THE REPRODUCTION OF THE AFRICAN ELEPHANT, *LOXODONTA AFRICANA*

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Between December 1946 and December 1948, and January to March 1950, 150 elephants made available in the course of control work carried out by the Uganda Game Department were examined in greater or less detail according to circumstances. Eighty-one were females, of which sixty-seven were adult and thirty-one had an embryo in the uterus. All the dissections were carried out in the field, and the present account includes observations on the terrain, the food of the elephant, and other aspects of its ecology. Linear measurements of the carcasses and photographs of the molar teeth provide a guide to the age of specimens. Tusk growth is nearly similar in males and females until puberty, after which those of females generally cease to grow. The reproductive organs of the male are briefly described; those of the female are described in more detail, and discrepancies between existing accounts are considered in the light of this relatively extensive series of specimens. The mode of formation of the ovarial sac is unusual and is described from foetal, neonatal and adult specimens. There is marked hypertrophy of the interstitial tissue of the foetal gonads during the later stages of gestation. Breeding occurs at all times of year, but mating is possibly more frequent in the period December to March than at other times. Both sexes reach maturity at 8 to 12 years, and the female continues to breed until old age. Parturition is followed by a lactation anoestrus, after which the female undergoes a number of brief oestrous cycles until pregnancy ensues, lactation being continued throughout the subsequent gestation period. The interval between parturition and subsequent conception is normally of the same order of duration as the gestation period, and the normal calving interval appears to be rather less than four years. The ovarian cycle of the adult is characterized by the occurrence of multiple ovulation and the presence of many apparently active and histologically indistinguishable corpora lutea in both ovaries at all the stages of pregnancy which were encountered. It is probable that the corpus luteum of pregnancy develops from one of a number of follicles which ovulate under the same hormonal stimulus, and that it persists together with the accessory corpora lutea, some of which arise from follicles which ovulate and some from follicles which luteinize without ovulating. The corpora lutea are replaced about mid-pregnancy by a second set, which are formed by the luteinization of all the follicles with antra in both ovaries; some at least of the larger ones ovulate while many smaller ones do not. Follicular growth is suppressed in the later stages of pregnancy. The cycle of events bears some resemblance to that which occurs in the mare, and the comparison is discussed in detail. The ovarian periphery is characterized by numerous subsurface crypts and papillose projections which increase the area of the germinal epithelium. A description of the placenta and foetal membranes is in preparation, and preliminary study reveals a striking similarity to *Hyrax*, particularly in the quadri-lobulate allantois. The findings are discussed with reference to the phylogenetic position of the genus, the probable role of the corpus luteum in pregnancy, and the significance of the results in relation to the conservation of existing wild elephant populations.

Introduction

(1) *Field work*

The control and conservation of the elephant population of Uganda has been an important part of the work of the Game Department since its establishment (originally as a department specifically for elephant control) in 1925, and a considerable number of elephants, usually between 600 and 1000, have been shot each year in the course of this work. In 1946 the writer was invited to work in Uganda for two years to make use of some of the biological material thus made available, and provision was made for the study of collected material in England afterwards. For although the elephant has always excited interest, surprisingly little was known about it beyond the scattered and often fanciful descriptions of its habits published by hunters. There is very scant knowledge of the details of the anatomy of the African, or even of the Indian, elephant, and still less of its physiology or its habits in the wild state. The original plan was for the writer to travel with a European Game Ranger and dissect elephants shot by him and his African staff of Game Guards. In the event, as the Senior Game Ranger, Captain R. J. D. Salmon, M.V.O., M.C., had to retire from active hunting owing to illness, I spent a few weeks with another European hunter, and thenceforward hunted only with African Game Guards, for part of the time in the capacity of an Honorary Game Ranger.

Most of the specimens were obtained in groups of more than one at a time, and as it was almost invariably necessary to carry out the dissection in a few hours, attention was perforce confined, in most cases, to the principal objects of the investigation. It was not often possible to carry out the dissection on the day the animal was killed, as it is impracticable to carry preservatives, etc., with a hunting party, and indeed the hunters are most effective when they form as small a party as possible. Furthermore, most of the specimens were obtained after several hours' hunting, often the greater part of the day, and there was not enough time left to carry out the dissection. It was not possible to leave the carcass overnight, once it was opened, as hyenas and vultures destroyed it. The routine adopted in the field, therefore, varied with the circumstances, and particularly with the number of specimens obtained, and their sex. The main object was kept strictly in view, the reproductive organs were examined as soon after death as possible, linear measurements were taken and the molar teeth photographed, and other anatomical points were investigated, and specimens sought, when time was available.

A certain amount of non-elephant material was obtained, including a series of specimens of *Hyrax* (*Procavia* sp.), upon which work has begun. Such material, of elephant and other animals, as the writer does not expect to be able to investigate has been passed on to other zoologists for study.

(2) *Localities where elephant specimens were obtained*

All the specimens were obtained in Uganda, and the areas where they were obtained are listed below. Areas 3, 4 and 5 are closely adjoining, the remainder are considerably more distinct. The locality of origin is given for each individual in the table of measurements in the Appendix.

Area 1. North of Gulu, in Acholi District.

Area 2. Toro District, east of Fort Portal.

Area 3. Bwamba Forest, near Semiliki River, south of Lake Albert.

Area 4 and area 5. The area adjoining the Lake Albert Game Reserve, to the south-east of the Reserve, and bounded to the north and east by the Victoria Nile and the Kafu River. Area 4 is separated from area 5 by the Masindi-Atura road, area 4 being to the north-west and area 5 to the south-east of this road. Area 4 includes part of the Budongo Forest.

Area 6. West Nile District, near the Moyo-Arua road, in the vicinity of the Koich Bridge.

(3) *Terrain, food, etc.*

Loxodonta africana is primarily an inhabitant of open tall-grass country (Shortridge 1934) and would appear to have taken to forest only as a result of being intensively hunted. Its food consists mainly of the most easily available fresh vegetation, eaten in great quantity but not very thoroughly digested. Elephants appear to be attracted by the scent of certain crop plants, and to raid gardens to obtain them. In Uganda the major item of the elephant's diet is grass, together with some twigs and leaves of trees. When in forest they browse, taking the most easily available food. The stomach of the youngest calf in table 2, p. 105 (E134) contained only milk, but that of the other very young animal (E119) contained some grass, and the crowns of its first teeth mm_2, and of three of the laminae of mm_3, were worn flat and were beginning to show the characteristic enamel-loop pattern.

Stories of the wild elephant's sagacity, cunning, or intelligence, according to the narrators' various interpretations, are numerous in the literature of safari experiences. The writer is not in a position to give a comprehensive account of the habits of elephants, and they obviously form a very difficult subject for study, but the difficulties would be equalled by the fascination of the task if it proved to be practicable. The behaviour of elephants, both as individuals and as a community, is evidently related to two outstanding attributes, the possession of a prehensile organ and their virtual immunity from predators (except, in modern times, man). A measure of our ignorance of their habits is the fact that the significance of the well-known phenomenon of 'musth' and the function of the temporal glands is unknown, even in the Indian elephant. Beyond the fact that 'musth' is apparently related to sexual excitement, although males which are not 'musth' will readily mate with a female that is in oestrus, little is known of this phenomenon. It does not occur simultaneously in all the males of a group, and does not appear to have a marked seasonal rhythm in the elephant population as a whole. The temporal gland sometimes secretes in a healthy female. In the African elephant these glands function, at least over a considerable part of the year, not only in adult males but also in juvenile males and in juvenile and adult females, including pregnant animals. The relation of 'musth' to breeding is obscure, and it is not even clear that the 'musth glands' have the same function in Indian and African elephants.

(4) *The anatomy of the elephant*

By far the most comprehensive account of the anatomy of an elephant is given in a series of papers by Dr N. B. Eales, based on the very thorough dissection of a single male foetus of *L. africana.* Eales reviewed the existing literature respecting all aspects of the anatomy of the elephant, collated the accounts of earlier authors and compared them with her own findings, set out the differences which had been observed between the Asian and African species, and considered the results in relation to the palaeontology and affinities of the Proboscidea as a whole. A preliminary account described the external features, temporal glands and skin of the foetus (Eales 1925), and was followed by a series of papers on the anatomy of the head (Eales 1926), the body muscles (1928) and the contents of the thorax and abdomen and the skeleton (1929). All the earlier references of importance concerning elephant anatomy in general are given in Dr Eales's series of papers, and she very kindly placed her bibliographical index at the present writer's disposal. Only papers to which direct reference is made in the text, some of which have been published since 1929, will be included in the bibliography appended to the present account. This work, however, involved the detailed study of the female reproductive organs and afforded some opportunity for the study of the general anatomy of the elephant and its habits, and the data obtained make it possible to clarify the existing accounts in some respects, apart from the study of the reproductive cycle, which constitutes the main object of the research. Thus the succeeding remarks are based upon a comparison of the existing accounts with what was observed during the present work.

The skeletal characters, upon which the study of the phylogeny of the group is necessarily based, are already well known. A series of linear measurements, some of which bear a close relation to particular skeletal measurements, is given in an appendix to the present paper. The skulls and lower jaws of a number of these animals were sent to England, and Dr T. C. S. Morrison-Scott has undertaken a study of their morphology which, together with the body measurements, may be expected to throw fresh light upon certain aspects of the subject, particularly as regards individual variation within a series collected from a restricted area and over a limited period of time.

The musculature of the elephant has not been thoroughly described except in the case of the foetus of *Loxodonta* (Eales 1928), and that of the adult was not studied in the present investigation. The blood vascular system and respiratory organs have been described in some detail by previous workers, and such observations as were found possible in the field dissections were in accord with the findings of previous workers. It was thought that the description by Todd (1913) and others of a condition in which the lungs adhere permanently to the walls of the chest might not apply to the wild animal. The point was investigated in a number of specimens, and it was found that the adhesion is in fact normal. Pleural cavities are present in foetal stages and are obliterated soon after birth; costal movements in breathing are thus reduced to a minimum and respiration is largely diaphragmatic. This fact contributes to the remarkable stillness of a standing elephant in repose. A very young elephant calf in distress was observed to call loudly and continuously, its chest heaving very much after the manner of the young of the domestic cow or sheep.

The anatomy of the alimentary system has been fairly thoroughly described in both Indian and African elephants, and nothing has been added during this research. Specimens of selected parts of the gut wall were preserved and await study.

The male reproductive organs of the (African) foetus were described by Eales (1929), and those of the (Indian) adult have since been described by Schulte (1937). A male foetus considerably nearer term than that which Dr Eales worked on is now available, and dissection of this and other foetuses should augment existing knowledge. The development and structure of the female reproductive organs are dealt with at some length in the present paper, and a description of the placenta and foetal membranes is in course of preparation. Attention is here drawn to certain findings relevant to the systematic position of the Proboscidea. In the first place, there is a remarkable similarity between the foetal membranes of *Loxodonta* and *Hyrax* (*Procavia*). Descriptions of these structures in the elephant are virtually non-existent and those of *Hyrax* appear to be inadequate in some respects. In both there is a large quadri-lobulate allantois and a zonary placenta. In the African elephant the placenta does not usually extend entirely around the circumference of the chorionic sac, but is divided into two or three portions. The histology of the placenta appears from preliminary study to be rather similar in *Loxodonta* and *Hyrax*, but it is evidently erroneous to describe it as non-deciduate as previous authors have done. Since Grosser devised a useful classification of the various types of placental membranes, and more recent authors, including Mossman (1937), have studied a variety of forms in considerable detail, the classification of placentae as deciduate or non-deciduate has been recognized as being of doubtful value, and as long ago as 1904 Robinson's description of some degree of trophoblastic invasion of the uterine epithelium in the pig showed that there exists a more intimate connexion between foetal and maternal tissue in this animal than is often attributed to it. It is clear from such examination of the elephant placenta as has already been made in the course of the present investigation that a considerable amount of maternal tissue comes away with the placental tissue of foetal origin when the afterbirth is shed.

The development and morphology of the peritoneal structures in the region of the ovary is peculiar and characteristic and is described in this paper. In the course of work in Africa a series of specimens of *Hyrax* was obtained, and the female reproductive organs have been examined to determine whether any similarity to the elephant could be discerned. No particular resemblance could be seen in the ovary itself or in the morphology of the neighbouring structures. The similarity between the placental and foetal membranes of the two forms is sufficiently striking to make it appear certain that it is of phylogenetic significance, while the differences between the two with regard to the structures near the ovary are probably the result of specialization on the part of the elephant, perhaps related to its great size. Their condition in *Hyrax* is more like that of the generality of mammals and is doubtless the less specialized of the two.

Anatomical differences between *Elephas maximus* and *Loxodonta africana* are relatively few, although they differ in average size, in the shape of the head and in the more 'rangy' appearance of the African elephant, with its relatively longer legs and evident adaptation for more rapid movement in open country. The two animals in fact differ more obviously than a list of diagnostic characters of each would suggest. The present material includes two specimens of the African 'forest elephant' (nos. 21 and 22), which has sometimes been described as a distinct species of *Loxodonta*. The characters and status of '*L. cyclotis*' have been discussed by Allen (1936) and by Morrison-Scott (1947). It was first distinguished as a species by Matschie (1900) and is characterized by being of smaller size than *L. africana*, by its relatively long thin tusks, the ivory of which is more brittle, and by the distinctive lobed ear. But though the forest elephant is recognizable as a race or subspecies of constant type, it is very doubtful whether it is sufficiently different from *L. africana* to warrant its classification as a distinct species. That the two races ('bush' and 'forest' elephants) mingle and interbreed to some extent is apparent from Offermann's account (1939, and see Morrison-Scott 1947).

(5) *Growth*

Linear measurements were made of nearly all the specimens examined, and in most cases the weight of the tusks was recorded. Whenever possible, the grinding surfaces of the molar teeth of the upper and lower jaws were photographed, and a set of prints to a standard scale has been prepared for reference, so that selected animals can be arranged in order of the stage of dentition and the degree of wear shown by individual teeth. The appropriate nomenclature is described by Morrison-Scott (1939, 1947), the first three teeth, in the succession of six which appears in each ramus of the jaws, being designated mm_2 to mm_4, and the last three M_1 to M_3. It was found possible to arrange specimens in order of the degree of wear of the molar teeth, to form a series which must bear a close relation to the true order of age. Wear is usually more advanced in the lower jaw than in the upper, but this is not invariably so, and some degree of variation must be presumed to occur.

Carcass measurements and records of dentition together provide information about body growth and tusk growth, which will be more fully considered elsewhere, and attention is here directed only to certain points relevant to the subject of this paper. By plotting a skeletal dimension against the position of the animal in the age-series, as indicated by its dentition, a diagram can be constructed which is closely related to an actual growth curve, and it can be seen that growth is notably consistent within the sample. The suggestion is that the sample is drawn from a relatively homogeneous population which has perhaps been stable for a considerable time. The rate of growth evidently slows, in both sexes, at or about the time of puberty, the flexure in the growth curve occurring earlier in females than in males. Generally speaking, the tusks of females are smaller than those of males, and it can be shown that tusk growth almost always ceases at puberty in the female (but see Dollman 1931), while it continues, at varying rates in different individuals, in the male. A further difference between the sexes lies in the greater proportionate width of the pelvic girdle in the female.

The breeding season

A number of contradictory statements about the breeding season of the African elephant occur in the literature, but the majority of authors state that mating usually occurs in the dry season, mainly in January and February. It has not often been observed, and the present writer has not seen elephants *in copula*, and no clear relation could be distinguished between the size or weight of foetuses and the time of year when they were obtained. Animals killed in early pregnancy, however, provide direct evidence as to conception dates, and those near term do so if the gestation period is known, and the same applies to all foetuses if their uterine age can be estimated.

Table 1. Pregnant animals in order of approximate size of the foetus

The animals indicated as having a foetus of '>80 kg' have been placed in order of the size of the foetus from linear measurements, the weight not having been recorded

no.	wt. of foetus (g)	date killed
E25	12	28. vii. 47
E36	20	9. ix. 47
E20	50	15. v. 47
E21	60	24. v. 47
E78	600	7. iv. 48
E24	600	28. vii. 48
E63	750	25. iii. 48
E3	900	7. iii. 47
	(kg)	
E15	2	14. iv. 47
E147	3	8. iii. 50
E115	3	18. i. 50
E122	3	6. ii. 50
E60	3·5	10. xii. 47
E90	5	16. vi. 48
E138	6	24. ii. 50
E31	8	11. viii. 47
E117	45	25. i. 50
E37	>80	9. ix. 47
E61	>80	24. iii. 48
E64	>80	25. iii. 48
E75	>80	7. iv. 48
E38	>80	9. ix. 47
E59	>80	8. xii. 47
E22	>80	24. v. 47
E43	91	26. ix. 47
E94	96	10. vii. 47
E84	96	11. v. 48
E26	100	2. viii. 47
E46	105	25. ix. 47
E148	120	8. iii. 50
E87	120	11. vi. 48

The pregnant animals are listed in table 1, with the weight of the foetus and the date. In four of them the foetus weighed less than 100 g. The smallest weighed only 12 g and was found at the end of July. It seems certain that mating must have occurred within three months of that time. The next (20 g) was found in September, and in this case, too, mating must have occurred at a time of year very different from the December-March 'dry' season. The next two animals in this series were both killed in May, with foetuses of 50 and 60 g, and in these cases mating must have taken place in the December-March period. The next group of foetuses to be considered includes those near term, which contribute further evidence about mating times if the duration and variability of the gestation period are known.

(1) *The gestation period*

There appears to be no instance where the duration of pregnancy has been accurately determined in an African elephant. Shortridge (1934) states that 'Recent observations in Kenya Colony indicate that the gestation period of the African elephant is approximately the same as that of the Indian species (which is between 18 and 22 months—Sanderson)'. The nature of the observations is not stated. The same author quotes other estimates, ranging from 18 to 23 months. Jeannin (1947), stating 'The gestation period is variable, from 18 to 28 months', provides no evidence and is probably quoting Shortridge. The Imperial Bureau of Animal Breeding and Genetics publication, *Gestation periods* (1947), quotes several authors with reference to the African elephant, but none of them provides any direct evidence. Colonel Offermann, Director of the Station for the Domestication of Elephants in the Belgian Congo, states (unpublished) that the gestation period is 22 months, without citing actual instances. He adds that the mammary glands swell markedly about the 16th month, an observation which tallies with what is known of working elephants in Burma and suggests a similarity between the two species.

For the present purpose the gestation period will be taken as being 22 months, accepting Shortridge's and Offermann's statements in the absence of any evidence to the contrary. There is definite evidence that the gestation period of the Asian elephant is usually 21 to 22 months. Reference may be made to Flower (1943) and Burne (1943) and to an account of the birth of a female calf in the Rome Zoo, where the parents were seen to mate on several occasions; the last was on 6 October 1946, and the calf was born on 6 August 1948. The gestation period was thus at least 22 months (Hindle 1950). Ferrier (1948), writing of working elephants in Burma, says that in some cases healthy calves have been born after a gestation of 17 months, but in others pregnancy has lasted 23 months, the usual time being about 21 months. There is always the possibility of error in such observations, in that the copulation which is assumed to have initiated the pregnancy may have been preceded or followed by another which in reality was the effective one. Some authors state the gestation period to be longer in the case of male calves; Ferrier remarks on this, but says that his own experience does not confirm it.

In the present material there are several foetuses which must have been near term, including two which weighed approximately 120 kg and were bigger than the smallest calf encountered. One was found in June, the other in March, and the suggestion that calving, and therefore mating, occurs at various times of year is further borne out by other animals nearing term, as can be seen from table 1. Even the considerable variation in the gestation period which various authors, including Ferrier (above), describe could not account for such diversity of season as is encountered in this material, but there may be some degree of concentration of mating times at one particular time of year which, because of this variation, is not apparent from the animals near term. This proviso does not, however, apply to the animals in early pregnancy; these, it has been shown, do not indicate a defined mating season, but they are few in number. The remaining pregnancies may throw light on the question if the foetal age can be approximately determined.

