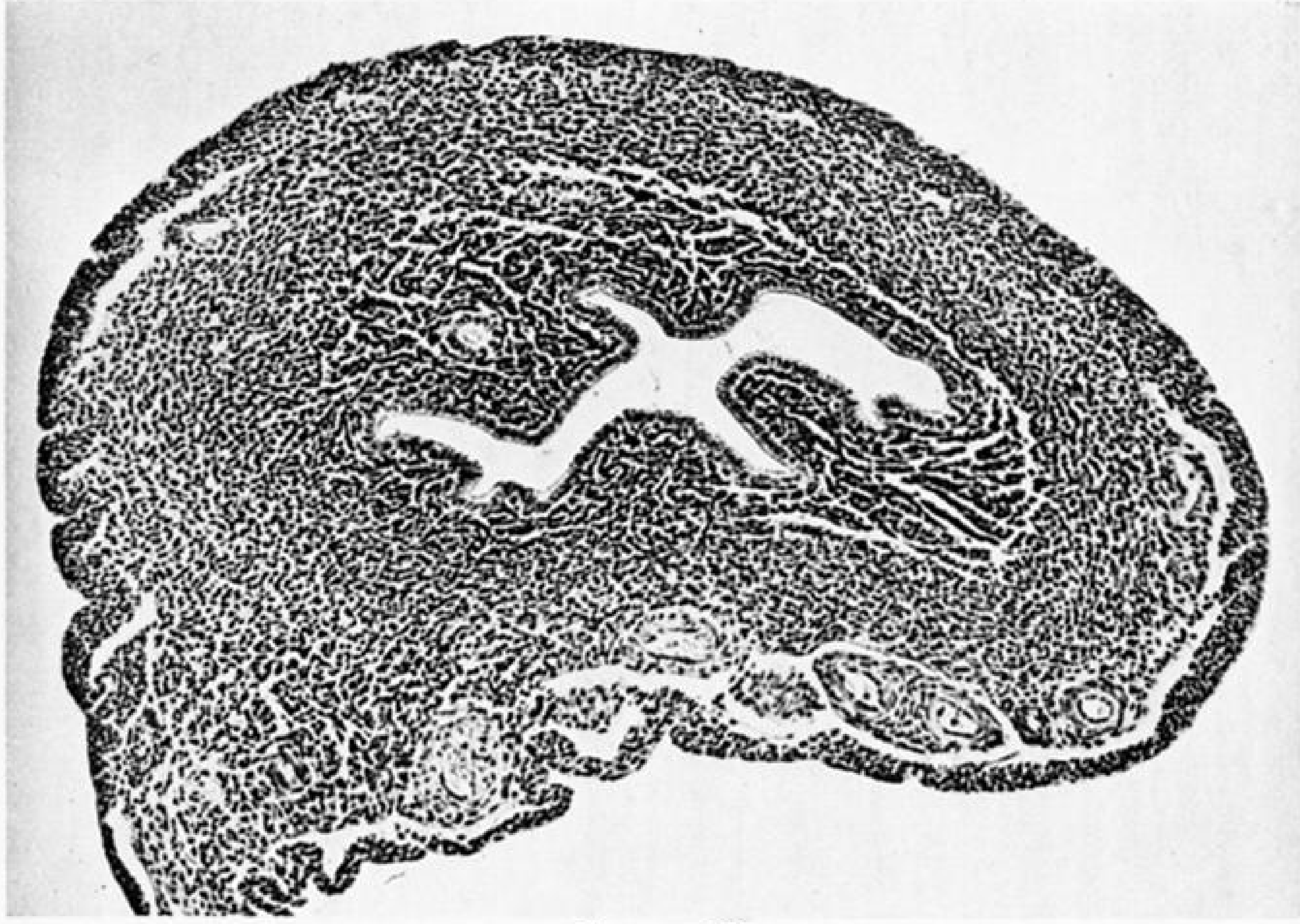

FIG. 19.