(2) *Foetal weight and age*

The subject of the relation of foetal weight to age has recently been reviewed by Huggett & Widdas (1951). These authors propound the general formula $W^{\frac{1}{3}}=a(t-t_0)$ as a means of using the average birth weight and gestation period to calculate the foetal weight/age relationship in species for which data of intra-uterine foetal weights and ages are not available. The term a is constant in respect of any particular species and is called by the authors the 'specific foetal growth velocity'. It is the slope of the line relating the cube root of the foetal weight (W) to conception age (t) in that segment of the curve where this relationship is linear. The term t_0 'is the intercept where the linear part of the plot, if produced backwards, cuts the time axis. It has no clear biological significance in foetal development, but if the numerical value of t_0 can be estimated by analogy with other mammals for which foetal weight and age data are available, then one known weight (W) and time from conception (t) would be sufficient to determine the value of a for the mammal concerned.' In figure 1 the birth weight has been taken as 120 kg and the gestation period as 22 months, while t_0 has been taken as $0{\cdot}1\,t$, which is the figure used by Huggett & Widdas, based on the observation that t_0 is greater when the gestation period is longer but represents a smaller fraction of the total gestation time.

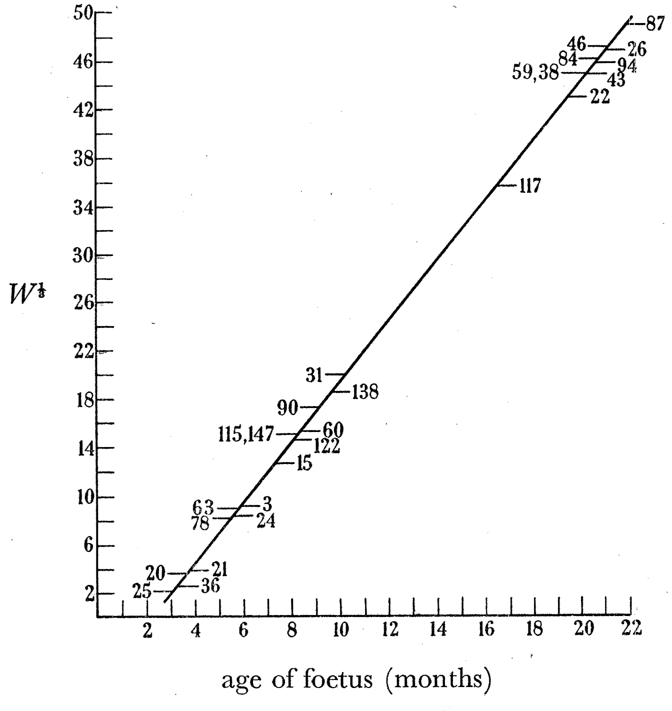

FIGURE 1. The foetal growth curve of the African elephant calculated from Huggett & Widdas's formula $W^{\frac{1}{3}}=a(t-t_0)$. The average weight at birth is approximately 120 kg, the gestation period is assumed to be 22 months, and t_0 is taken as $0{\cdot}1t$.

Huggett & Widdas, in the paper referred to above, were concerned with comparative aspects of foetal growth. They calculated the 'specific foetal growth velocity' for a number of species, using available data, and using Przibram's (1927) data of birth-weight and gestation periods they show that a is decidedly low in primates as compared with many other mammals, with a numerical value near 0·05 in this group, whereas in the majority of species studied its value lay between 0·12 and 0·15. The value of a is very high in the whales, the foetus reaching a relatively enormous size in a gestation period of only one year, and it was found to be higher in eland and hippopotamus than in the generality of mammals, and lower than most others, except the primates, in seal, donkey and rhinoceros. This is when allowance is made for those animals in which implantation is believed to be delayed, a phenomenon which may also account for the low value of a in the seals, though there is no reason to suspect its occurrence in the donkey or the rhinoceros. The data now available make it clear that if the gestation period of the African elephant is similar to that of the Indian, both occupy an intermediate position in Huggett & Widdas's figure, with a specific foetal growth velocity very near that of the rhinoceros, higher than that of the primates but lower than that of the majority of mammals studied. The weight at birth of the Indian elephant is rather less than that of the African, so the slope of the line relating foetal weight to age will be slightly different in the two forms if the gestation period is the same. In both, however, the value of a is near to 0·08.

In figure 1 the straight line has been calculated as described above, and the position of a number of foetuses, the weight of which was known, has been marked in accordance with their weight. The age which each may be supposed to have reached is therefore shown on the time scale. This estimate of the age of individual foetuses is obviously subject to considerable error, especially from individual variations, but the figure nevertheless illustrates a number of points of importance. In the first place it shows that the foetuses of 90 kg and over were all likely to be within the last two months of gestation, and if this is so it is not possible to reconcile the dates on which these various late foetuses were taken, with the assumption of a restricted breeding season. In the second place, the diagram illustrates the distribution of the specimens in the first half of gestation and the gap which occurs in the series after mid-pregnancy. The calculated age of the smallest foetuses is greatly affected by the point at which t_0 is assumed to fall, a factor which affects the calculation of the age of later foetuses to a much smaller degree. By analogy with other mammals, however, this point is unlikely to be less than 0·1 of the total gestation time, so that if the smallest foetuses have reached the stage of growth at which the graph becomes linear, they are probably over two months post-coitum. The data show a slight preponderance of animals either near mid-pregnancy or near term in the early months of the year, which accords with the suggestion of a higher rate of breeding at that time. These data do not by themselves point to this conclusion with sufficient clarity to be significant, but taken in conjunction with the reports of other observers they do suggest that mating is more frequent during those months. On the other hand, the most prominent feature of the evidence about the 'breeding season' which the present material affords is the clear demonstration that mating may occur at various times of year.

(3) *Elephant movements in relation to breeding*

There is a widespread impression that for a great part of the year bull elephants wander in small groups away from the breeding herd, and join the cows only at the mating season. In the course of the elephant control work from which the present material was obtained, regular patrols were continuously maintained in the area within the loop of the Victoria Nile near Atura, and from the middle of July to the end of October 1948 no female elephants were shot, although eighteen bulls were killed. But it was clear that the animals were moving in small groups and covering great distances daily. There had also been intensive hunting in the area for many months and the whole elephant population must have been disturbed. Indeed, the purpose of this hunting was to check the elephants' habit, well recognized locally, of spreading from the Reserve into the cultivated area to the south-east with the advent of the dry season. This purpose was to a great extent achieved, and it must be concluded that the behaviour of elephants in such a locality is little or no guide to their natural behaviour when undisturbed.

The writer is inclined to attribute much of the confusion which exists with regard to the breeding and migratory habits of the African elephant to three causes. In the first place, they are very difficult animals to observe over a period of time in their natural habitat, for even when the nature of the vegetation allows of their being seen from some distance, they cover such distances in their diurnal, and particularly nocturnal, wanderings, that it is impossible to maintain contact with them for long, and a group will split up and rejoin and mingle with other groups, so that it is impossible to define a 'herd'. This term, in fact, is very loosely used, and at present it cannot be said that we know anything of the social structure of an elephant 'herd'. The term is perhaps best confined to a geographical connotation, as it is used by Pitman (1925). In the second place, it is difficult to determine the sex of an elephant by casual observation, except when the tusks are really large. It quite frequently happened, in the course of the present work, that a Game Guard reported shooting a bull when in fact the animal proved to be a cow. The converse error never occurred. That this error is fairly general is indicated by the reports of the numbers of cows and bulls shot during control work each year in Uganda, as given in the Game Warden's Reports from 1925 onwards. Sir William Gowers has pointed out (in correspondence with the writer) that if the number of bulls reported shot is approximately correct, it is impossible to explain the continued existance of male elephants in Uganda unless an extraordinary degree of immigration from surrounding territories is assumed, if the population was of the order it was estimated to be when control work began. It seems certain that the number was not greatly under-estimated, and it is obvious that cows do not in fact greatly outnumber bulls in the present population. Gowers endorses the writer's suggestion that the explanation lies partly in the faulty identification of sex. In the same way, the difficulty of identifying the sex of an individual elephant in many cases may be expected to lead to confusion in reporting seasonal movements of the animals, and mating habits. In the third place, as it has now been shown conclusively that mating may occur at various times of year, and that the 'breeding season' is in consequence ill-defined, it will be seen that scattered observations will not readily yield the complete story of the elephant's breeding habits.

(4) *The musth glands*

Ferrier remarks of the Asian elephant that it resembles the majority of mammals in that mating only takes place when the female comes into season. He adds: 'It is very rare, however, that any marked signs can be observed of a female's being on heat, and this, coupled with the very marked symptoms of sexual excitement in male elephants when musth, for long tended to obscure the true facts.' The same author states further that healthy male elephants are always ready to mate, and that mating takes place 'at all times of year, but certainly among working elephants most cases occur during the hot weather. In my opinion the time of the year has a definite significance, as wild tuskers molest tame herds much more during the hot weather than at any other time, but in the case of working elephants the absence of severe physical strain also has its effect.' The elephants are lightly worked during the hot weather.

As males will mate at any time, the significance of 'musth', even in the Asian elephant, is not understood. Generally speaking it is a seasonal phenomenon; some individual males experience 'musth' regularly at the same time each year, but others do not. 'Musth' does not occur at the same time in different males, but it is more frequent during the hot season (in Burma). Ferrier adds that 'Very occasionally a female elephant in very good condition exudes fluid from her temporal glands'. During the present investigation it was noted that, for a considerable part of the year at least, the temporal glands of the African elephant are active in all individuals of both sexes, including pregnant females and quite young calves probably not more than two years old. In this respect, therefore, the African elephant seems to differ from the Indian. At other times of year activity of the temporal gland was less general, and the observation of peak activity of the gland at the time of year when mating is thought to be most frequent suggests that the two are indeed related, as has been generally supposed.

It must be concluded that beyond the fact that mating does occur at all times of year and is probably more frequent during the dry season, there is a dearth of reliable information about the breeding habits of the African elephant, or, for that matter, of the Indian species in the wild. It is evident that the movements of elephants are governed to some extent by food and water requirements, but to what extent they are related to breeding habits, if at all, is uncertain. Continuous observation of a group of elephants would perhaps be the ideal way of solving such problems, and if it were feasible it would certainly yield a great deal of interesting information. The difficulties of such work are formidable, however, and a first step would be the integration and evaluation of the information already available. Such information is necessarily fragmentary, and very little of it is in published form, but the experience of European and African hunters, particularly those concerned in game control and conservation, as distinct from ivory seekers, is far from negligible.

FERTILITY

Several aspects of the reproductive life of the female will be discussed under this general heading, including the onset of puberty and senescence, the frequency of calving and the duration of the reproductive life. From evidence provided by the present material it is clear that the African elephant in the wild state often begins to breed at an age of 10 years or less. This accords with the instance cited by Hindle (1950) of a female Indian elephant calf born in Rome Zoo, the age of the parents being approximately 10 years at the time of mating. Hediger (1950) says that elephants in the Belgian Congo do not reach puberty until about 15 years of age. This may refer to captive elephants, in which case the statement agrees with that of Williams (1950) that in Burma working elephants do not breed until they are 16 or 17 years old. But it is not surprising that what may be exceptional in captivity may be usual in the wild. Neither in Asia nor in Africa can the elephant be said to be truly domesticated. The animals are captive, tamed and trained, but they are far from having been bred in captivity for a sufficient number of generations to have regained the fecundity of the wild animal. The history of domestication of a species follows a well-marked pattern, the breeding rate being depressed at first and only slowly recovering over a number of generations, after which the domestic strain may be more prolific than the wild stock.

The way in which the stage of replacement and wear of the molar teeth can be used to arrange the animals of the present series in approximate order of age has been described above (p. 98). There appears to be no case where the successive stages of dentition have been recorded in an African elephant of known age, but it was found possible to examine the molar teeth of one in the London Zoo, in 1949 and in 1950, and this animal has been included at two points in table 2, where the younger females are listed in approximate order of age, as indicated by the molar teeth. It is probable that tooth wear will differ in such an animal from that in the wild state, and as the series in table 2 is arranged in order of the stage of dentition it will be seen that in fact this captive animal, Dicksie, was longer and taller than the wild animals at similar stages of dentition. The circumference of the forefoot did not exceed that of the wild animals of similar dentition, but this is probably due to the fact that Dicksie was relatively poorly developed in muscle and fat, and would be judged to be much lighter than a typical wild animal of similar skeletal dimensions. The implication is that the captive animal wears its teeth more slowly than the wild one, so that using its age as an indication of that of wild animals at a similar stage of dentition will give a maximal estimate of the age of the wild ones. When captured on 31 October 1940, this elephant was believed to be 6 to 9 months old, but the height at the withers is given as

TABLE 2. THE YOUNGEST SPECIMENS IN ORDER OF AGE, AS JUDGED FROM THE CONDITION OF THE MOLAR TEETH, AND COMPARED WITH A FOETAL SPECIMEN AND WITH A CAPTIVE AFRICAN ELEPHANT (DICKSIE), WHICH WAS BORN IN THE WILD IN 1940

no.	length: occiput to tail-base (cm.)	height: scapula to sole of foot (cm.)	forefoot: perimeter (cm.)	teeth	condition
E87 (♂ foetus)	122	92	48	mm_2/mm_3	near term (120 kg)
E134	104	96	45	mm_2/mm_3	very young
E119	130	110	51	mm_2/mm_3	very young
E27	211	163	76	mm_3/mm_4	immature
E70	—	—	—	mm_3/mm_4	immature
E131	198	173	76	mm_3/mm_4	immature
E54	188	160	67	mm_4	immature
E150	235	178	82	mm_4/M_1	immature
E144	241	205	92	mm_4/M_1	immature
E83	254	200	92	mm_4/M_1	immature
E149	254	213	92	mm_4/M_1	immature
E121	—	213	99	mm_4/M_1	immature
Dicksie (1949)	—	226	96	mm_4/M_1	?
E8	—	—	—	mm_4/M_1	immature
E45	260	213	99	mm_4/M_1	immature
E7	267	213	99	mm_4/M_1	immature
Dicksie (1950)	297	—	—	mm_4/M_1	?
E147	275	224	97	mm_4/M_1	1st pregnancy, about 8 months
E48	282	229	99	M_1	lactating
E59	305	250	105	M_1	pregnant and lactating
E140	—	229	97	M_1/M_2	lactating
E17	297	—	104	M_1/M_2	lactating
E75	295	241	104	M_1/M_2	2nd pregnancy, 17 to 20 months

80 cm a few days later, less than that of the smallest calf or the largest foetus in the present series. Furthermore, although Dicksie was not weighed at the time, her first owner reports that he could lift her clear of the ground, which indicated that she could not have been much, if any, heavier than at birth. In fact, the estimate of 6 to 9 months was based on the belief that the animal must have been born during the preceding dry season, and it has already been shown that mating, and therefore calving, may occur at widely different times of year. Thus this animal could not have been much over 9 years, and certainly could not have reached 10 years of age, when measured in May 1949. The smallest, and apparently the youngest, adult female in the present material (E147) was pregnant, probably for the first time, and nearing mid-pregnancy. The condition of the molar teeth suggests that E147 was older than Dicksie was when measured in 1950, at an age of 10 years or a little over, but the wild animal was considerably the smaller of the two and may well have been less than 10 years old. It will be noticed that the last milk molars were still in use nearly half-way through gestation. The next animal in the series, E48, was a little bigger and had just shed the last remains of the last milk molar. This animal was lactating; it is not possible to determine how long post-partum it was, but it must have become pregnant some two years before its death, perhaps more. The next specimen, E59, was a parous animal which was pregnant and nearing term, while accompanied by a suckling calf. Only the first molar (M_1) was in use in each jaw, yet this animal had been pregnant for some 20 months, and before that it had presumably experienced a lactation anoestrus preceded by another pregnancy of nearly two years' duration. Thus it probably reached puberty 5 or 6 years prior to death. Another animal, E75, was pregnant for the first time when killed, and in this case the second molar tooth had come into use, so that the age at first pregnancy must vary considerably between individuals. In general, however, it is evident from the cases described that the wild African elephant may begin to breed at about 9 years of age, and that puberty is usually reached when the animal is not much more than 10 years old.

(1) *Puberty, first pregnancy and lactation*

In the above account, two animals have been described as being pregnant for the first time. That E147 was in fact pregnant for the first time seems certain from the size of the animal compared with others which were nulliparous, but the condition of the mammary glands appears to afford convincing evidence on the point. The mammary glands were accessible and were examined in twenty-four of the pregnant animals, and milk could easily be expressed from nineteen of them. There were two doubtful cases, but in three animals, all of which were small, the mammary glands were definitely inactive. Two of these are shown in table 2, and have been commented upon above. The third was of the subspecies *Loxodonta africana cyclotis* and therefore cannot be fitted into this series, but it too was evidently a young animal. Of the two doubtful cases one, E115, was a young animal and was possibly pregnant for the first time, but the other, E31, was large, and certainly parous, and had possibly completed a lactation before becoming pregnant again. On the other hand, lactation may have been terminated by the loss of the calf; the condition of the mammary glands was doubtful because it was not possible to examine them until a considerable time after death, and decomposition was advanced.

The fact that no milk was expressible from the mammary glands of several pregnant animals, including one near term, which from their size would appear to be pregnant for the first time, suggests that the presence of milk, easily expressed from the nipples, indicates the occurrence of lactation. The observation that milk cannot be expressed from the nipples of the pregnant animal which is not feeding a calf agrees with statements by Ferrier (1948), for the Asian, and Offermann (1949 unpublished), for the African elephant, to the effect that milk cannot be squeezed from the nipples of a pregnant elephant with no calf until very shortly before parturition. Thus in nineteen of the pregnant animals—indeed, in all to which the test could be applied except the three first pregnancies and two doubtful cases—pregnancy was apparently accompanied by lactation. In all except one of the adult non-pregnant animals to which the test could be applied, milk was expressible, so that, with this exception, an old animal to which further reference is made below, no adult females were found which could be shown to be neither pregnant nor lactating, and no pregnant animals could be shown not to be lactating at the same time, except for the three which were evidently, and one which was possibly, pregnant for the first time, and one other doubtful case (E31, above). Lactation must therefore overlap the subsequent pregnancy in the great majority of cases, and some indication of the average interval which elapses between parturition and a subsequent conception may be gained from the relative numbers of pregnant and non-pregnant adults. There were thirty-one pregnant animals and thirty-four which were diagnosed as being in lactation anoestrus. The distribution of the adult females between the two classes, pregnant and non-pregnant, may be regarded as a binomial where $n_1+n_2=1$, when n_1 is the average gestation period and n_2 is the average interval from parturition to conception. Taking n_1 to be 22 months, the best estimate of n_2, applying Fisher's method of maximum likelihood, is 23·4 months, and the 95 % confidence limits are 21·0 and 25·8 months. The writer is indebted to Mr R. C. Campbell for these calculations, which imply that the average calving interval is nearly 4 years. This accords well with Ferrier's statement that in the case of working elephants in Burma, the minority which do breed 'are likely to have calves regularly at three to four year intervals'. The average calving interval among these elephants will evidently be much longer than this, for many failed to breed at all, but the suggestion is that 3 to 4 years is the 'normal' interval, and would be close to the average in a wild population, except for the effect of such accidents as loss of the foetus or loss of the calf. In the case of the African elephants, there are certainly some, though probably not many, cases where a calf dies or is killed before the end of the lactation anoestrus, and in such cases the interval between parturition and conception, and hence the calving interval also, will be shortened. In so far as the calculation quoted above does not allow for this factor, it would seem that the 'normal' lactation anoestrus is longer than the calculated average interval. Another factor is the possible incidence of pre-natal mortality. After the loss of the embryo, the cow will presumably become pregnant again relatively soon, so that the time between the termination of the one pregnancy and the beginning of the next will, again, be shorter than the normal lactation anoestrus. But at the same time the duration of such a pregnancy will be less than the normal gestation period, and a calculation based on an assumed average pregnancy of 22 months will give an estimate of the average non-pregnant interval, and hence of the average calving interval, longer than the true one. No evidence of pre-natal mortality was in fact encountered, but it does appear that 22 months is a maximal estimate of the average gestation period, and hence that the calculated average calving interval of nearly 4 years is similarly maximal.

(2) *Senescence*

In no case could it be shown conclusively that a female had ceased to breed. In one animal, E4, only the last remnants of the last molar tooth, M_3, remained in the lower jaw, worn down below the level at which the enamel loops give the characteristic pattern. The teeth of the upper jaw were not quite so advanced in wear. The stomach contents were decidedly less well masticated than in other animals living in the same conditions and eating similar food. This animal was clearly lactating, and milk could be easily squeezed from the nipples. Only one non-pregnant adult female was found which could definitely be said not to be lactating. This was E135, which was found wandering alone, and had every appearance of age. The ovaries contained the remains of old corpora lutea, but had no macroscopically visible follicles. The last molar teeth were in use but were not as worn as those of E4. The absence of macroscopically visible follicles was also noticed in one other animal, E57, but in this case it was not possible to reach the mammary glands, owing to the position in which the animal was lying. It can be said, therefore, that E4 had reached a very advanced age while apparently retaining the capacity to produce young, while E135 had either lost this capacity or was experiencing a longer interval between calves than was general among younger animals, and that this probably applies also to E57.

From the sum of these observations it is evident that the female East African elephant in the wild state generally begins to breed at about 10 years of age, sometimes earlier, that calves are usually produced at fairly regular intervals, the lactation period associated with one calf extending over most or all of the succeeding gestation period, and that the capacity to produce young is, in some cases at least, maintained until extreme old age. It is probable that the interval between calves is longer in very old females, and it is possible that some may completely lose the capacity to breed, but this cannot be shown to have occurred in any of the specimens examined.

THE REPRODUCTIVE ORGANS OF THE MALE

During the collection of material in Africa there were few occasions when it was found possible to devote any considerable time to the dissection of a male elephant. In most cases the abdomen was opened, and portions of the testis and epididymis were removed and preserved, but it was not possible to do more than confirm existing descriptions of the reproductive tract as a whole. One male foetus weighing 45 kg was carefully preserved, and it is hoped that dissection of this specimen will supplement the account given by Eales (1929) of the urogenital system and other organs of a considerably smaller foetal African elephant. The material brought to England includes several earlier foetuses of both sexes.

Existing accounts of the structure of the male reproductive organs in both Asian and African elephants are briefly reviewed by Eales (1929), and since then Schulte (1937) has described those of the Asian species. This author also reviews the literature in some detail, with the notable omission of any reference to Eales's description, although reference is made to an earlier paper by Eales describing the external features of a foetal specimen. The different accounts do not entirely agree in all respects, but the discrepancies are far less marked than those between some of the descriptions of the female reproductive organs. It has been shown, and the present work confirmed, that the lobes of the kidney, which in the foetus are very distinct, become fused in the adult to form an organ which is only partially divided into lobes. The foetal African elephant at about mid-term has no ductus ejaculatorius, the vasa deferentia and seminal vesicles opening separately into the urethra (Eales 1929). The occurrence of a ductus ejaculatorius has been described in the adult males of both African and Indian elephants, in the former by Mojsisovics (1879) and Hofmann (1923), and in the latter by Watson (1873), Petit (1924) and Schulte (1937). Some of the other accounts are less clear on this point, and the statement that the seminal vesicles and vasa deferentia open separately into the urethra appears to be due to Owen (1868), and as it is not clear that he had the opportunity of examining a male elephant himself, the statement is perhaps based on a dissection by another worker whose name is not given. In the present investigation the urogenital system of the male African elephant was not found to differ significantly from that of the Indian elephant as described by Schulte.

The testes of the elephant lie medial to the kidneys and are rather more nearly equidistant from the pelvis than are the kidneys. To judge from existing descriptions, it appears to be usual to find very little fat deposited in the body, even around the kidneys, in elephants kept in captivity, but in this investigation all the animals examined were found to have large amounts of fat, and the kidneys were only just discernible when the peritoneum was exposed. The testes protruded from the body wall into the abdominal cavity, but the course of the renal blood vessels and the ureters was obscured by the amount of fat deposited in the connective tissue of this region.

Each testis usually weighs between 2 and 3 kg. The epididymis is somewhat indefinite in shape, and Eales (1929) says that 'The vasa efferentia unite, at right angles to the efferent ducts, to form a longitudinal duct which becomes the convoluted vas deferens'. This description, of course, applied to a foetal specimen. The condition in the adult African elephant is similar to that described by Schulte (1937) for the Asian, the epididymal portion of the tubule of each side being extremely convoluted within a thick cord which is somewhat bunched around the medial surface of the testis. A short distance behind the testis the cord becomes reduced to about the thickness of a finger, and for most of the remainder of its length it remains fairly uniform in thickness and follows a direct course to its junction with the duct of the seminal vesicle of its own side very near the opening into the urethra. The junction of the epididymis with the vas deferens is, therefore, not clearly demarcated, but the epididymal portion of the tube is ciliated. In those specimens which have been examined histologically the epithelium was found to be of a high columnar type, the cilia arising from dark-staining basal granules. The lobulate prostate glands are situated near the bases of the seminal vesicles and open into the urethra by several ducts at about the same level. Cowper's glands are situated farther down the urethra, and their ducts open into it some distance below the level at which the glands themselves lie. The penis is large and very extensible. There is no true prepuce but the glans penis is concealed by a fold of skin.

The reproductive cycle of the male

Ferrier (1948) states that the male elephant in Burma will mate at any time of the year, and nothing has been found to indicate that this is not true of the African elephant. In no case could it be shown that spermatozoa were absent from the testes and epididymides of an animal which appeared to be adult. The male appears to reach puberty at about the same age as the female.

In most published accounts dealing with the breeding habits of the elephant, the phenomenon known as 'musth' is given considerably prominence, but its true nature remains obscure. Some observations on this subject are given in the section of the present paper dealing with the breeding season.

THE REPRODUCTIVE ORGANS OF THE FEMALE

(1) *General structure*

The principal published accounts of the reproductive organs of the female elephant were all written prior to 1900. The descriptions by Perrault (1734), Forbes (1879) and Chapman (1880) relate to the African genus, and those of Mayer (1847), Owen (1857), Miall & Greenwood (1878), Watson (1881, 1883) and Paterson & Dun (1898) to the Indian. There are notable discrepancies between the different accounts, and it is clear that they are chiefly due to individual differences between the various specimens examined, rather than to constant differences between the two genera of elephant. In most cases the authors were able to examine only one specimen, but Watson dissected one in 1881 and another in 1883, and was also able to examine the material described by Forbes and that of Miall & Greenwood. He realized that the condition described from his first specimen must have been an unusual abnormality. Nevertheless, Watson's (1881) illustration showing the disposition of the reproductive organs in the abdomen and pelvis is admirable. In 1937, Neuville collated the existing descriptions and discussed the significance of the differences between them; the present investigation has yielded further information, and the whole subject is reviewed later in this account. It must be remembered that all the earlier descriptions are of specimens which died in captivity, and which for the most part were reared in unnatural conditions. Shortcomings in the earliest descriptions are not surprising in view of the nature of the material and the conditions in which the dissections were carried out. The later authors emphasized the need for a greater number of specimens.

In the course of the present investigation, it was usually impossible to attempt a complete dissection of the reproductive organs, but of the considerable number which were examined in greater or lesser detail, none differed significantly from the description which follows. Figure 2 is based on drawings and photographs made in the field; only in one case was the reproductive tract completely dissected out, the organs normally being examined *in situ*. The tract of one advanced foetus (E84, figure 4) and that of a very young calf were preserved entire and brought to England for study. No other female foetus was found at an advanced stage of gestation, but several earlier foetuses were preserved entire and brought to England, and it is hoped that they will provide material for more detailed study of the anatomy. Specimens were fixed for histological examination, and the findings are incorporated in another section of the present paper.

Figure 3 shows how the reproductive organs lie in the abdomen and pelvis of the adult. The outline of the body was traced from a photograph taken in Kenya by Sir Geoffrey de Havilland. The diagram indicates the relatively anterior position of the ovaries, which lie near the kidneys, as do the testes of the male, so that in neither sex do the gonads move posteriorly in the course of development as happens in the males of most mammals and to a lesser degree in the females of many. The outline of the whole adult tract is shown in figure 2, drawn from photographs of a pregnant specimen dissected out of the body and with the mesometrium and surrounding structures removed. A striking characteristic of the anatomy of the elephant is the long urogenital canal, which extends through the perineal area to carry the vulva to a position on the belly of the animal, anterior to the hind legs and similar to that of the male genital opening.

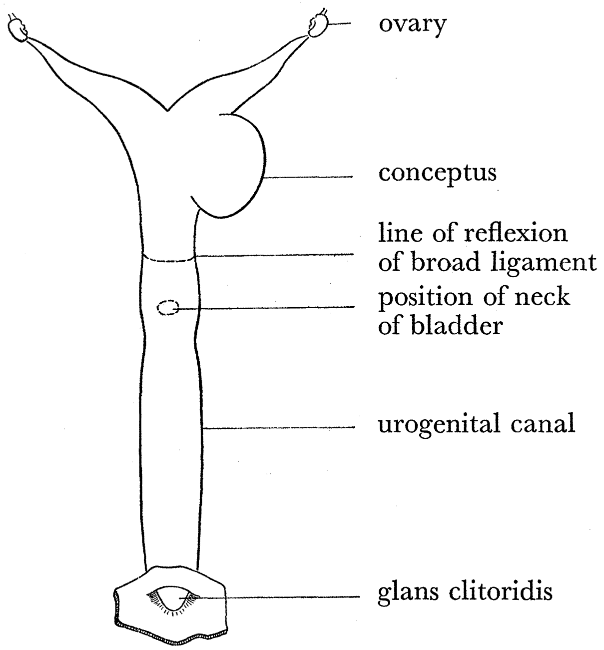

FIGURE 2. E 3, pregnant about 6 months post-coitum. Outline of reproductive tract dissected out and straightened. Ventral view.

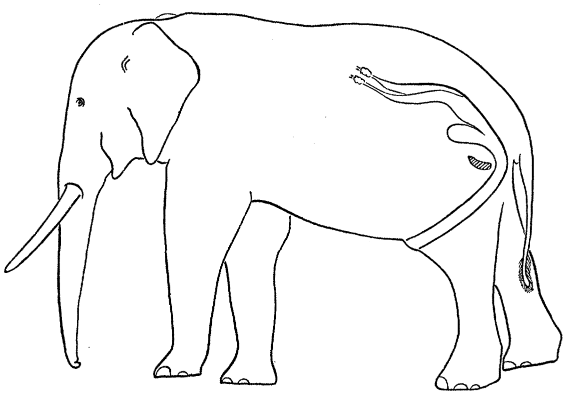

FIGURE 3. Outline of adult elephant; position of reproductive tract in the body. The long urogenital canal carries the tract through the perineal region so that the vulva lies below the abdomen, just anterior to the hind limbs.

The morphology of the structures in the region of the ovary is shown in figure 5 (E144). The ovary is almost completely enfolded by an expansion of the fimbrial funnel of the Fallopian tube, which forms an ovarial sac whose outer wall is covered with peritoneal epithelium. It is anchored to the uterine horn by the ovarian ligament, and to the body wall, anteriorly, by the suspensory ligament. Both ligaments are strongly developed and are continuous with the hilum of the ovary. The ovarial sac is widely open medially and is divided into two compartments; the ovary lies in the inner compartment and the Fallopian tube opens on the inner (fimbrial) surface of the outer wall of the outer compartment. The arrangement differs from that shown by Watson (1881) for an Indian elephant, in that the

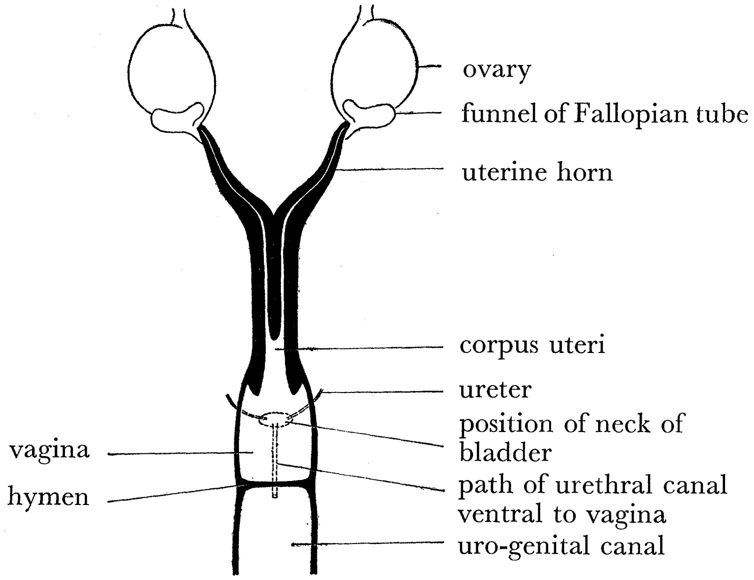

FIGURE 4. Foetus of E 84. Upper portion of reproductive tract; the ovaries are enlarged, and are not enclosed by the ovarial sac, which at this stage is a simple fimbriated funnel.

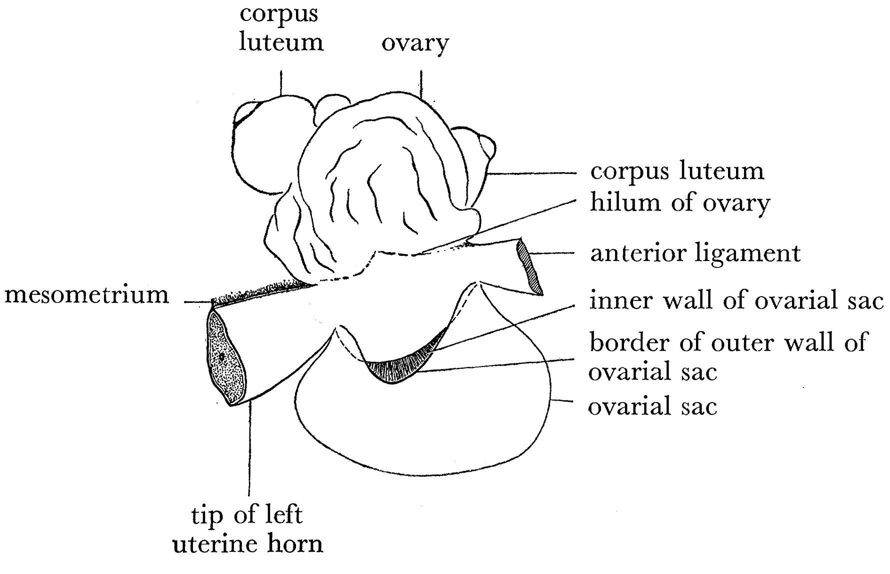

FIGURE 5. The adult ovary: a sketch of the ovary of a pregnant animal, to show the relations of the ovarial sac and the ovarian ligaments. The left ovary from the medial aspect, the ovary being taken out of the ovarial sac and raised above its hilum.

ostium abdominale lies much nearer to the free edge of the sac, and the course of the Fallopian tube is less easily apparent than his drawing suggests. The portion of the tube proximal to the ovary runs beneath the peritoneum in the outer wall of the ovarial sac. In a fresh specimen its course can just be made out by stretching this wall, and it is not visible from the inner surface. As the course of the tube is followed towards the uterine horn it sinks farther in from the peritoneal surface, and the junction of the tube with the lumen of the horn is deep in the musculature and connective tissue and can only be found by dissection. That Watson's illustration differs from the arrangement here described may be due to his specimen being one of the Indian genus, but it may equally well be due to its being an animal whose development has been affected by a life in captivity, to which fact it is at least safe to attribute the small size and apparently inactive condition of the ovary itself. The outer compartment of the ovarial sac is fimbriated, while the inner compartment is lined with peritoneum. The arrangement of the peritoneal structures in this region would appear to be different from that of other mammals as yet described. As developmental stages are available in the present material, it has been possible to trace the manner in which the adult condition is arrived at, and the subject is dealt with in greater detail below (p. 118).

The lumen of the Fallopian tube leads directly into that of the uterine horn, but it was found impossible to force a perfusing fluid through the lumen past this junction, either in the intact organs or when the tube, with the surrounding musculature, had been dissected out. In the latter case, however, if the tube was severed immediately above its junction with the uterine horn, it was very easy to perfuse it from the ovarian end, using a simple syringe. That the passage is simple, without an intussusception or other complication, is shown by serial sections. The lumen of the Fallopian tube narrows gradually as it approaches the junction with the uterine lumen, and at this point is very small. The muscularis forms a thick collar round the lumen here, and the constriction so caused is probably sufficient to prevent perfusion by the methods available in the field. In the case of one immature animal (E121) it was found that the lumen of the Fallopian tube was actually occluded for approximately 2 mm just above its junction with the tip of the uterine horn. The epithelium was extremely attenuated, but strands of epithelial cells occurred in each of a series of sections throughout this portion of the tube, and the uterine lumen was found to be quite well defined. The lumen of the Fallopian tube was found to be patent in another immature animal (E146), which was slightly bigger and evidently somewhat older than E121, and the same was true of a very young calf (E134) and a late foetus (E84).

The lumina of the right and left uterine horns remain distinct for some distance beyond the point where the horns themselves fuse, as is shown, for instance, in figure 4, and then open by simple orifices into a common lumen in the body of the uterus. In pregnant animals it was found that the embryo was usually situated in that part of the uterus where the horns are fused but where the right and left lumina are distinct. That this is the usual site of implantation was confirmed by the fact that in many lactating animals the site of a former placental attachment could be seen in this region.

Within the uterine horn the lumen gradually increases in diameter as it progresses towards the junction of the right and left horns, and the surrounding muscle layer becomes more massive. In the adult the uterine horn increases in diameter from about 4 cm near the insertion of the ovarian ligament, to about 14 cm near the junction of the horns. These measurements are necessarily very approximate, but they serve to give some idea of the size and proportions of the uterus. It should be mentioned that the lumen is reduced to a minute tube in the upper one-third or so of the uterine horn, while the external proportions of the horn are massive. Another striking feature of this region is the smooth surface of the uterine lining, which is creamy in colour and only slightly vascular in the non-pregnant animal. The lining of the lumen in the body of the uterus is similar to that of the two horns.

The os uteri, by which the single cavity of the posterior part of the body of the uterus opens into the vagina, was found to be well defined in a late foetus, the passage being narrow and carried in a relatively massive papilla which projects into the vaginal cavity (figure 4). This is still so in the case of a very young calf, but in the adult there is no definite valve. There is no difficulty in identifying the junction between uterus and vagina because the former has thick muscular walls, while those of the vagina are thin and very extensible, but the os uteri is only constricted by an annular thickening of the wall. There is no sudden change in the histological character or macroscopic appearance of the lining of the lumen between the vagina and the lower part of the uterus.

Just as the junction between the uterus and the vagina becomes progressively more open in the course of development, so does that between the vagina and the urogenital canal. In the foetal specimen already referred to (that of E84, the only female foetus that was encountered at a late stage of gestation), the two cavities were completely separated by a transverse partition or hymen (figure 4). In the very young calf the vaginal cavity was found to narrow posteriorly, finally opening into the bottom of a groove in the dorsal wall of the urogenital canal, flanked on each side by a fold of tissue. These longitudinal hymeneal folds continue for a little distance along the urogenital canal, and a tongue of tissue which projects from the ventral wall further closes off the dorsal groove. The bladder lies against the ventral wall of the vagina, and its neck is encircled by a massive sphincter muscle. Because at this stage of development the cavity of the urogenital canal extends back a little way, ventral to the urinary canal and the surrounding sphincter muscle, three cavities can be seen in a single transverse section about the middle of the flexure of the genital tract, which is so curved (figure 3) that in the erect animal the bladder is in front of the vagina, and the clitoris is above the urogenital canal, to which it is of course morphologically ventral. The urethra opens into the extension of the urogenital canal which has been mentioned, while the opening from the vagina lies nearer the vulva, that is, morphologically posterior to the urethral orifice. In the adult condition, the passage from the vagina to the urogenital canal is widely open, and the urethral orifice appears as a simple opening on the ventral wall of the tract. The ureters open into the bladder near its neck.

The urogenital canal continues so far along the abdominal wall that its length is about equal to that of the whole of the rest of the tract from ovaries to os vaginae. The glans clitoridis is large, and the corpora cavernosa of the clitoris extend along the wall of the urogenital canal for about half of its length. The retractor muscles of the clitoris originate from the ischium and insert into a tendon which extends to the glans and which, for part of its length, is cartilaginous.