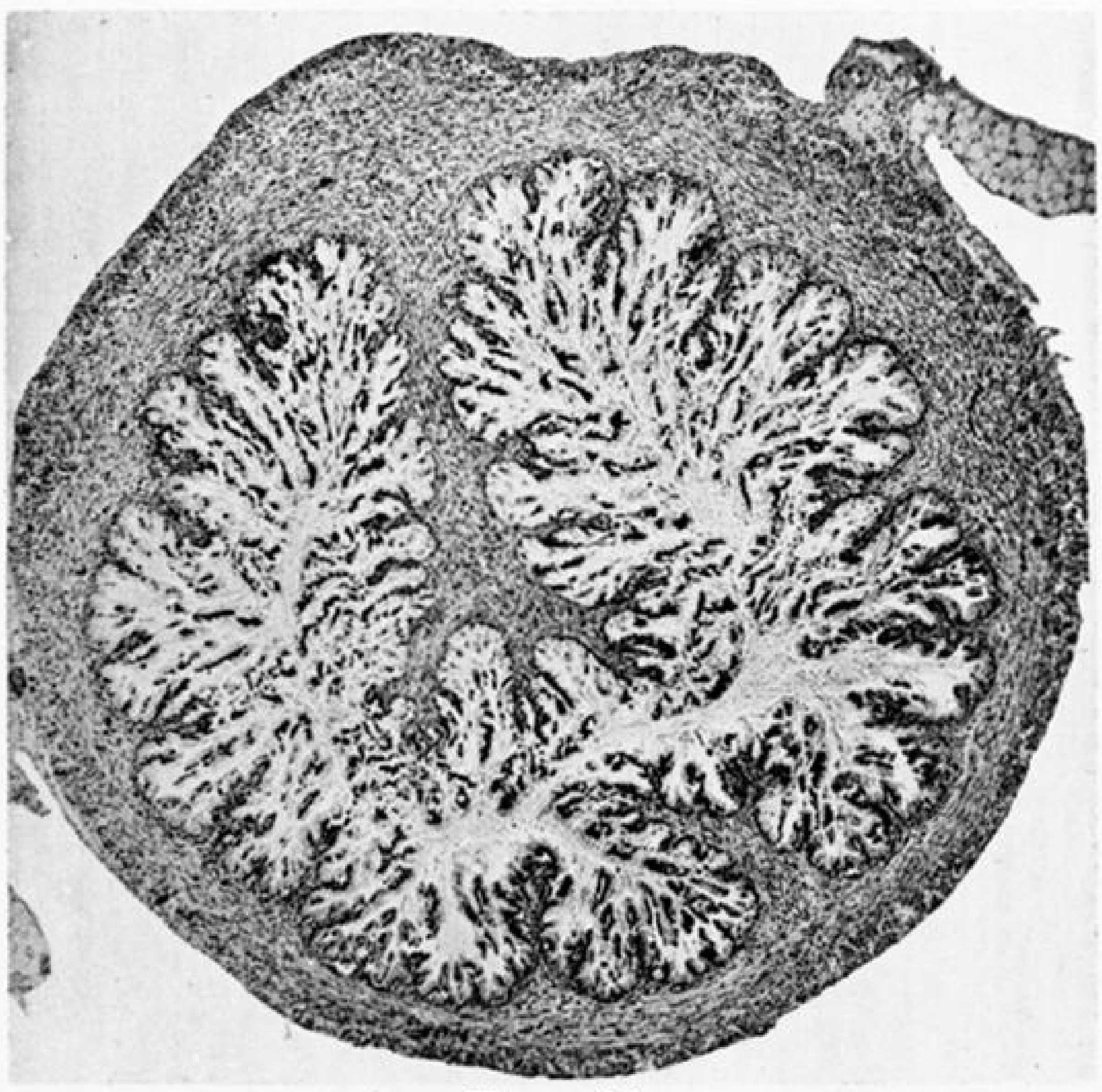

FIG. 21.