It is clear, from a study of existing descriptions, that the female reproductive organs of the African and Indian elephants are very similar, and that differences between the various accounts are due to individual variation among the specimens described. They all agree in general with the description which has been given above for the African elephant, but the extent to which the uterus and vagina are divided into right and left halves is evidently variable, at least in Indian elephants in captivity. The two extreme cases in the literature are (*a*) one described by Watson (1881), in which a longitudinal septum divided not only the uterus, but also the vagina, and (*b*) one described by Paterson & Dun (1898), in which the body of the uterus was entirely unilocular. In 1883 Watson described a second specimen, the condition of which was normal. In the specimen described by Miall & Greenwood (1878) the os uteri was single and the vagina was unilocular, but a fibrous bar divided the opening of the vagina into the urogenital canal. This bar, which the authors 'ventured to call a hymen', was longitudinal. This account was published prior to that of Watson, and the latter had an opportunity of examining Miall & Greenwood's specimen. He confirmed their description but suggested that the longitudinal fibrous bar was not in reality a hymen but simply a vestige of the septum which in his own first specimen was so remarkably complete. Neuville (1937), in his review of the existing descriptions, discusses the significance of the differences between them. He concurs with Watson's view of Miall & Greenwood's specimen, and ascribes the different extent of the septum in different specimens to individual variations in the extent to which the right and left halves of the utero-vaginal tract, derived from the Mullerian ducts, have become confluent. He cites parallel cases from human teratology, and relates the apparently greater frequency of abnormality in elephants to their being phylogenetically isolated and specialized ('Types extrêmes terminant une lignée'). The elephant described by Stukeley (1723) apparently resembled that of Miall & Greenwood in the division of the os vaginae, and can presumably be interpreted in the same way, but the present writer has not studied this account at first hand. The account given by Paterson & Dun (1898) of a very complicated hymeneal valve at the junction of the urogenital canal and the vagina is very difficult to assess. In the first place, this specimen diverged widely from the normal in the structure of its reproductive tract, as described above, and it was a large animal which had spent all its life in captivity. In the second place, Paterson's figure is at least partly diagrammatic, and though the description in the text is quite definite, it is very possible for a chance form, or a temporary fold, to be mistaken for a characteristic structure in so difficult a subject. Neuville concludes that the 'hymen' of Paterson & Dun's account was wrongly so called, and that in any case it is not a normal or usual structure. Of the three female African elephants, the reproductive tracts of which have previously been described, one, that of Perrault (1734), appears to differ from the normal form. This is an early account, and it may be doubted whether the specimen was in fact other than normal. In the text, Perrault describes the uterus as being divided longitudinally into right and left halves, with separate openings into the vagina (which he called the 'corps de la matrice'). But he figured this region as having a curious transverse septum, convex towards the vagina, and pierced not by two but by four orifices, of irregular outline. In this case, as Neuville says, one may take one's choice between the text and the figure, but whatever this sieve-like structure may have been, it seems possible that Perrault's specimen was in fact normal, the description being faulty owing to the peculiar difficulties of the dissection. This seems, also, to be the most likely explanation of the peculiar valvular structures which Perrault described as occurring at the junction of the vagina with the urogenital canal. Neuville, however, having accounts of only three African elephants available (Perrault 1734; Forbes 1879; and Chapman 1880), and accepting one, that of Perrault, as being abnormal, concluded that variability was characteristic of both African and Indian elephants. It is surely significant, however, that the African elephants examined in the course of the present investigation displayed no major deviations from the normal type. It may be that the Indian and African elephants do in fact differ in the frequency with which abnormalities occur, but it is suggested that such a difference is more likely as between captive animals and those in natural conditions in the wild state. It should be added that, whereas Neuville attached some importance to variations of minor detail, the present investigation furnished no comparable details over a large series owing to the fact that it was possible to devote only a limited time to the dissection of each specimen. It was noticed, however, that, because of the size of the animal, minor variations of form, and details of structure, were often brought to notice when in a small animal they would have been invisible. This was true, for instance, of folds in the uterine wall, where it was often difficult, even in quite fresh material, to distinguish between permanent structures, or such features as an old implantation site, and quite temporary folds. Similarly, the dimensions of the reproductive tract varied enormously according to whether it was measured soon after death, when it was greatly contracted and thick, or after the muscles had relaxed, when it would be twice as long but much less in thickness.

The most striking feature of the reproductive organs of the female elephant is the long urogenital canal, resulting in an unusually forward position of the vulva. There was formerly considerable discussion of the possible mode of copulation, since mating is infrequent in captive animals and is not often observed in the field. It is evident, however, that the behaviour of the elephant in coitus is not markedly different from that of such animals as the horse. The present writer has not observed the act, and was able to obtain little detail from hunters who have seen it in Uganda. But nothing that was learned in Uganda, or from those who have had a great deal to do with elephants in Burma, suggests that the excellently clear description given by Slade (1903) is other than accurate. The male, having placed his forelegs on the female's haunches, has to crouch in a semi-sitting position for the initial insertion of the penis, afterwards straightening his hind legs and rising so that the vulva is dragged into a more 'normal' position. It may be noted that this type of behaviour in coitus has been described in the spotted hyena (*Hyena crocuta*) by Schneider (1926). In this animal the female organs very closely resemble those of the male, and intromission takes place via the urogenital canal, which, in the immature animal, opens at the tip of the clitoris, which is almost identical in size and form with the penis of the male. In the adult female, the urogenital canal is enlarged so that it occupies the lower part (morphologically dorsal) of the clitoris. Watson (1881) observed: 'If we imagine the urogenital canal and clitoris of the elephant, instead of being entirely concealed by the abdominal integuments, to be free for a part of their course, we shall then have a pendulous organ closely resembling the genital member of the opposite sex, an arrangement which actually obtains in *Hyena crocuta*.' Watson believed the clitoris of the elephant, like that of the hyena, to be comparable in size with the penis of the male. This is not really so; the clitoris is large, even for the size of the animal, but the penis is very much larger and more extensible. To what extent the clitoris of the elephant is erectile is unknown; that it is sensitive is obvious from observation of captive elephants.

Notwithstanding its usually sluggish movements, the elephant is in fact a supple and agile animal. It is sometimes forgotten that its usefulness in the Burma teak forests depends not only on its strength but on its ability to work in very difficult terrain. The writer has seen wild African elephants climb with ease up rough slopes which he would have judged impassable to them, and which would perhaps have deterred an agile pony. In forest, elephants disturb the vegetation very little as they move, and on one occasion when accurate observation was possible, a group of elephants was found to have passed over a fallen tree trunk, an obstacle just 3 ft high, without scratching its smooth bark. There is therefore no occasion for surprise at the degree of agility called for on the part of the male elephant during copulation as described by Slade.

The length of the urogenital canal, together with the narrowness of the passage from it to the vagina, as it appears in most of the existing accounts, has led to the supposition by many authors that the penis does not reach into the vagina during copulation. This view was held by Hunter, for instance, and Watson, after examining the first of his two specimens, accepted it. Neuville (1937) takes the same view, believing that the degree of rupture that would be caused by the passage of the penis into the vagina would, at least in nulliparous animals, be greater than the animal could conceivably sustain. Paterson (1898), on the other hand, thought that in his specimen the vagina was so completely closed off by what he called the hymen that spermatozoa would be unable to find their way past this point unless the penis ruptured the 'hymen' to deposit the semen beyond it. It has been stated above that the vagina was completely closed off from the urogenital canal in a late foetus, that the two cavities communicated by a narrow passage in a young calf, and that in older animals the passage was not markedly constricted. Information about the condition of the reproductive tract in the foetus and very young animal was not previously available; study of a series of stages suggests that, of the variations described in the literature and reviewed by Neuville, those concerning the demarcation of these successive segments of the tract might reasonably be ascribed to imperfect development from a juvenile form. It is suggested, therefore, that the narrowness of this passage in many of the animals previously described was due to feeble development of the reproductive organs associated with their life in captivity. These animals had failed to breed, and it is probable that the oestrous cycle was partially suppressed, so that the growth of the reproductive organs may not have received the normal growth stimuli of the endocrine cycle. The same explanation may be suggested to account for the finding, discussed by Neuville (1937), that in some cases the urethral opening is posterior to that of the vagina. His description of an animal said to be about 33 years old, which he examined himself, accords with the condition which was noted by the present writer at the autopsy of a young adult female Indian elephant which died in the Zoological Gardens, London. The opening from the urogenital canal to the vagina was very small, being, as Neuville remarked, of about the same calibre as the urethral orifice. It will be seen from the description above (p. 114 and figure 4) that in the foetus the urethra opens into the urogenital canal posteriorly to the partition which separates the canal from the vaginal cavity. In the course of development the relations of the parts in this region normally become altered, but if development proceeded no farther than the piercing of the partition shown in figure 4, then the urethral orifice would continue to be posterior to that of the vagina, and a condition like that described by Neuville would result.

Mayer's (1847) account led Watson (1878) to suppose the vagina to be only slightly demarcated from the uterus in the female Indian elephant, and he compared this species with the hyena in this respect. Miall & Greenwood's paper was published in 1878 and that of Forbes in the following year, and these authors described a well-defined vagina, the former in the Indian and the latter in the African elephant. Watson then dissected a female Indian elephant, which he described in 1881, and found a condition differing from all previous accounts (see p. 115). In fact, the structure he found has not been reported in any other specimen. Assuming this specimen to be normal, he wrote: 'There are few (mammals) in which the vagina, in respect of anatomical structure, presents so close a resemblance to the uterus as does that of the elephant.' In a second specimen, however, which was of normal configuration, Watson (1883) found the vagina quite clearly distinguishable. In the present investigation it was always found possible to insert the hand from the cavity of the vagina, when that organ was cut across *in situ*, into that of the urogenital canal. There is therefore no reason to suppose that the vagina is not normally used in copulation in the elephant. As for the comparison with the hyena in this particular respect, which was taken up by Neuville, a later paper by Matthews (1939) has made it clear that the vagina of the hyena is in fact distinguishable from the uterus, both morphologically and histologically, and that here again there is no reason to suppose it is not functional in coitus.

(2) *The development of the ovarial sac*

The structure of the ovarial sac of the adult elephant has been briefly described above (p. 112, figure 5). The most comprehensive account of the comparative morphology of the peritoneal structures in the region of the ovary of mammals is that of Zuckerkandl (1897), who showed that the form of the sac varies within each order of mammals, while in some cases the same form of sac appears in members of several different orders. In general, the ovarial sac is formed by the mesosalpinx, or ala vespertilionis. This is that portion of the broad ligament in which the Fallopian tube is suspended from the body wall. The tube sometimes runs along the free edge of the mesosalpinx, as in man, but more frequently runs somewhat dorsal to the free edge. In this case the part of the mesosalpinx between the tube and the free edge is conveniently referred to in Zuckerkandl's term as the 'Superior mesosalpinx'. Both ends of the Fallopian tube are fixed in position. The ostium abdominale lies in close relation to the ovary, and the other end of the tube connects with the tip of the uterine horn. But in the adult mammal the oviduct is always longer than a direct line between these two points, so that it follows a more or less sinuous course and carries the mesosalpinx with it. In the simplest cases the mesosalpinx is thus expanded to form a bowed screen partially covering a shallow depression, within which the ovary lies, e.g. in man. In many forms, of which the pig is typical, the oviduct is some distance from the free edge of the mesosalpinx, and the free edge is not so greatly elongated as is the oviduct itself. In such a case a deeper sac is formed, with the Fallopian tube running within its wall, and the ovary is almost completely, although loosely, enfolded. A further modification is found in the seals, where the ovary is almost completely encapsulated, and in the rat and mouse, where the capsule is completely closed.

In the elephant the broad ligament is progressively reduced in extent anteriorly, until at the tip of the uterine horn it has virtually disappeared, so that the massive ovarian ligament projects only slightly, and by virtue of its own thickness, above the peritoneal surface of the body wall in that region. In the foetus, the oviduct leads almost directly, after leaving the uterine horn, into a fimbriated funnel. In the late foetus of E84, as shown diagrammatically in figure 6*a*, the funnel lies alongside the ovary, which at this stage is enlarged by development of the interstitial tissue, probably under the influence of maternal or chorionic hormone (see p. 124). The funnel is more or less symmetrical at this stage, but in the very young calf (E134) represented in figure 6*b*, in which the ovary has become much smaller with the regression of the interstitial tissue, the wall of the funnel which lies away from the ovary has grown very greatly and has covered, and almost completely enfolded, the ovary. The ostium abdominale, however, still lies at the base of the funnel, and both walls of the funnel are fimbriated. The shorter wall of the fimbrial funnel, which we may for the moment refer to as the inner wall, is also drawn up so as partially to enclose the ovary, and it is in this way that the two compartments of the ovarial sac of the adult are formed.

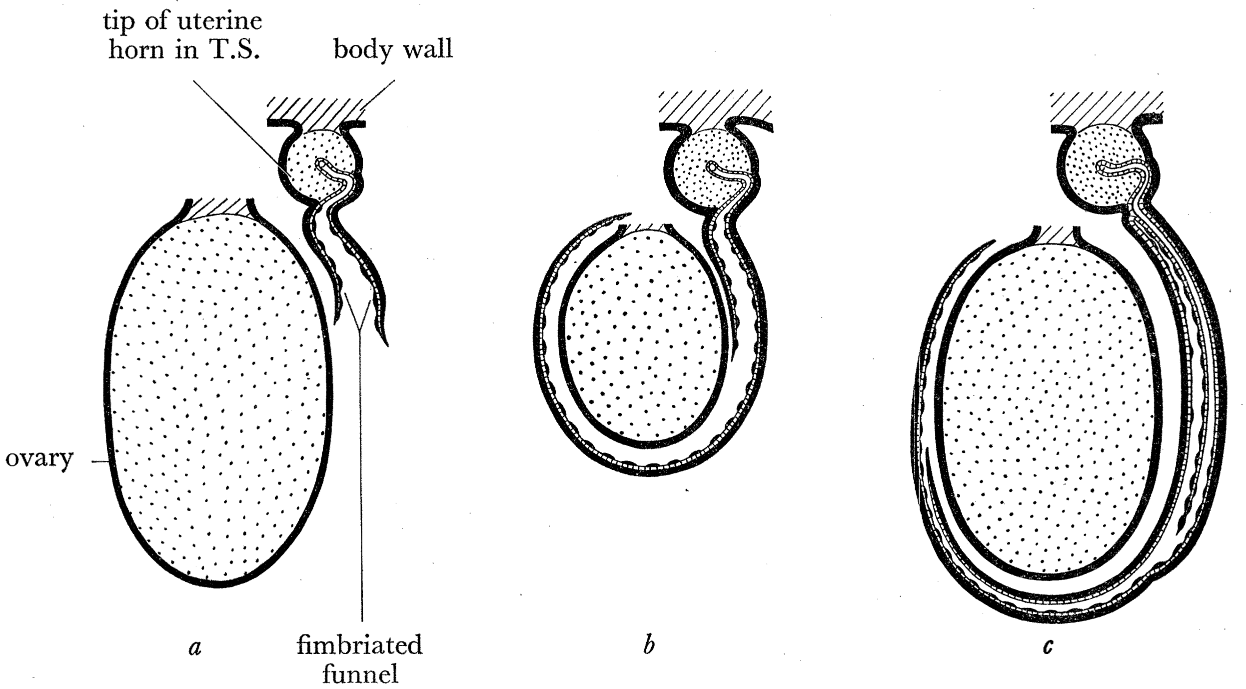

FIGURE 6. Diagram of stages in development of the ovarial sac of the elephant. (*a*) Condition in a late foetus (of E84, cf. figure 4). (*b*) Condition in a very young calf (E134, cf. figure 9, plate 5). (*c*) Condition at puberty (E144). Each figure is a diagrammatic representation of a transverse section through the trunk in the region of the ovary, drawn as if the ovary and the tip of the uterine horn were in the same plane. The peritoneum is represented by a heavy black line.

In figure 9, plate 5, the ovarial sac of the left side, *a*, remains in its normal position, while that of the other side, *b*, has been drawn away from the ovary.

The adult condition is shown diagrammatically in figure 6*c*. Thus in figure 6 are shown: (*a*) the condition in the late foetus of figure 4, (*b*) that of the very young calf photographed in figure 9, and (*c*) the adult condition, where the ostium abdominale has been carried some distance up the outer wall of the sac, to open on its inner (fimbrial) surface some distance from the base of the sac.

It seems reasonable to suggest that this unusual arrangement is related to the great size of the elephant, for it is noteworthy that in most mammals the Fallopian tube is so arranged as to be longer than the direct distance from ovary to uterus. The ovum, in all the species so far investigated, takes a fairly constant time to traverse the Fallopian tube, and its development is jeopardized if it arrives in the uterine lumen either too soon or too late. Normally, the Fallopian tube governs the rate of passage of the egg, and this function can be upset experimentally by hormone treatment. How long the ovum takes to traverse the Fallopian tube in the elephant is not known, but it is reasonable to suppose that it is not markedly different from other mammals in this respect; the relative reduction of the peritoneal structures in the region of the ovary makes the actual length of the Fallopian tube about 25 to 30 cm, comparable with that of many Ungulates.

(3) *Histology of the female reproductive tract*

The present account will be limited to the description of the histological characteristics of the several regions of the reproductive tract in the non-pregnant female. Changes associated with pregnancy will be described in relation to placentation in a further account, and the material includes only three adult animals which were not either pregnant or in lactation anoestrus, and none which demonstrates the changes which may be expected to occur at oestrus. Little difference was observed between the reproductive organs of young nulliparous animals, adults in lactation anoestrus, and the three specimens which, while lactating, were diagnosed as undergoing a succession of infertile cycles prior to a further pregnancy.

The opening of the Fallopian tube is easily located but is not very sharply defined. The fimbrial folds and grooves extend from the 'funnel' into the tube itself and continue for a considerable part of its length. The lumen grows progressively narrower, and the surrounding muscle layer becomes stronger. Apart from the fact that the Fallopian tube in the elephant is not suspended by a mesosalpinx but lies beneath the peritoneum, as already described, it resembles that of such animals as the pig, a strongly fimbriated and ciliated segment gradually giving way, as one proceeds towards the uterine horn, to a strongly muscular and non-ciliated segment.

The uterus may conveniently be divided into three regions, that of distinct right and left uterine horns, that in which the cornua fuse but the lumina remain distinct, and that with a single uterine lumen. The first two are histologically distinguished from the third by the fact that the uterine wall is glandular in the first two segments, while in the third it is not. This portion of the uterus, in fact, which is about one-third of the 'body' of the uterus as seen at dissection, resembles the vagina as regards the inner lining of the lumen. In the quiescent state the lining of both consists of a single layer of cuboidal epithelium supported by a layer, four to six cells thick, of fairly compact tissue which is not sharply demarcated from the underlying muscle and connective tissue. The two regions, lower uterus and vagina, differ in the total thickness and muscularity of the wall, and may well do so in other respects at certain times during the oestrous cycle, but the present material does not show whether this is so or not.

In a very young calf (E119) the development of glands was seen to be beginning in the mucosa of the uterine horns, though not in the middle region of the uterus. At this stage the glands consisted of short invaginations of the epithelium; later they become considerably coiled, but they appear to remain simple in type, with few or no branches, and without anastomoses. In lactating animals in which the placental scar was still prominent the glands were in an active condition and their lumina were distended. It has already been noted that placentation usually occurs in the middle region of the uterus and sometimes in the region where the uterine horns are distinct. The glandular mucosa becomes progressively attenuated towards the upper end of the uterine horn, as the lumen becomes progressively narrower.

The wall of the urogenital canal is relatively thin and extensible, like that of the vagina, but is complicated along part of its length by the clitoris and associated organs. Above this region, however, the wall of the canal is thick and spongy in texture, and was found to be relatively strongly vascularized.

An attempt was made to follow changes in the lining of the vagina and urogenital canal of a living elephant in captivity, but the results were inconclusive. The vagina was found to be inaccessible, and smears were taken from the urogenital canal by the animal's keeper, over a period of time, at weekly intervals. They were found to consist of mucus, but varied greatly in amount, and sometimes contained considerable amounts of blood. The keeper also reported the extrusion of mucus from the vulva at intervals. The occurrence was not regular, but suggested a possible cycle of approximately 6 weeks' duration. The captive animal appears unlikely to yield more precise information, and none is available from the experience of those who have had to deal with working elephants in Burma. Ferrier (personal communication) says he has made repeated attempts to settle this point, both by personal observation and by questioning those in charge of elephants, but without success. He inclines to the opinion that the female elephant experiences oestrus once a year, but it must be remembered that some of these animals calve at regular intervals and others usually fail to breed at all, so that in the former the unmated cycle will be supplanted by one of pregnancy and lactation as in the wild African elephants, and in the latter the cycle is in all probability suppressed or partly so. It will be shown that the elephant apparently undergoes several infertile cycles before becoming pregnant, and from the relative infrequency with which animals in this phase of the reproductive cycle were encountered it would appear that the cycles cannot be of long duration.