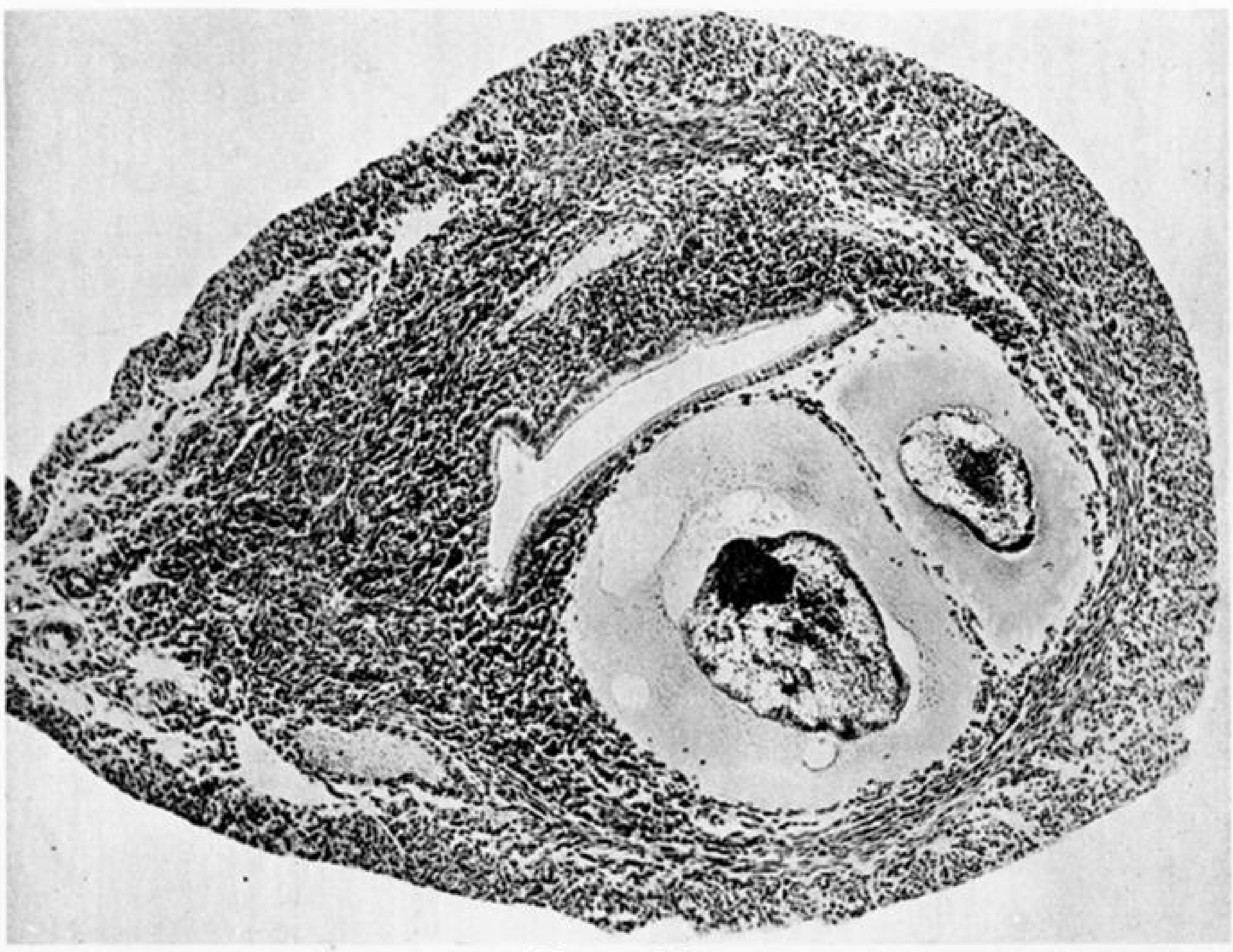

FIG. 20.

PLATE 11

FIG. 15—Photomicrograph of a transverse section of a mature follicle about to ovulate (E 189). The oocyte was in metaphase of the heterotypic division although the chromosomes do not appear in this section. × 87.

FIG. 16—Photomicrograph of a transverse section of the uterine cornu during oestrus (E 501). The extreme distension of the uterus with fluid and the consequent thinning of the uterine wall are apparent. × 24.

FIG. 17—Photomicrograph of a transverse section of the uterine cornu of a non-parous animal (E 402) during winter anoestrus. × 120.

FIG. 18—Photomicrograph of a transverse section of the uterine cornu of a parous animal with unimplanted uterine blastocysts obtained in October (E 968). Comparison with figs. 17 and 19 shows that the uterus is passing into the anoestrous condition and that implantation presumably would not take place. × 120.

FIG. 19—Photomicrograph of a transverse section of the uterine cornu of a parous animal (E 419) during winter anoestrus. Comparison with fig. 17 shows the difference in size and structure of parous and non-parous uteri during anoestrus. × 120.

FIG. 20—Photomicrograph of a transverse section of the uterine cornu of a pregnant animal (E 603), in which the uterine blastocysts were becoming implanted, showing two abnormal giant cells in the mucosa. × 75.

FIG. 21—Photomicrograph of a transverse section of the vagina at the end of pregnancy showing mucification of the epithelium. Part of the epithelium is shown at a higher magnification in fig. 13, Plate 10. × 22.