(4) *The ovary*

General

The ovaries of each female were first examined *in situ* at the time of dissection, and then removed from the body as soon after death as possible. After further macroscopic examination in the fresh condition they were preserved in formalin. Considerable deformation occurred if the ovary was cut before fixation, but the fixative penetrated only slowly into the bulk of the organ when it was preserved whole. In order to obtain well-fixed material for critical examination, small pieces of tissue were placed in Bouin's fluid, and it was found that whole ovaries were best preserved by placing them in 'formol-alcohol' (1 part of formalin to 9 parts industrial spirit) for about 24 hours, then transferring to 5 % formalin for storage and transport.

As will appear from the descriptions below, it was not possible to count, or even in many cases to identify, the corpora lutea and follicles in the intact ovary, but the appearance of the surface features before fixation helped in the interpretation of the condition of the gonads at subsequent examination. In the laboratory, the preserved ovary was sliced into 'leaves', each a few millimetres thick. The cuts were made from the free edge of the ovary towards the hilum, and parallel to the long axis of the hilum in most cases, but not extending through it, so that the slices or 'leaves' remained attached. This made it possible to identify and count the corpora lutea to determine the condition of the ovary in relation to the reproductive cycle, by macroscopic examination supplemented by histological study of selected regions.

The ovaries of pregnant animals were characterized by the presence of corpora lutea, bright yellow in colour and obviously 'active'. More than one such corpus luteum occurred in every pair of ovaries in pregnancy, and there was only one pregnant animal (E117) in which one of the ovaries had no active corpora lutea. The corpora lutea ranged in size from about 50 mm down to about 2 mm in diameter, and in some cases a pair of ovaries contained as many as twenty corpora lutea over 5 mm in diameter as well as others of smaller size. The ovaries of non-pregnant lactators were characterized by the absence of active corpora lutea and the presence of old corpora lutea in various stages of regression. In animals which had given birth to a calf shortly before they were killed the corpora lutea were still well defined and not greatly reduced in size as far as could be judged, although they evidently begin to darken in colour a short time before full term. Further stages of regression were marked by continued shrinkage and progressive darkening in colour, until eventually the site of a former corpus luteum was seen at the cut surface of the ovary as a minute patch of very dark brown tissue of irregular outline. Histologically, such an area was indistinguishable from the surrounding stroma in a section except for the persistent pigment granules (figure 27, plate 8). It is therefore clear that corpora lutea which may be regarded as 'active' are found at all stages of pregnancy, while parturition is followed by the onset of a lactation anoestrus which lasts until the approach of a subsequent pregnancy.

Only three non-pregnant adults (E130, E145, E146) were found to have corpora lutea of relatively recent formation. These animals, all of which were lactating, are considered in detail below, and the conclusion is formed that they were undergoing a series of ovulations with the production of relatively short-lived corpora lutea. It was not possible to determine whether or not these ovulations were accompanied by oestrus and mating, but these animals were all killed during the time of year when mating is frequent, and it appears certain that in the normal course of events there would soon have followed an ovulation at an oestrous period accompanied by fertile mating. A series of cycles of ovarian activity prior to fertile mating, after a prolonged anoestrus, is not uncommon in mammals, and indeed the basic rhythm of the ovarian cycle appears generally to be maintained throughout the animal's reproductive life, without ever being entirely suppressed even in pregnancy or anoestrus. The transition from anoestrus to full breeding activity is often gradual and is sometimes characterized by a series of 'dioestrous' cycles, as in the wild brown rat (Perry 1945), or by a series of 'silent heats' where ovulation occurs without oestrus, as in the sheep, or even by a number of oestrous cycles accompanied by infertile mating, as in the hedgehog (Deanesly 1934). In the sheep, it has been suggested that the presence of a waning corpus luteum is necessary before heat can occur at a subsequent ovulation, so that the first ovulation after an anoestrous period is necessarily a 'silent heat' (Robinson 1951).

The foetal ovary

An account of the gross anatomy of the ovary and its relation to the surrounding peritoneal structures has already been given in the section on the structure of the female reproductive tract. During the second half of gestation the ovary of the foetus is found to be enlarged by the development of the interstitial tissue, as has been described in the case of the horse (Cole, Hart, Lyons & Catchpole 1933; Amoroso & Rowlands 1951). This enlargement of the gonads occurs in both sexes (figures 10 and 11, plate 5), and in the series of foetuses listed in table 1 the gonads were obviously and markedly hypertrophied in that of E117 (estimated foetal age 16 months) and in all those at later stages. The foetus of E117 was a male, and only one of the larger foetuses was a female (E84). It was found that the ovaries of this animal were very similar in size to the testes of males at similar stages of gestation, and that they were approximately four times as heavy as the ovaries of a neonatal calf. Figure 10 shows the cut surface of the ovary after it had been bisected, and the photograph clearly shows the relation of the cortex, with the light-coloured hypertrophied interstitial tissue, to the medulla, carrying the major ovarian blood vessels. The testis of a male foetus (E61) at a similar stage of gestation is shown in figure 11, and it will be seen that the degree and type of hypertrophy is similar in the foetal gonads of both sexes. The medulla forms a central core of connective tissue, dividing into a series of radial bars or partitions between blocks of tissue comprising epithelial and interstitial elements. These partitions subdivide to form an anastomosing framework throughout the cortex, a condition clearly seen in the section of the testis photographed in figure 19, plate 7. Graafian follicles occur throughout the cortex of the foetal ovary, but most of the larger ones, which attain a diameter of about 2 mm, occur near the periphery. There are also many follicles without antra, many of them with only a single layer of epithelium. One of the larger follicles, which is polyovular, is shown in figure 20*a*, plate 7.

The most striking feature of the ovary at this stage is undoubtedly the great degree of hypertrophy of the interstitial tissue. A small proportion of the excess of bulk of the foetal as compared with the neonatal ovary is due to slight enlargement of the peripheral follicles, but by far the greater part of it is due to the interstitial tissue. It may be remarked at this point that the elephant ovary resembles that of the mare, not only in that the interstitial tissue is rendered conspicuous during foetal life, but also in the fact of its being remarkably inconspicuous in adult life. In both animals the increase in weight of the ovary during pregnancy appears to be attributable almost entirely to the growth of the corpora lutea and the increased vascular supply involved in their development. This is in contrast with the sequence of events in some other animals, in which the interstitial cells are conspicuous in the reproductive processes of the adult. The most extreme example yet described is that of the water shrew, *Neomys fodiens*, where the interstitial tissue hypertrophies during pregnancy to such an extent that the whole ovary at first sight appears to consist of a single mass of luteal tissue, and the individual interstitial cells are indistinguishable from the true luteal cells. (Brambell, Marshall's *Physiology of reproduction*, vol. 1; also Price, M., in preparation.)

The resemblance which the hypertrophied interstitial tissue bears, macroscopically, and at low magnification, to the tissue of an active corpus luteum is more than superficial, for, as can be seen from figure 20*b*, the individual cells bear a striking resemblance to the true luteal cells, although they are smaller than, for instance, the luteal cells of the ovaries of the pregnant animal E138 shown in figures 23 and 24, plate 7. It is possible that they have passed the stage of their maximum development, as no intermediate stages are available between the female foetus of E31, estimated at about 10 months, and the male foetus of E117, estimated at about 16 months. It will be shown that some of the animals approaching mid-pregnancy have undergone a phase of ovarian activity which must presumably have been initiated by the release of gonadotrophin into the blood-stream, but it is likely, by analogy with the mare, that this hormone does not directly affect the foetal ovary. In the horse it has been shown (Cole *et al.* 1933) that the gonadotrophins which are responsible for the changes in the maternal ovaries, leading to ovulation and the formation of accessory corpora lutea during pregnancy, do not cross the placental barrier. Growth of the foetal ovaries, with hypertrophy of the interstitial tissue, is greatest after gonadotrophin ceases to be demonstrable in the maternal blood, and it is probably due to oestrogen (Amoroso & Rowlands 1951). Although the histological appearance of the interstitial tissue in the foetal ovary at this time suggests that it has an endocrine function, Catchpole & Cole (1934) showed that the foetal ovaries do not contain a conspicuously large amount of the hormone compared with other tissues, and it is probably not of embryonic origin.

The neonatal ovary

The material includes the ovaries and uteri of two very young calves (see table 2). One, E134, was probably not more than about a week old, and the other, E119, was probably at least a month old. The intact ovaries of E134 are shown in figure 9; figure 12 is a photograph of a section, 12μ in thickness, through one of them, and figure 21, plate 7, shows a portion of the same section at a higher magnification. The two ovaries of this animal together weighed about 20 g, as compared with 80 g, the approximate weight (from preservative) of the ovaries of the foetus of E84. As the photographs show, the reduction is mainly accounted for by the regression of the interstitial cells from their hypertrophied condition. The interstitial tissue is still conspicuous, however, and in fact up to this stage its regression has for the most part consisted of a reduction in the size of the individual cells. The ovaries of the second calf, E119, are similar in size and in general appearance to those of E134, but the interstitial tissue has changed considerably in character. The cells are somewhat dispersed and the cytoplasm shows a greater degree of vacuolation. In parts of the ovary blocks of interstitial cells are evidently being altered in form and redistributed in the stroma after losing their characteristic glandular appearance (figure 22, plate 7). The vacuolation bears no resemblance to that which is so conspicuous a feature of regression of the luteal cells of the corpora lutea, where the individual cells eventually break down and are replaced by invading connective tissue cells. The interstitial cells, after losing their hypertrophied glandular appearance, contribute to the general structure of the stroma. Such de-differentiation of the interstitial cells has been described in several cases, particularly in the dog (Jonckheere 1930), man (Tropea 1930) and opossum (Martinez-Esteve 1942), and it has been suggested that in some animals these cells may undergo cycles of hypertrophy and de-differentiation in the adult in relation to the oestrous cycle. In the present material the only adult females available were either pregnant or lactating, or both, and in these the interstitial tissue was found to be extremely inconspicuous. This includes the three lactating animals which had apparently passed through a lactation anoestrus and were undergoing a series of relatively brief cycles prior to mating and subsequent pregnancy.

It is noticeable, in comparing the ovary of the advanced foetus with that of the very young calf, that the regression of the hypertrophied interstitial tissue is accompanied by the elimination of the follicles, which, in the advanced foetus, had attained a diameter of as much as 2 mm. This contributes to the shrinkage in the size of the ovary as a whole, and while the cortex of such an ovary as is shown in figure 12, that of a neonatal animal, contains very many follicles throughout its extent, all of them are very small.

The pre-pubertal ovary

As may be seen from table 2, the remaining immature animals must all have been considerably older than the two very young calves which have been described. No sound data are available on which to base an accurate estimate of their age, but it is thought that all of them were at least 1 year old. Single ovaries from these young animals ranged in weight (from formalin) from 15 to 60 g. With the growth in size the lenticular form becomes more pronounced, just as was the case during the temporary enlargement of the ovary during foetal life. The ovary is now about as deep, from the hilum to the free edge, as it is long, and it retains this form throughout life, except for the temporary distortions which are caused by the development of corpora lutea during pregnancy. During the lactation anoestrus the ovary resembles that of the immature animal except that it always remains larger. In the earliest stage represented among this group of immature calves the interstitial tissue has already become inconspicuous, and the increased volume of the organ is due to growth of the other elements, particularly those of the connective tissue. The bulk of the cortex is reduced, relative to the medulla, and now forms a well-demarcated peripheral zone. This condition persists, and the cortex is always seen, at the cut surface of an ovary sliced across in the manner described, as a light-coloured border. This border varies in thickness with the condition of the gonad; it is thickest when there is follicular growth, and shallowest when follicular growth is suppressed, as in the latter half of pregnancy (figure 14, plate 5). The clear demarcation of the cortical region is shown in figure 13 (E45), particularly in the lower part of the figure. This is the ovary of an animal approaching puberty. That follicles occur throughout most of the cut surface in this photograph is due to the cut having been made near to the rather flattened surface of the ovary, so that the section is here tangential.

In the youngest animals in this group, that is to say, in animals believed to be about a year old, the ovary is characterized by the reduction of many of the follicles in the cortex, by a form of atresia. This releases epithelial elements which are then available to contribute to the cortical stroma of the ovary during its considerable pre-pubertal growth. In all these animals, the cortex contained some follicles several millimetres in diameter, and with the approach of puberty such follicles are numerous, as shown in figure 13.

The adult ovary

The cycle of events which was found to occur in the life of the adult female has already been briefly indicated. Parturition is followed by a lactation anoestrus which lasts until the approach of a subsequent pregnancy, and only three non-pregnant animals, all of which were still actively lactating, were found to have active or relatively recent corpora lutea. One other animal, also lactating, had large follicles, and it is evident that these four animals represent stages in the resumption of the oestrous cycle after the lactation anoestrus. In order of the stage they have reached in the sequence of events, these animals are E116, E145, E146 and E130. They proved to be of great importance in the elucidation of the reproductive cycle, and they illustrate what appears to be the normal manner of corpus luteum formation in the African elephant, so the ovaries will be described in some detail.

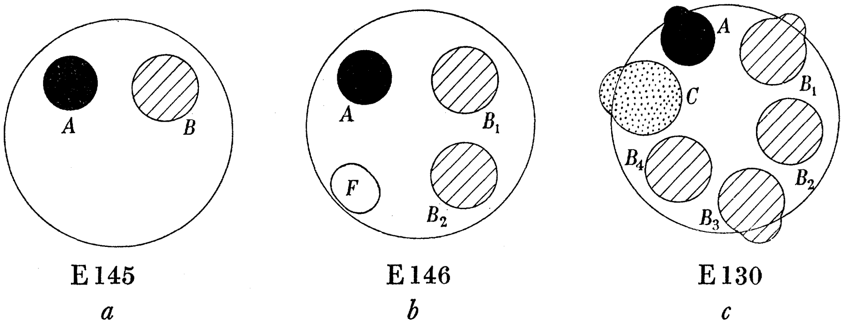

FIGURE 7. Schematic representation of the condition of the ovaries of E145, E146, E130. Each figure represents a pair of ovaries (see text and cf. figure 17, plate 6).

The first, in order of the course of events, is E116, in which two follicles, in the left ovary, have attained a diameter of between 15 and 20 mm (as big as any follicles encountered in the present material), but in which ovulation or atresia and luteinization of the follicles has not yet occurred. The other three animals all had corpora lutea of relatively recent formation, and one ovary of each of these animals is shown in figure 17*a*, plate 6, while the condition of the corpora lutea is represented diagrammatically in figure 7, where each circle represents a *pair* of ovaries. We are at present concerned only with corpora lutea which are, from their histological condition and macroscopic appearance, too recent to be interpreted as the regressing corpora lutea of the preceding pregnancy. Moreover, there is more than one corpus luteum in each pair of ovaries; and the ovaries differ from those of pregnant and post-partum animals in that some of the corpora lutea can be seen, in each case, to have been formed at different times. The ovaries also contain the remnants of older corpora lutea, such as have been seen in all lactating animals and represent the former corpora lutea of pregnancy.

The ovaries of E145 contain two corpora lutea, the histology and macroscopic appearance of which show that they have been formed relatively recently, but at different times. This is shown in figure 7*a*, where they are shaded differently and labelled *A* and *B*, to represent their difference in age; they are shown as not breaking the circle to represent the fact that they appear to have been formed, as far as can be judged, without ovulation. The older of them, *A*, had reached a stage of regression somewhat similar to that of the corpora lutea of pregnancy just after parturition. The two occurred in the same ovary, and both can be seen in the photograph of this ovary in figure 17*a*, plate 6. The darker corpus luteum which lies between them is considerably older, and has lost its regular outline. It is thus impossible to distinguish it from the remains of the corpora lutea of pregnancy such as could be found in the ovaries of all the lactating animals, so that although it may in fact represent a still earlier member of the post-partum series, it has been omitted from the diagram. The ovary of E145 photographed in figure 17*a* was sliced across at several levels; the uppermost portion has been removed completely, and a central portion has also been cut out so as to reveal a cut surface about 1 cm lower than that in which the above-mentioned corpora lutea lie. In this lower cut surface can be seen several follicles of a diameter up to 5 mm, and a dark brown patch of irregular outline which is the persistent remains of a very old corpus luteum.

The ovaries of E146 contain three corpora lutea, all of which appear to have been formed without ovulation. As indicated in the diagram (figure 7*b*), one of them has regressed farther than the other two, and it is labelled *A*, as corresponding, in the sequence of events, to that labelled *A* in the diagram of E145. The other two corpora lutea of E146 are labelled B_1 and B_2 because they are indistinguishable from each other in appearance and histological condition and appear to have been formed at approximately the same time and certainly under the same endocrine stimulus. They both correspond, therefore, to the single corpus luteum *B* of E145. It must be made clear that by labelling these corpora lutea *A* and *B* it is not intended to indicate that those of different animals are in the same histological condition, or of the same age. What is intended is to indicate that the corpora lutea labelled *A* were, in each case, the first to be formed after a long lactation anoestrus, while those labelled *B*, and that which in E130 will be called *C*, represent successive 'generations' of corpora lutea, formed at successive oestrous periods or under successive gonadotrophic impulses.

There is also, in one of the ovaries of E146, a large follicle. It is seen in the photograph of this ovary in figure 17*a*, and just above it is one of the corpora lutea of 'generation *B*', which has been cut across. The dark shadow farther to the right is caused by a portion of the other corpus luteum of this 'generation', which is considerably smaller, having been cut out for histological study. The corpus luteum *A* of this animal was found in the other ovary. All three of these corpora lutea appear to have been formed without ovulation as far as can be judged, and this is represented in the diagram in figure 7*b*, as it was in the case of the corpora lutea of E145.

The third animal of this series, E130, had six corpora lutea sufficiently recent in appearance to indicate their formation in the course of a series of oestrous cycles following the lactation anoestrus. One of them, here referred to as *A*, was definitely older than the other five, and it appears to have been formed by ovulation, for it is surmounted by a prominent protuberance, the tip of which appears to be unmistakably a trauma of ovulation. Its form will be referred to later, when the mode of formation of the corpus luteum is considered. One other corpus luteum in this pair of ovaries was, equally obviously, newer than the others, and it too was evidently formed by ovulation.

The remaining four corpora lutea of E130 were intermediate in age and indistinguishable from each other histologically. They must, in fact, have been formed at approximately the same time, and under a single endocrine stimulus. Two of them were evidently formed from follicles which ovulated. These several corpora lutea are represented diagrammatically in figure 7*c*, and some of them can be seen in the photographs in figures 17*a*, *b*.

It is notable, with regard to the relative longevity of the corpora lutea in these three animals, that as many as three 'generations' can be distinguished in one pair of ovaries, the newest being developed before the oldest has regressed sufficiently far to have lost its definite form. Further consideration will be facilitated if at this stage the probable mode of ovulation and corpus luteum formation is described. The follicle of E146, and the two similar follicles in one of the ovaries of E116, were the largest encountered in the present material. If such a follicle were to rupture without much further increase in size, the former antrum being filled by luteal tissue, one might expect the formation of a corpus luteum a great part of the bulk of which would be contained in a relatively large protuberance, such as is seen in the older corpora lutea of E130, one of which is seen in figure 17*a*. In fact, the appearance of the ovaries suggests that these corpora lutea were formed in just such a manner from follicles very like those of E116 and E146. Further growth of such corpora lutea would lead to an appearance very like that of the newest one of E130 (*C*), seen in figure 17*b*. Still further growth would produce the condition in the large corpora lutea of the pregnant animals, such as are shown, for instance, in figures 16 and 18, plate 6. Four stages in the formation and development of the elephant corpus luteum are represented diagrammatically in figure 8. Each of these diagrams represents a stage actually seen in the ovaries, as described above, and there is no evidence of a pre-ovulation growth of the follicle such as occurs in the mare, where the follicle may reach a diameter of 60 mm before rupture. It seems likely that the size of the mature follicle of the elephant is not much greater than that of the cow.

The oldest corpus luteum of E130 (*A* in figure 17*a* and figure 7*c*), and B_1 and B_2, the two of the second 'generation' which were formed by ovulation, ceased to develop, and began to regress, when they reached the stage of growth represented by stage *b* of the diagram in figure 8. In the fresh specimen these three corpora lutea, as well as the newer one, *C*, were at first thought to be of very recent formation because the traumata of ovulation were not completely healed, and traces of extruded blood were still to be seen even in the case of the oldest, *A*. The suggestion is that these corpora lutea are relatively short-lived, the successive 'generations' (*A*–*B*–*C*) being produced at a series of oestrous cycles. There is, of course, no evidence as to whether these cycles are like the so-called 'silent heat' of the ewe, i.e. growth, rupture and luteinization of follicles without the symptoms of heat, or whether they are accompanied by oestrus, with or without infertile mating.

There remains the problem of the status of the most recently formed corpus luteum of E130, that which has been called *C*. It is possible that this was in fact the corpus luteum of conception (see p. 132) and that the animal was actually pregnant. If this was the case, the embryo must have been minute, and lying free in the uterine lumen. The Fallopian tubes were carefully dissected out within an hour of death, and thoroughly transfused with fluid which, after the addition of a preservative, was subsequently searched for the presence of an ovum, without success. The uterine lining was smooth and creamy in texture, and the uterus was carefully removed and searched as thoroughly as possible. It was thought at the time that a structure of as much as, say, 3 mm diameter would have been located. The histological condition of this corpus luteum is illustrated in figures 23*b* and 24*b*, plate 7, and may be compared with that of one of the larger corpora lutea of E138, a pregnant animal, shown in figures 23*a* and 24*a*. Of these two corpora lutea, it should be remembered that the one from E130 had the external form shown at stage *c* of figure 8 and the one from E138 had reached stage *d* (figure 16, plate 6). In the absence of a sequence of known stages for comparison it is difficult to interpret the histology of a single corpus luteum, but those of E138, the histology of which is seen in figures 23*a* and 24*a*, and the external form of which is shown in figure 16, would not seem likely to represent a stage of development leading up to the condition of the corpus luteum *C* of E130, figures 23*b*, 24*b* and 17*b*. The extent of the connective tissue, which so markedly partitions the luteal tissue into a series of bands, in figure 23*b*, suggests in fact that this corpus luteum had already entered upon changes which would lead to regression. The likelihood is that, like those of the preceding 'generations' in the same ovary, it was destined to regress without ever reaching the final form of the fully developed corpus luteum of pregnancy. It would seem, therefore, that in the normal course of events this animal would have undergone a further oestrous cycle before becoming pregnant.

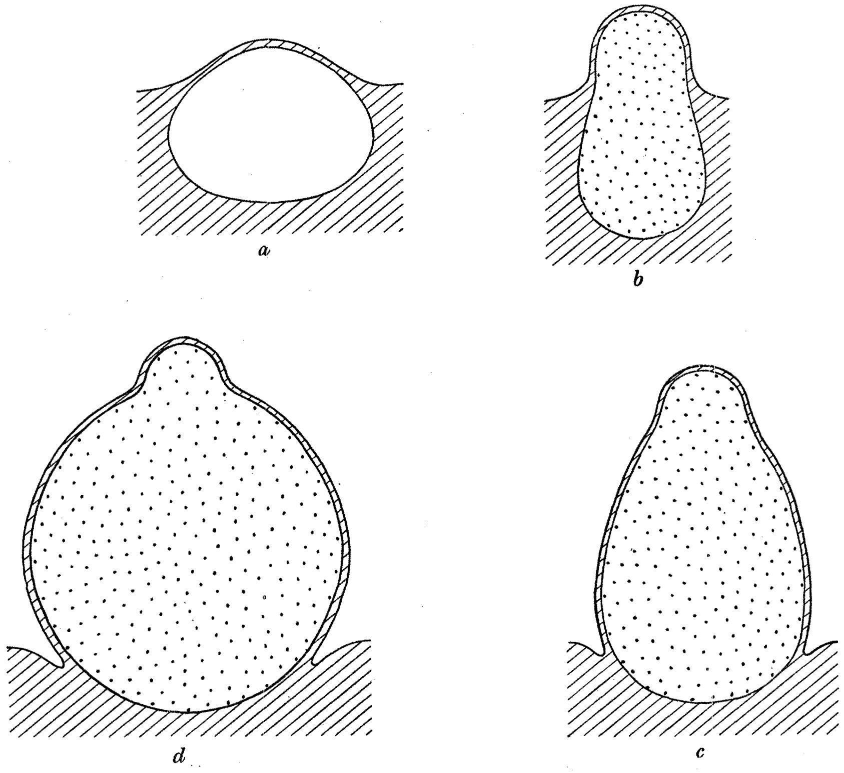

FIGURE 8. Probable mode of corpus luteum formation in the elephant. Based on actual specimens, as described in the text.

The corpora lutea B_1 and B_2 of E146, and the four B_1, B_2, B_3 and B_4 of E130 (figure 7), were so similar histologically as to render it inconceivable that they were not formed in each animal under the stimulus of a single endocrine impulse. This fact is illustrated in figure 25, plate 8, where sections of the six corpora lutea of E130 are shown at the same magnification. The sections were cut at the same thickness and mounted on a single slide for staining, and the photomicrographical procedure was as nearly identical as possible in each case. It will be seen that, of the six corpora lutea, one is evidently newer, and one older, than the remaining four, and that the histological condition of these four is identical. Reference will be made later in this account to the occurrence of multiple ovulation as a regular feature of the reproductive cycle of the elephant (p. 133).

All the animals which have been described as undergoing oestrous cycles after a lactation anoestrus were killed during the period of the year when mating is thought to be most frequent (see p. 102). It will be noticed that although two large follicles appear to be maturing in the ovaries of E116, the first ovulation after the quiescent period resulted in the formation of a single corpus luteum, while multiple ovulations occurred subsequently. This suggests that the ovaries require to go through one or more cycles of activity before they respond fully to gonadotrophic stimulus, or that the whole endocrine system only slowly regains its full activity after a long quiescence. But one animal (E21) was encountered in an early stage of pregnancy, with a foetus of about 60 g, in which the ovaries contained no traces of corpora lutea other than the active corpora lutea of pregnancy. By analogy with other animals it seems very unlikely that corpora lutea formed shortly before conception, like those considered above, would have disappeared completely so early in pregnancy, so that in this instance the first oestrous cycle after a quiescent period was evidently accompanied by multiple ovulation and fertile mating. This specimen belonged to the subspecies *Loxodonta africana cyclotis*, and it is conceivable that the forest elephant differs from the bush elephant in this respect. It would seem more likely, however, that while it is usual, in the genus *Loxodonta*, for pregnancy to be preceded by a series of oestrous cycles, it is possible for the first oestrus after an anoestrous period to be accompanied by ovulation and fertile mating, with the production of sufficient luteal tissue to maintain the ensuing pregnancy.

It may be that multiple ovulation is preceded by a single ovulation in most cases, not merely because the physiological mechanism takes some time to regain full activity, but because multiple ovulation is only possible after a corpus luteum has previously been functioning in one of the ovaries. That the corpus luteum may have this positive effect is suggested by the finding of Marden (personal communication) that multiple ovulation can be experimentally induced in the calf only if a single corpus luteum has previously been functional, and by the fact that, in the cow, experimental induction of multiple ovulation was most successful when a waning corpus luteum was present in the ovary, or when progesterone was injected in the case of an animal from which the corpus luteum had been removed (Rowson 1951). Further evidence that progesterone plays a part in the initiation of oestrus is given by Robinson (1952).

The ovaries during pregnancy

The thirty-one pregnant animals which were encountered had, in every case, a foetus *in utero*. The foetuses ranged in weight from about 12 g to about 120 kg, and in overall length from 60 mm to about 1400 mm. These animals are shown in table 1, where they are arranged in order of the size of the foetus, and it will be seen that there are sixteen with foetuses up to 8 kg in weight, and fourteen with foetuses over 80 kg, and only one specimen intermediate between these two groups, with a foetus of 45 kg. It has been shown in a previous section of the present paper (p. 102 and figure 1) that in all probability the sixteen foetuses below 8 kg represent a series of stages of gestation up to about half-term, while the fourteen of 80 kg and over represent a group of animals nearing full term, and E117, with a foetus weighing 45 kg, was probably about 16 months post-coitum. Thus there is a gap in the series of pregnancies, and stages immediately after half-term are not represented. This has to be borne in mind in the interpretation of the condition of the ovaries, together with the fact that early implantation and pre-implantation stages are also not represented.

The ovaries of several animals at different stages of pregnancy are shown in figures 14, 16 and 18, plates 5 and 6. The available material covers the gestation period from an early uterine stage to very near term, and post-partum animals are also available. Throughout this period the ovaries are characterized by the presence of a number of apparently active corpora lutea, bright yellow in colour in most of the specimens, and only beginning to darken with the near approach of parturition. As the photographs show, many of these corpora lutea bear a protuberance which can only be regarded as marking the point of rupture of the follicle from which the corpus luteum developed. The pregnant animals fall, however, into two groups according to whether or not the ovaries contain follicles with antra. Some such follicles, sometimes very small and sometimes as much as 5 mm in diameter, were found in the ovaries of every animal in the first half of gestation, that is to say, in all stages up to and including that of E31, with a foetus of about 8 kg. No follicles with antra were found in any of the later stages of pregnancy. Follicles of about 5 mm diameter are seen in the photograph of one of the ovaries of E24 (figure 18*a*, plate 6). During the latter part of pregnancy, sections of the ovarian cortex reveal the presence of follicles of which the epithelium is only a few cells, or sometimes only one cell, in thickness.

The presence, as a normal condition, of a considerable number of corpora lutea of approximately the same age in the ovaries of a monotocous animal during pregnancy invites comparison with the condition in the mare, the only other example known at present (Cole, Howell & Hart 1931), although other equines are probably similar. In this species the original corpus luteum of pregnancy regresses after about 30 days (Cole *et al.* 1931, and Kimura & Lyons 1937) and is replaced by a set of corpora lutea formed by the luteinization of all or nearly all of the follicles with antra which are present in both ovaries. The follicle which ruptures at oestrus, to give rise to the corpus luteum of pregnancy, properly so-called, attains a diameter of about 60 mm before rupture, and the corpus luteum formed from it grows to a similar size. For a time, from about the 40th to about the 180th day, gonadotrophin occurs in the blood serum of the pregnant mare (Day & Rowlands 1940), and the production of the accessory corpora lutea presumably occurs under the influence of this substance. The larger follicles ovulate (Amoroso, Hancock & Rowlands 1948), while the smaller luteinize without the release of the ovum. None of them attains the size of the single follicle which ruptured at oestrus. These corpora lutea persist, in an apparently active condition, for a considerable time, but they have completely regressed by about the 180th day, and from then until the end of pregnancy (about 360 days in the mare) the ovaries contain neither corpora lutea nor large follicles, and appear to be in a state of complete quiescence.

A point of nomenclature arises with the need to distinguish conveniently between the corpora lutea of different origin which are found during pregnancy in such a case. In their description of the changes in the pregnant mare's ovary, Cole *et al.* (1931) confine the term 'corpus luteum of pregnancy' to the corpus luteum which is associated with conception, and there can be no doubt that this is correct. Amoroso *et al.* (1948) use the term 'primary corpus luteum of pregnancy', but no convenient term for the corpora lutea which are formed during pregnancy is suggested. In the present account it is proposed to refer to the true corpus luteum of pregnancy (i.e. that which is formed from the follicle from which came the ovum which was fertilized and developed into the embryo) as the 'corpus luteum of conception', while all corpora lutea formed subsequent to this one, during pregnancy, will be termed 'accessory corpora lutea of pregnancy'. These appear to be self-explanatory terms and to facilitate discussion of the conditions met with in the mare and in the elephant.

In comparing the ovaries of the elephant in pregnancy with those of the mare, the first notable difference lies in the presence of active corpora lutea throughout pregnancy in the elephant, in contrast with the quiescence of the ovary, and the absence of corpora lutea, in the later stages of pregnancy in the mare. Pursuing the comparison, several questions present themselves regarding the fate of the corpus luteum of conception, the stage at which accessory corpora lutea are first formed, and whether, once formed, they persist throughout gestation or are replaced once or several times. In the earliest stage of pregnancy covered by the present material, the embryo is some 60 mm in length and the zonary placenta is established. It is not possible to age the embryo accurately, but it is likely to be more than 1 month, and is probably 2 months, post-coitum. The ovaries of the mother, like those of most of the pregnant animals examined, contained the remains of several corpora lutea in advanced stages of regression, but there is no evidence that the corpus luteum of conception had regressed to this degree. Some, and as far as can be seen all, of these very old corpora lutea can be accounted for by the fact that conception is preceded by the formation of a number of corpora lutea whose remains may be expected to persist in the ovaries for a long time. There is therefore no one corpus luteum in any one of the ovaries which can be identified as that of conception by its being older than those which were active at the time of death. The ovaries of E25, the earliest pregnancy, contained five corpora lutea which appeared, macroscopically and histologically, to be fully active. There was one in the left ovary, with a prominent rupture-point, and four in the right ovary, of which two had prominent rupture-points. These five active corpora lutea, like those of each of the pregnant animals encountered, were histologically indistinguishable from each other. The corpus luteum in the left ovary was the biggest and the embryo was in the left horn of the uterus, but other specimens had more than one corpus luteum in both of the ovaries and no relation could be discerned between the location of the embryo and the number or size or condition of the corpora lutea in the respective ovaries.

Amoroso *et al.* (1948) concluded that during the second and third months of pregnancy in the mare 'It is highly probable that...a succession of follicles ovulate, from which corpora lutea are rapidly formed to maintain gestational requirements'. It is clear from the description given by Cole *et al.* (1931) and from examination of the ovaries of the mare during these stages, (*a*) that additional corpora lutea are formed from follicles which do not ovulate, and (*b*) that the earliest accessory corpora lutea continue to function while the later ones are being formed, until by the 80th day of pregnancy both ovaries contain a considerable number of fully active corpora lutea. Amoroso *et al.* do not describe the histological condition of the individual corpora lutea of the mare's ovary during the period concerned, and whether or not these accessory corpora lutea of pregnancy can be distinguished from each other, or, as it were, 'aged' histologically, appears not to have been investigated as yet. These authors, however, found one or more ova in the Fallopian tubes of nine out of fourteen mares killed between the 46th and 73rd day of pregnancy, so that, in some cases at least, it must have been possible to distinguish the newest of the accessory corpora lutea from the remainder. The corresponding stages of pregnancy in the elephant are fairly well represented in the present material, and the fact that in no case could a clear histological distinction be seen between the several active corpora lutea in a pair of ovaries very strongly suggests that they were formed not over an extensive, but over a restricted period of time. This conclusion is strengthened by the fact that the number of active corpora lutea was not found to increase with successive stages of pregnancy during this phase. All the corpus luteum formation which will occur in the earlier months of pregnancy has in fact been accomplished by the earliest stage represented in the available material (E25). As the corpus luteum of conception could not be identified in any of the available stages, even the earliest, it must either have regressed completely by this stage, or else it must persist in an active condition throughout the period of formation and activity of the accessory corpora lutea. That it should already have regressed to a minute remnant indistinguishable from the remains of corpora lutea which developed and waned before conception occurred seems unlikely. Furthermore, the sample includes one specimen of *L. a. cyclotis* (E21) in early pregnancy, the ovaries of which contain no corpora lutea other than the fully active ones (p. 130), and as the site of an old corpus luteum is recognizable for a very long time in the elephant it would seem that the corpus luteum of conception must be among those which were active at the time of death. If, as appears very probable, this is always the case, and if the accessory corpora lutea are in fact formed over a restricted period of time very early in pregnancy, as the evidence suggests, the implication is that multiple ovulation occurs as the normal process at the time of fertile mating. It has already been shown (p. 128) that multiple ovulation does in fact occur during the oestrous cycle of the non-pregnant animal, and it is therefore concluded that pregnancy is in all probability initiated by a multiple ovulation and the formation of a number of corpora lutea, some of which are formed from the follicles which ovulate and others from follicles which luteinize without ovulating.

If this is the case, the similarity between the ovaries of the elephant and those of the mare during certain stages of pregnancy is seen to be the result of very different processes in the two animals. It is of course clear that they differ markedly in the later stages of pregnancy, and during the stages which have just been described there is a difference in that the ovaries of the elephant always contain some follicles with antra, as if in preparation for further follicular activity, while the ovaries of the mare rapidly reach a condition in which all the Graafian follicles appear to have luteinized.

At this point attention must be drawn to the later stages of gestation in the elephant. It has already been stated that bright yellow and evidently active corpora lutea were found in the ovaries of every one of the pregnant animals encountered, up to full term. Those of animals very near full term show definite signs of the onset of regression, and it is evident, from a study of the ovaries of lactating animals, that the corpora lutea rapidly shrink, with the breakdown of the luteal cells, very soon after parturition.

It is evident, however, that one set of corpora lutea does not last throughout pregnancy. Instead, it appears that those which are found in the ovaries in the earlier stages of pregnancy are replaced, usually near mid-term, by a very similar set, formed in a similar manner. The clearest available example is that of E138, an animal killed on 24 February, with a foetus weighing approximately 6 kg and estimated as being 9 or 10 months post-coitum. The ovaries of this animal are shown in figure 16, plate 6, and the histological condition of the corpora lutea can be seen from figures 23*a* and 24*a*. There were fourteen bright yellow corpora lutea, histologically indistinguishable from each other, in the right ovary. Four of them were 20 mm or more in diameter, six were between 3 and 10 mm in diameter, and the remainder were intermediate in size. The left ovary contained twelve corpora lutea similar in gradation of size, and in histological condition, to those of the right ovary. There were prominent rupture-points on four of the corpora lutea in the right ovary and on five of those in the left ovary. A few follicles occurred in these ovaries, up to 3 mm in diameter. At the time of dissection, when the ovaries were examined in the fresh condition, it was recognized that ovulation had occurred not long before, although it was long enough for the traumata to have healed over and for the corpora lutea to have reached what would probably have been their maximum size, with the form shown diagrammatically in figure 8, stage *d*. Old corpora lutea were present as well, but they were far regressed, very dark in colour and only about 5 mm in diameter. Such structures, sometimes recognizable in even more advanced stages of elimination, were found in the ovaries of almost all the pregnant and lactating animals, and they evidently persist for a very long time, so that it is difficult to interpret their origin in any one case.

The relatively recent formation of the corpora lutea of E138 was indicated by the very clearly defined rupture-points, by the condition of the tunica albuginea over these points, and, in particular, by the histological condition of the luteal tissue. In this respect this animal was in marked contrast with others killed earlier in pregnancy. In most of these the corpora lutea were remarkably similar, being characterized by a marked degree of vacuolation which is described in greater detail below and which can be seen in figure 26, plate 8. The degree of vacuolation varied somewhat, and was not always the same in different parts of one corpus luteum, but it was always conspicuous and appears to represent a stage of long duration in the 'life' of the corpus luteum. The example shown in figure 26 is that of E3, an animal with a foetus of about 900 g as compared with that of about 6 kg in the uterus of E138. There can thus be no doubt that the active corpora lutea of E138 were formed at an intermediate stage of pregnancy.

Attention has already been drawn to the unequal distribution of the sample of pregnant animals between successive stages of pregnancy. E138 was one of the most advanced of a fairly complete series of pregnancies in the first half of gestation. One other animal of this group appeared to have undergone the same process of replacement of the corpora lutea. This animal (E147, figure 18*c*, plate 6) was at a slightly earlier stage than E138, and the replacement had taken place less recently before death, so it must have occurred at a less advanced stage of gestation. A seasonal influence may account for the fact of one animal having experienced this wave of ovarian activity at an earlier stage of gestation than another, the difference being of the order of 2 months. It is probably significant that both animals were killed during the time of year when mating is apparently most frequent, for the long gestation period, continuing through nearly 2 years, carries the animal through the usual breeding season some time near the middle of pregnancy, and as E147 became pregnant at a later date than did E138, any response of its ovaries to a seasonal influence would overtake it earlier in pregnancy. That these corpora lutea were in fact 'active' was shown by the demonstration of the presence of progesterone in the preserved material. This was done by Mr D. G. Edgar at Cambridge, using a method of paper chromatography (Edgar 1952).

It has been remarked that the ovaries contain none but minute follicles without antra in the late stages of gestation, but follicles with antra always occurred in the ovaries of animals in the first half of pregnancy, and the series is perhaps not sufficiently extensive entirely to preclude the possibility that the process whereby the corpora lutea are replaced during pregnancy, as just described, may be repeated more than once. There is, however, no evidence for it in the available material, and except for the two animals mentioned, the active corpora lutea were remarkably similar in every case.

It is concluded, therefore, that the significant features of the ovarian cycle of the elephant in relation to pregnancy are as follows.

First, the animal passes through a series of oestrous cycles, with the formation of one or several corpora lutea, some by ovulation and some by atresia, before there occurs an oestrus accompanied by fertile mating and conception.

Secondly, a number of accessory corpora lutea are formed early in pregnancy, and most probably at the same time as the corpus luteum of conception, some of the accessory corpora lutea being formed from follicles which ovulate.

Thirdly, the corpora lutea formed at the beginning of pregnancy last until about mid-term, when they are replaced by a similar set, of which again some are formed by ovulation and some not.

Fourthly, these replacement corpora lutea persist to term, when they rapidly decline.

Fifthly, there is complete suppression of follicular growth during the late stages of pregnancy.

The lactation anoestrus

Lactation appears to be a continuous process throughout the reproductive life of the adult elephant (see p. 108), but after parturition the ovaries rapidly take up the quiescent condition which was encountered in about half of the adult females. The corpora lutea shrink in size and are soon reduced to small irregular-shaped blocks of dark brown tissue distinguished histologically only by the presence of numerous pigment granules which are responsible for the colour. A number of follicles grow to a diameter of about 5 mm but do not develop further. This appears to be the normal size attained by some of the follicles at all stages from before puberty until old age, with the exception of the late stages of pregnancy, when follicular growth is suppressed. The condition of the ovary in lactation anoestrus is well illustrated by that of E77, figure 15, plate 5, which shows the well-demarcated cortex, the follicles, and one of the dark brown patches marking the site of a former corpus luteum.

The histology of the corpus luteum

The present material does not include early stages in the development of the corpus luteum of the elephant, but certain characteristics of the stages of activity and regression call for description. In the first place, the corpora lutea of pregnancy, which never occur singly, together constitute a relatively large mass of luteal tissue which maintains an apparently active condition for nearly a year. It is estimated that in some of the pregnant animals the ovaries contained over 200 g of luteal tissue. For some time after the corpus luteum is fully developed, the luteal cells are large, rounded and sometimes binucleate, and the cytoplasm has a frothy appearance. They present, in fact, the structure characteristic of this type of cell in the fully developed condition (figures 23*a* and 24*a*). But in most of the available specimens the cytoplasm of the luteal cells is occupied by large spherical globules which stain black with osmic acid and which appear as vacuoles in preparations in which they are not preserved (figure 26, plate 8). This very marked degree of vacuolation is evidently a process of fatty degeneration, but nevertheless appears to represent a functional phase of the corpus luteum which persists for a long time. It would seem that during this time substances are slowly released from the vacuoles in a process which involves the eventual destruction of the cells. With the exhaustion of the vacuoles the luteal cells in fact disappear, and are replaced by connective tissue elements.

Another feature is the marked orientation of the luteal tissue in a framework of connective tissue, seen in figures 23 and 24. The orientation is related to the vascular supply, and particularly to the arrangement of prominent channels, presumably lymphatic in nature, which are lined by a well-defined epithelium and which evidently function as a drainage system. They are present in the earliest stages in this material, and persist until the corpus luteum finally and rather suddenly declines, a process which, in the present material, is illustrated by stages immediately before and after parturition. These channels are more prominent in the structure of the corpus luteum than are the actual blood-vessels, except in the region of the periphery, near the theca interna from which the blood-vessels ramify into the luteal tissue.

Numerous granules occur in the cytoplasm of the luteal cells from a relatively early stage. Their presence gives the active corpus luteum its bright yellow colour, as in some other species, and their persistence after the destruction of the cell in which they were formed identifies the site of a former corpus luteum for a long time, even after the disappearance of the theca interna. The latter forms a thick investment around the corpus luteum and retains its shape for some time after the sudden reduction in size of the corpus luteum, brought about by the collapse of the luteal cells.

The germinal epithelium and the ovarian periphery

At all the stages of development that have so far been examined, the periphery of the elephant ovary is to a greater or less degree folded, in such a way that pits extend from the surface into the stroma, and as these pits are lined with germinal epithelium in common with the rest of the free surface of the ovary they bring about an increase in the total area of the germinal epithelium. At certain stages the folding is accentuated and the periphery is not only pitted but is produced into papillose projections, so that the surface area is further increased. A description of some of the present material has been incorporated into an account of subsurface crypts in the ovaries of a very wide range of mammals by Harrison & Matthews (1951), who describe a variety of ways in which the germinal epithelium appears to penetrate the tunica albuginea. These authors found it 'difficult to associate crypt formation directly with the reproductive pattern', although they noted that most of the species in which crypt formation was a regular feature of the ovarian histology were ones which are believed to be monoestrous, and in which ovulation is possibly induced by copulation. They conclude that crypt formation, when it occurs, is associated with the migration of cells from the germinal epithelium into the cortical stroma, contributing to the epithelial (granulosa) elements of the follicles. There is no evidence that the phenomenon is associated with the development of epithelial cells into oocytes, and, indeed, in the whole of the large series of ovaries which were studied, no oocytes were found near the bases of the epithelial crypts.

In the present study the elephant material has been extended and includes the ovaries of foetal and neonatal animals, as described above, and it is possible to amplify to some extent the description of the ovarian periphery given by Harrison & Matthews. Thus, for example, it was found that although surface crypts were sometimes shallow and few, they were never entirely absent from any of the ovaries studied. In no case was the germinal epithelium found to proliferate so as to form a layer more than one cell in thickness, and, on the other hand, it never appeared to be greatly attenuated by being stretched over the bulging surface of a projecting corpus luteum or follicle. Crypts were few and shallow in the surface of the ovary of the foetus of E84, an advanced foetus whose ovaries were greatly enlarged by hypertrophy of the interstitial tissue. They were very little more prominent in the ovaries of the two very young calves whose ovaries had shrunk with the regression of the interstitial tissue, and it was noticeable that the surface of the ovaries of these animals was extremely smooth and free from wrinkles, while the tunica albuginea was little thicker, if at all, than that of the enlarged foetal ovary. The 'shrinkage' brought about by the regression of the interstitial tissue from its formerly hypertrophied condition must, therefore, be accompanied by the resorption of a considerable amount of epithelial and connective tissue in the region of the periphery. The degree of crypt formation in the remaining pre-pubertal animals varied to some extent but was not found to be extreme in any of them. The material does not include any animals actually in oestrus, but it does include three non-pregnant animals which were evidently undergoing successive cycles of ovarian activity resulting in the production of corpora lutea and accompanied by ovulation. There was a considerable degree of crypt formation in these, but the most extreme examples were found in the ovaries of pregnant animals near mid-pregnancy. Part of the periphery of one such animal, E138, is shown in figure 28, plate 8. This animal is the one which affords the clearest example of mid-pregnancy ovulation and luteinization within the present sample. It will be seen that the area of the surface covered by the germinal epithelium is increased not only by the formation of crypts but, more especially, by the projection of papillae from the ovarian surface. In this case it should be noted (*a*) that the surface of the ovary is rendered very irregular, and therefore very extensive, by the projection of many corpora lutea, and (*b*) that this ovary is not one which is about to require epithelial elements for the development of a large number of follicles, but one which has recently ovulated with the conversion of many follicles into corpora lutea. Thus, although it seems certain that the surface activity must be related in some way to the phase of follicular activity through which the ovary has recently passed, the formation of crypts and papillae cannot be regarded as a preparation for the mechanical requirements of an increase in the ovarian surface, or its volume, or as a means of storing large numbers of epithelial cells to be used up in the development of follicles. If this extreme example of crypt formation were seen some time after ovulation in the non-pregnant animal, it might be thought to be related to the requirements of the next oestrus, which would follow after a short interval, but this ovary was not destined, as far as is known, to undergo further follicular activity for a very long time. In the last few months of pregnancy, crypt formation, together with follicular activity, is at a minimum.

Harrison & Matthews considered the possibility that crypt formation might be concerned with the development of oocytes from epithelial elements, but found no evidence to suggest that this was so. Examination of further elephant material in the present investigation similarly fails to demonstrate the likelihood of this possibility. It appears certain that the periodic increases in the number and extent of the surface crypts of the ovary are associated with the oestrous cycle, but it must be concluded that the nature of the relationship remains obscure.

Conclusions

The investigation described in the present paper covered a number of different aspects of reproduction in the elephant, and the findings have been discussed under the several heads as they have been described. That the reproductive cycle should present a number of features unique among known forms is not surprising in view of the isolated systematic position of the elephant and the small number of species whose reproduction has been studied compared with the large number of which we have little or no knowledge. Although the resemblance between the elephant and the mare in the behaviour of the ovaries during pregnancy is not as close as superficial study might suggest, it is nevertheless striking, and the occurrence of multiple ovulation as a normal feature of reproduction in both forms is remarkable among monotocous animals. The two species differ in that multiple ovulation plays a different role in each, and they have markedly different mechanisms for the maintenance of pregnancy, while they resemble each other in the behaviour of the interstitial tissue of the gonads during foetal and adult stages. The placenta and foetal membranes of the elephant are very different from those of the mare and very similar in some respects to those of *Hyrax*. On the other hand, the structure of the ovaries and the pattern of the ovarian cycle differ very greatly in *Loxodonta* and *Hyrax*. Resemblance in some respects, together with marked dissimilarity in others, is not uncommon among members of related groups, and the present findings must be considered to afford additional evidence for regarding the elephants as being phylogenetically related in some degree both to the Perissodactyla and to the Hyracoidea.

The provision of numerous corpora lutea, which comprise a considerable mass of luteal tissue throughout gestation, and their precipitate decline at term, with the destruction of luteal cells, suggests that they play a vital part in the maintenance of pregnancy for a total period which is apparently about 22 months. That the accessory corpora lutea which are formed at about mid-term and replace those of the earlier part of gestation are in fact 'active' in the sense that they produce or contain progesterone has been demonstrated by Mr D. G. Edgar's work on the preserved material. It has sometimes been suggested that the corpus luteum may lose its function some time before it regresses in size, but the author inclines to the opinion that in some forms, including the elephant, the corpus luteum may act as a reservoir from which hormone is slowly drained off, for some time after the luteal tissue has been brought to a condition resembling extreme fatty degeneration. Physical methods of identifying and estimating progesterone will doubtless be applied to the corpus luteum of such animals as the cow at successive stages of pregnancy and will have a bearing on this point. At present, however, the mode of action and utilization of progesterone remains obscure.

Existing descriptions of the female reproductive organs have been reviewed in relation to the present findings, and the marked discrepancies which characterize them have been attributed to the fact that the authors were describing animals kept in captivity. It has been shown that some of the ways in which the descriptions vary may be attributed to varying degrees of retention of infantile characters in the reproductive organs of elephants in captivity. It may be added that it is difficult to estimate the age of an elephant in captivity if the date of birth is not known, and African elephants in zoological gardens appear to differ from wild ones much more markedly in body conformation than do Indian elephants.

This investigation could not have been carried out without the co-operation and financial help of the Uganda Protectorate Administration, and one of its aims was to provide information which could be taken into account in framing government policy with regard to the conservation of the elephant population and the sale of licences to ivory-hunters. The information is, of course, of biological interest as well, covering such aspects of the life cycle as the breeding season, age at puberty, the probable 'productivity' of the population, and tusk growth in relation to age and sex. These points have been considered in the preceding sections of this paper. It has been clearly shown that breeding occurs at all times of year, and it is less clear, but probable, that mating is somewhat more frequent from December to March than at other times of year. It has also been shown that an adult female will calve at an average interval of approximately 4 years, or rather less, and the probable sequence of events in the individual has been discussed. In relation to the population as a whole it seems safe to assume that each adult female will produce a calf every 4 years on an average, and it has been shown that puberty is reached at an age of about 10 years. The average life span remains a matter for conjecture, but conservation measures can be based on an estimated average life span, and an estimated or counted total population, taken in conjunction with the facts just quoted.

The relation of tusk growth to age is another characteristic of interest in relation to administrative policy. Work by the author (in preparation) has shown that the rate of growth of tusks varies enormously in different males, and that large tusks usually indicate rapid growth rather than old age. Exceptionally large tusks are probably the result of both rapid growth and unusual longevity, but no examples were included in the present material. The bearing which this has upon ivory-hunting and conservation is somewhat complex. Thus, although a pair of tusks of, say, 100 lb. each, does not necessarily take a long time to grow, in terms of an elephant's lifetime, it must be remembered that many males will never produce big tusks however long they survive, so that the number of potential big tuskers is only a proportion of the total male population. It is also conceivable that genetic factors control the rate of tusk growth, so that intensive hunting for big ivory might affect the proportion of potential big tuskers remaining in the population.

In considering the African elephant in relation to its environment, it is evident that the environment is no longer a 'natural' one, in the sense that human interference has undoubtedly altered the status of the elephant within the regions which it inhabits. It is conceivable that the major factor controlling elephant numbers in former times was probably the water supply, since this would control elephant movements and the range of individual animals, and may be imagined as likely to expose large numbers of them to epidemic disease at times when they were concentrated in particular areas. No evidence was found that predators, in the ordinary sense, affect the elephant population in Africa as they are said to do in Asia, where tigers are reported to destroy a significant proportion of elephant calves.

Limitations are imposed upon a study of this kind in that the time available for work upon individual specimens is very limited, and the bulk of the observations are derived from work on dead specimens, each of which represents a point in the life cycle, so that their interpretation depends upon linking up these isolated points to reconstruct the sequence of events that makes up the reproductive cycle as a whole. Opportunities for direct observation of the habits of the elephants were very limited, and although records of captive animals provide a guide to the age at puberty (African and Indian) and to the gestation period (Indian), there are no records for captive or 'domesticated' animals which would make it possible to relate the stage of the molar tooth succession of the wild animal to actual age. Furthermore, the length of the oestrous cycle of the unmated animal is quite unknown as yet in either genus. There is some evidence in the present material that the interval between successive oestrous periods preceding fertile mating is relatively brief.

It is possible that our present information may be supplemented by more systematic observation of elephants in captivity, but it would seem that a much more fruitful source of information would lie in the extension of work of the kind here described, to comprise a larger sample of material. If more consistent and systematic observation of the elephant in the wild state than has yet been possible could be combined with such a study, it would greatly extend our knowledge of a form which occupies a unique position both in the animal kingdom and in mankind's interest in that kingdom.

This research owes its inception to Professor P. A. Buxton, F.R.S., of the London School of Hygiene and Tropical Medicine, and Captain C. R. S. Pitman, C.B.E., D.S.O., M.C., who was then Game Warden of Uganda. Professor Buxton convened an Elephant Research Committee and was assisted in organizing the expedition by Dr L. Harrison Matthews, Dr A. S. Parkes, F.R.S., Professor F. W. Rogers Brambell, F.R.S., and Captain C. R. S. Pitman. The expenses of the work in Uganda were borne by the Administration, while the writer received a Colonial Research Fellowship. The trustees of the Percy Sladen Memorial Fund provided equipment and apparatus, and a grant was made by the Royal Society. The work would not have been possible without the ready help of many people in Uganda, not only European and African members of the Game Department staff, but members of the Administration and other Departments both at Headquarters and up-country, and the good-natured co-operation of the local population in the districts where operations were carried out. I should like especially to acknowledge the hospitality extended to me by Makerere College and by Dr S. G. Wilson, then Director of the Veterinary Research Laboratory, Entebbe.

Laboratory work upon the collected material was carried out from January 1949 until June 1950 in the Department of Zoology, University of Bristol, and I am greatly indebted to Professor J. E. Harris for the hospitality of his Department. My special thanks are due to Dr L. Harrison Matthews, until lately of Bristol University and now Scientific Director of the Zoological Society of London. Dr Matthews acted in the capacity of treasurer to the Elephant Research Committee and took the closest interest in the progress of the work in Africa. It was through his good offices that I was offered laboratory facilities in the University of Bristol, and he has taken an active interest in the progress of the work throughout and has been most helpful in the preparation of this manuscript.

My thanks are also due to the authorities of the British Museum and to the Discovery Expeditions for the loan of containers and advice upon the transport of preserved material. In addition, the work has brought me into contact with many scientists and others who have assisted with various problems as they have arisen, among whom I should especially like to thank Professor E. C. Amoroso for his very active interest in the research.

APPENDIX

Sex, linear measurements and tusk weights

In table 3, the 150 elephants which were examined are listed in order of the date of death, and linear measurements and tusk weights are given when available. The measurements taken were selected as being the least likely to be affected by chance flexure of the head or limbs after death, and as representing truly linear growth of particular parts of the skeleton, and as providing a basis for comparison with other records. The localities where the specimens were obtained (areas 1 to 6) have been described (p. 95); the measurements referred to by letters are as follows:

Measurement A. The length along the surface of the skin from the crest of the occipital region of the skull (the supra-occipital) to a point at the base of the tail dorsal to the post-anal notch. The latter is well defined and is about the junction of the 7th and 8th caudal vertebrae. This is a good measurement in that it is little affected by the position of the animal except in a few cases, and it bears a close relation to the length of the vertebral column.

Measurement B. A caliper measurement from the ear orifice to the post-anal notch. This is clearly related to measurement *A*, but it was found to be rather more subject to

TABLE 3. LINEAR MEASUREMENTS

no.	date	loc.	sex	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*	*K*	*L*	*M*	*N*	*O*	*P*	tusk wt. (lb.) *Q*	*R*
1	16. i. 47	1	♂	322	267	252	229	—	125	41	122	49	—	—	—	—	—	—	—	—	—
2	16. i. 47	1	♂	317	269	247	219	—	117	41	122	49	—	—	—	—	—	—	—	—	—
3	7. ii. 47	1	♀	292	247	191	212	91	115	41	107	44	—	—	—	—	—	—	—	—	—
4	10. ii. 47	1	♀	332	272	284	244	—	127	46	122	51	—	—	—	—	—	—	—	—	—
5	10. ii. 47	1	♀	312	264	254	239	—	115	41	112	46	—	—	—	—	—	—	—	—	—
6	21. iii. 47	2	♂	317	279	284	244	—	127	46	117	51	—	112	117	100	105	35	33	—	—
7	21. iii. 47	2	♀	267	237	214	202	—	100	33	97	39	—	69	69	66	66	18	18	—	—
8	21. iii. 47	2	♀	—	—	—	—	—	—	—	—	—	—	59	59	56	56	15	15	—	—
9	30. iii. 47	2	♂	344	284	279	—	—	142	51	140	56	—	168	140	142	120	49	44	59	57
10	30. iii. 47	2	♂	334	294	254	—	—	135	51	130	54	—	—	127	—	112	—	33	—	30
11	4. iv. 47	2	♂	304	249	—	—	—	110	39	117	46	—	89	91	79	81	24	24	7½	8
12	11. iv. 47	2	♀	317	274	264	244	—	117	41	117	49	—	91	91	81	81	23	23	9	9
13	11. iv. 47	2	♂	297	249	259	232	—	117	41	117	51	—	110	110	91	91	30	30	14	14
14	11. iv. 47	2	♂	314	289	274	—	—	117	44	115	46	—	102	105	86	89	30	30	15	15
15	14. iv. 47	2	♀	319	294	224	—	—	120	41	115	46	—	91	91	84	84	24	24	11	11
16	10. v. 47	2	♀	—	—	—	—	—	—	—	—	—	—	89	95	79	84	26	26	10	11
17	10. v. 47	2	♀	297	259	—	—	—	105	—	—	—	—	95	95	84	84	21	21	6	6
18	10. v. 47	2	♀	—	—	—	—	—	—	—	—	—	—	102	102	86	86	23	23	8	9
19	15. v. 47	2	♀	309	269	244	219	—	110	35	107	42	—	95	91	79	79	26	28	11	11
20	15. v. 47	2	♀	324	297	249	252	91	117	41	112	46	—	86	89	102	105	25	26	11	12
21	24. v. 47	3	♀	259	239	214	191	—	89	30	86	33	—	61	61	56	56	16	15	4	3
22	24. v. 47	3	♀	264	242	217	217	—	95	33	91	35	—	71	69	66	64	16	15	5	3½
23	15. vii. 47	4	♂	339	302	304	—	—	140	51	135	54	—	135	130	115	110	42	42	42	41
24	28. vii. 47	4	♀	324	274	239	222	—	115	35	102	41	—	105	107	96	100	21	21	10	11
25	28. vii. 47	4	♀	279	272	229	229	—	105	35	102	41	—	89	89	79	79	21	21	10	10
26	2. viii. 47	5	♀	319	302	237	239	97	117	41	115	46	—	—	—	—	—	—	—	—	—
27	2. viii. 47	5	♀	214	178	162	155	—	76	28	79	33	—	—	—	—	—	—	—	—	—
28	2. viii. 47	4	♀	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
29	6. viii. 47	4	♂	—	—	—	—	—	—	—	—	—	—	107	112	89	97	33	33	17	18
30	9. viii. 47	4	♂	309	284	239	209	—	107	35	105	44	—	—	—	—	—	—	—	—	—
31	11. viii. 47	4	♀	322	297	267	—	—	120	42	115	46	—	97	95	81	75	25	25	13	11
32	11. viii. 47	4	♂	344	292	272	—	—	120	44	115	49	—	127	120	110	107	33	33	22	21
33	14. viii. 47	4	♂	334	292	284	—	97	130	44	125	49	—	—	—	—	—	—	—	—	—
34	17. viii. 47	5	♂	363	322	309	—	110	145	52	132	56	—	171	171	142	140	47	47	67	66
35	18. viii. 47	5	♂	259	—	204	214	—	112	41	110	46	—	110	115	89	94	31	31	18	18
36	9. ix. 47	5	♀	289	267	252	—	97	110	39	105	44	—	91	97	79	84	26	28	11½	14
37	9. ix. 47	5	♀	302	277	257	—	97	117	41	115	49	—	102	100	86	86	25	25	14	13
38	9. ix. 47	5	♀	329	292	259	—	—	120	41	115	46	—	95	97	84	86	23	24	11	12
39	21. ix. 47	5	♀	289	259	254	—	91	108	39	103	43	—	91	89	84	83	24	23	12	10
40	24. ix. 47	5	♂	353	299	302	—	105	132	46	127	54	—	130	130	115	115	35	34	27	26
41	24. ix. 47	5	♀	353	292	244	—	95	112	39	107	44	—	110	102	97	89	26	26	17	16
42	24. ix. 47	5	♂	400	332	319	—	117	142	50	135	55	—	166	166	142	140	45	44	55	53
43	26. ix. 47	5	♀	339	302	274	—	100	122	45	117	47	—	117	115	97	97	24	25	15	15
44	28. ix. 47	5	♀	324	274	254	—	95	117	40	115	45	—	—	—	—	—	—	—	—	—
45	28. ix. 47	5	♀	259	237	214	—	86	100	35	96	36	—	—	—	—	—	—	—	—	—
46	28. ix. 47	5	♀	314	287	274	—	100	125	44	115	46	—	—	—	—	—	—	—	—	—
47	10. x. 47	4	♂	327	274	262	—	97	120	42	115	46	—	107	108	94	94	34	33	18	18
48	10. x. 47	4	♀	282	247	229	—	84	100	33	97	41	—	82	76	71	69	22	22	7	6½
49	27. x. 47	4	♀	309	252	244	—	86	105	35	100	41	—	115	117	100	100	25	25	15	15
50	4. xi. 47	4	♂	365	312	284	—	—	122	44	117	49	—	147	150	127	132	39	39	35	36

51	22. xi. 47	4	♀	299	279	264	—	—	112	41	110	49	—	101	95	80	84	24	25	12	12
52	22. xi. 47	4	♀	307	274	254	—	—	112	40	110	45	—	97	91	89	84	23	23	10	10
53	23. xi. 47	4	♀	314	279	257	—	91	110	39	107	44	—	—	—	—	—	—	—	—	—
54	23. xi. 47	4	♀	188	176	160	—	—	67	23	67	26	—	—	—	—	—	—	—	—	—
55	23. xi. 47	4	♂	252	209	222	—	79	96	33	95	39	—	—	—	—	—	—	—	—	—
56	24. xi. 47	4	♀	307	282	252	—	97	107	36	105	44	—	—	—	—	—	—	—	—	—
57	24. xi. 47	4	♀	368	329	274	—	102	127	45	122	49	—	—	—	—	—	—	—	—	—
58	6. xii. 47	5	♂	319	277	269	—	98	115	42	112	48	59	—	—	—	—	—	—	—	—
59	8. xii. 47	4	♀	304	267	249	—	100	106	40	103	42	51	—	—	—	—	—	—	—	—
60	10. xii. 47	4	♀	307	269	244	—	97	105	33	102	41	51	—	—	—	—	—	—	—	—
61	24. iii. 48	6	♀	304	269	257	—	—	112	40	110	46	—	—	—	—	—	—	—	—	—
62	24. iii. 48	6	♂	284	244	239	—	89	107	37	102	41	49	86	85	79	75	23	23	9	9
63	25. iii. 48	6	♀	317	244	234	—	—	105	35	105	44	54	—	—	—	—	—	—	—	—
64	25. iii. 48	6	♀	277	262	237	—	—	115	40	107	45	—	—	—	—	—	—	—	—	—
65	25. iii. 48	6	♂	317	264	274	—	—	127	45	119	49	—	150	161	130	135	39	39	32	33
66	25. iii. 48	6	♂	327	282	294	—	—	132	45	122	50	—	127	130	107	112	33	34	24	25
67	25. iii. 48	6	♂	319	272	277	—	—	117	41	112	46	—	98	—	84	—	29	—	16	—
68	25. iii. 48	6	♂	360	317	312	—	—	135	49	130	54	—	140	157	118	132	41	39	35	36
69	25. iii. 48	6	♂	322	274	282	—	—	127	45	117	49	—	—	—	—	—	—	—	—	—
70	28. iii. 48	6	♀	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
71	28. iii. 48	6	♂	304	282	267	—	—	125	46	122	51	—	137	134	122	122	33	33	24	23
72	28. iii. 48	6	♂	322	274	274	—	—	125	45	120	51	55	108	117	95	102	31	31	20	21
73	28. iii. 48	6	♀	279	247	232	—	84	106	37	100	41	52	87	88	79	81	19	20	8	8
74	7. iv. 48	6	♂	287	244	242	—	81	110	40	107	44	52	111	102	102	91	26	28	15	14
75	7. iv. 48	6	♀	294	254	244	—	86	105	39	102	41	51	86	66	76	56	20	20	7	5
76	7. iv. 48	6	♂	214	181	168	—	61	79	28	76	31	39	54	54	49	49	18	18	3	3
77	7. iv. 48	6	♀	294	252	232	212	86	107	37	102	42	51	115	—	105	—	23	—	12	—
78	7. iv. 48	6	♀	319	264	249	227	87	112	39	107	45	54	110	107	97	97	25	25	13	13
79	7. v. 48	6	♂	267	239	234	209	86	107	37	105	44	47	91	99	81	86	23	23	7	8
80	7. v. 48	6	♂	304	252	257	219	91	117	43	110	45	55	132	120	120	107	33	31	21	21
81	7. v. 48	6	♂	259	214	219	198	76	100	35	95	41	46	110	91	94	79	25	25	12	9
82	11. v. 48	6	♀	317	287	264	—	86	122	43	116	47	54	117	117	100	102	28	28	18	20
83	11. v. 48	6	♀	254	227	202	—	76	91	33	93	39	46	61	64	54	56	16	15	3	3
84	11. v. 48	6	♀	319	274	—	—	87	—	—	—	—	52	97	95	86	81	22	22	8	9
85	11. v. 48	6	♀	317	284	254	—	86	117	41	115	46	54	120	112	105	95	28	25	20	16
86	11. v. 48	6	♂	299	247	—	—	—	—	—	—	—	49	99	99	91	86	25	25	12	12
87	11. vi. 48	6	♀	322	272	267	—	100	120	44	—	—	57	107	109	95	95	26	25	15	15
88	11. vi. 48	4	♂	327	284	269	—	100	122	43	115	46	56	99	99	84	86	33	33	16	16
89	16. vi. 48	4	♂	294	259	239	—	87	106	35	105	42	50	87	87	79	79	25	25	10	9
90	16. vi. 48	4	♀	297	264	254	—	97	108	39	107	44	52	—	—	—	—	—	—	—	—
91	16. vi. 48	4	♂	324	319	—	—	—	—	—	—	—	—	101	107	91	95	23	23	13	12
92	30. vi. 48	5	♂	307	274	262	—	95	117	41	115	46	54	105	99	95	95	29	29	17	16
93	10. vii. 48	5	♂	322	284	267	—	97	122	44	115	46	55	—	86	—	76	—	29	—	13
94	10. vii. 48	5	♀	314	279	262	—	100	112	39	107	44	54	83	86	71	76	23	24	10	10
95	15. vii. 48	4	♀	312	282	257	—	97	110	39	107	44	51	83	87	79	81	21	21	9	8
96	23. vii. 48	4	♂	327	292	274	249	105	135	47	130	51	57	—	—	—	—	—	—	—	—
97	26. vii. 48	4	♂	327	272	282	237	96	120	41	115	49	54	116	114	101	100	31	31	18	18
98	6. viii. 48	4	♂	339	287	259	—	—	122	42	115	48	56	123	124	107	110	39	38	30	30
99	6. viii. 48	4	♂	332	282	274	244	97	125	42	117	46	60	132	134	115	117	35	35	27	28
100	6. viii. 48	4	♂	319	284	264	244	97	124	41	117	47	54	124	121	110	107	35	35	26	26
101	6. viii. 48	4	♂	324	294	267	254	95	120	41	116	46	55	106	109	89	94	30	30	16	16
102	6. viii. 48	4	♂	347	312	289	262	101	125	45	117	49	59	124	124	105	102	35	35	27	28
103	9. viii. 48	4	♂	344	297	292	249	—	131	44	122	50	—	166	168	150	142	40	42	46	44
104	9. viii. 48	5	♂	304	287	—	—	—	137	46	131	49	—	137	137	118	125	41	40	35	33
105	9. viii. 48	5	♂	347	307	294	—	—	131	45	127	50	—	141	146	122	125	41	39	34	34
106	15. ix. 48	5	♂	383	329	319	—	115	145	49	133	56	61	—	—	—	—	—	—	—	—
107	20. ix. 48	5	♂	299	269	244	—	86	110	39	105	44	51	—	—	—	—	—	—	—	—
108	20. ix. 48	5	♂	297	267	242	—	86	112	39	107	44	53	—	—	—	—	—	—	—	—
109	20. ix. 48	5	♂	337	304	294	—	—	132	45	127	49	61	—	—	—	—	—	—	—	—
110	5. x. 48	4	♂	304	259	247	222	—	112	39	107	44	51	99	102	84	89	26	26	12	12

TABLE 3 (*cont.*)

																			tusk wt. (lb.)	
no.	date	loc.	sex	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*	*K*	*L*	*M*	*N*	*O*	*P*	*Q*	*R*
111	5. x. 48	4	♂	355	307	292	—	—	140	49	132	54	60	142	157	120	132	40	41	32	36
112	5. x. 48	4	♂	319	274	244	234	—	115	39	111	46	51	99	107	86	91	26	26	14	14
113	16. x. 48	5	♂	342	304	309	—	—	142	51	130	54	—	—	—	—	—	—	—	—	—
114	16. x. 48	5	♂	360	307	302	—	—	145	51	135	54	—	—	—	—	—	—	—	—	—
115	18. i. 50	4	♀	299	262	232	—	—	102	35	102	44	47	—	—	—	—	—	—	—	—
116	25. i. 50	4	♀	319	244	254	229	—	107	39	105	44	—	—	—	—	—	—	—	—	—
117	25. i. 50	4	♀	342	294	267	—	—	119	41	115	47	—	—	—	—	—	—	—	—	—
118	1. ii. 50	4	♀	294	262	242	214	89	—	—	—	—	—	—	—	—	—	—	—	—	—
119	1. ii. 50	4	♀	130	112	110	74	—	51	19	52	21	—	—	—	—	—	—	—	—	—
120	4. ii. 50	4	♂	353	304	294	—	—	135	46	128	51	—	—	—	—	—	—	—	—	—
121	6. ii. 50	4	♀	287	267	214	—	—	100	33	97	39	46	—	—	—	—	—	—	—	—
122	6. ii. 50	4	♀	324	287	—	—	—	—	—	102	40	51	—	—	—	—	—	—	—	—
123	7. ii. 50	4	♀	314	274	257	—	—	110	39	110	45	—	—	—	—	—	—	—	—	—
124	11. ii. 50	4	♂	297	237	239	—	—	117	40	115	46	—	—	—	—	—	—	—	—	—
125	11. ii. 50	4	♀	342	284	282	—	—	125	46	121	49	—	—	—	—	—	—	—	—	—
126	11. ii. 50	4	♂	277	232	232	—	—	106	39	102	42	—	—	—	—	—	—	—	—	—
127	16. ii. 50	4	♂	299	264	264	—	—	117	42	112	46	—	—	—	—	—	—	—	—	—
128	17. ii. 50	4	♂	279	239	227	202	—	105	35	102	41	—	—	—	—	—	—	—	—	—
129	17. ii. 50	4	♂	284	244	242	204	—	102	35	100	41	—	—	—	—	—	—	—	—	—
130	18. ii. 50	4	♀	289	262	247	217	97	109	39	103	42	—	—	—	—	—	—	—	—	—
131	18. ii. 50	4	♀	198	181	173	142	64	76	30	—	—	—	—	—	—	—	—	—	—	—
132	18. ii. 50	4	♀	269	257	232	217	95	105	36	100	40	—	—	—	—	—	—	—	—	—
133	18. ii. 50	4	♀	317	289	267	—	97	120	40	115	46	—	—	—	—	—	—	—	—	—
134	18. ii. 50	4	♀	105	86	97	—	29	46	16	47	18	—	—	—	—	—	—	—	—	—
135	22. ii. 50	4	♀	327	289	262	217	—	117	40	112	49	—	—	—	—	—	—	—	—	—
136	23. ii. 50	4	♂	334	294	304	234	—	132	49	125	52	—	—	—	—	—	—	—	—	—
137	23. ii. 50	4	♂	360	312	309	342	—	133	49	130	54	—	—	—	—	—	—	—	—	—
138	24. ii. 50	4	♀	307	284	249	—	—	109	36	106	44	—	—	—	—	—	—	—	—	—
139	24. ii. 50	4	♂	302	257	257	—	—	117	41	112	46	—	—	—	—	—	—	—	—	—
140	24. ii. 50	4	♀	—	249	229	—	89	98	33	98	39	—	—	—	—	—	—	—	—	—
141	6. iii. 50	4	♀	302	274	267	234	—	120	40	116	45	—	—	—	—	—	—	—	—	—
142	6. iii. 50	4	♀	314	284	269	—	—	120	42	113	46	—	—	—	—	—	—	—	—	—
143	7. iii. 50	4	♀	332	287	264	—	—	120	41	113	46	—	—	—	—	—	—	—	—	—
144	7. iii. 50	4	♀	242	212	207	—	—	91	30	89	35	—	—	—	—	—	—	—	—	—
145	8. iii. 50	4	♀	319	279	259	232	—	111	39	107	44	—	—	—	—	—	—	—	—	—
146	8. iii. 50	4	♀	360	312	—	—	—	—	—	118	47	—	—	—	—	—	—	—	—	—
147	8. iii. 50	4	♀	274	227	224	—	—	99	35	96	40	—	—	—	—	—	—	—	—	—
148	8. iii. 50	4	♀	317	292	252	—	—	116	41	110	46	—	—	—	—	—	—	—	—	—
149	8. iii. 50	4	♀	254	222	214	—	—	91	30	91	37	—	—	—	—	—	—	—	—	—
150	8. iii. 50	4	♀	234	188	178	—	—	81	29	79	33	—	—	—	—	—	—	—	—	—

alteration with the position of the animal. Both are very much less valuable in the case of animals lying in a 'couchant' position.

Measurement C. Along the skin from the crest of the scapula to the sole of the foot. This measurement is closely related to the length of the forelimb and has the advantage that the crest of the scapula is easily located before dissection. It has been found with living elephants that this measurement is greater than the true height at the withers when standing, but less than the caliper measurement of the 'height at the withers' of a recumbent animal, as sometimes recorded by hunters. Thus the elephant 'Dicksie' at the London Zoo was about 220 cm at the withers in a standing position in May 1949. From the top of the scapula to the sole of the forefoot, recumbent, was about 226 cm, while the caliper measurement of the 'height at the withers' in this position was nearly 230 cm. It was found that the measurement along the skin was not greatly affected by the position of the animal, while the caliper measurement of the 'height at the withers' varied considerably with the animal's position.

Measurement D. The girth, or, in most cases, the distance from the ridge of the backbone to the mid-ventral line, was measured, but in most cases it was found that distension of the belly by the rapid accumulation of gases after death destroyed the value of this measurement. This does not apply to foetuses, or when it was possible to make the measurement soon after death, and only such cases are given in table 1.

Measurement E. Width of the pelvic girdle, across the anterior extremities of the iliac processes.

Measurements F to I. Foot measurements: *F*, around the edge of the base of the forefoot; *G*, antero-posterior length of the forefoot; *H* and *I*, similar measurements for the hindfoot.

Measurement J. Width across skull, from the posterior and ventral corners of the zygomatic arch (the jugal bone). Caliper measurement.

Measurements K to R. Tusk measurements and weights, after extraction: *K*, length of right tusk, along convex ventral curvature; *L*, length of left tusk, along convex ventral curvature; *M*, length of right tusk, along concave dorsal curvature; *N*, length of left tusk, along concave dorsal curvature; *O*, girth of right tusk at level of gum; *P*, girth of left tusk at level of gum; *Q*, weight of right tusk in lb.; *R*, weight of left tusk in lb.

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DESCRIPTION OF PLATES 5 TO 8

PLATE 5

FIGURE 9. The ovaries of a very young calf (E134): (*a*) the left ovary, with ovarial sac in place, (*b*) the right ovary, with ovarial sac pulled away. This shows how the ovarian ligament appears to be continuous with the uterine horn. The Fallopian tube cannot be distinguished externally. The ovary was withdrawn from the inner compartment *ic*; *oc* is fimbriated outer compartment, *ut* is the tip of the uterine horn, and *al* the anterior ligament.

FIGURE 10. The ovary of the foetus of E 84, bisected in the axis of the hilum, and showing the cut surface. Light-coloured blocks of hypertrophied interstitial tissue can be seen throughout the cortex.

FIGURE 11. The testis of the foetus of E 61, bisected in the axis of the hilum, for comparison with the foetal ovary shown in figure 10. (Slightly reduced.)

FIGURE 12. Section through the ovary of a very young calf (E 134, cf. figure 9). (Magn. × $2\frac{1}{2}$.) The interstitial tissue is regressing.

FIGURE 13. The cut surface of the ovary of an animal approaching puberty (E 45) bisected. Follicles up to 5 mm in diameter can be seen in the peripheral region.

FIGURE 14. The cut surface of the ovary of a pregnant animal nearing term (E 26) bisected in the axis of the hilum. Three corpora lutea, which were histologically indistinguishable, (*acl*) and two very old corpora lutea (*ocl*) are seen.

FIGURE 15. The ovaries of a lactating animal (E 77) bisected in the axis of the hilum (upper figure) and at right angles to it (lower figure). Follicles over 5 mm in diameter, and the remains of very old corpora lutea, are seen in the peripheral zone.

PLATE 6

FIGURE 16. The ovaries of an animal in mid-pregnancy (E 138): (*a*) medial aspect of right ovary; (*b*) left, cut surface of left ovary; right, lateral aspect of right ovary. Several rupture points are clearly seen. All the corpora lutea shown in the photographs were histologically indistinguishable.

FIGURE 17. The ovaries of three animals which are regarded as undergoing infertile oestrous cycles. Their condition is shown diagrammatically in figure 7, and is described in the text.

FIGURE 18. Typical specimens of the elephant ovary during pregnancy. Some of the largest corpora lutea which were encountered are shown in (*c* and *d*) E 147 and E 60. Others, histologically indistinguishable from these, were as small as 2 to 3 mm in diameter.

PLATE 7

FIGURE 19. Portion of the periphery of a foetal testis (late pregnancy). (Magn. × 4·8.) The section was 12μ in thickness. Many spermatic tubules can be seen, imbedded in blocks of hypertrophied interstitial tissue in a framework of connective tissue. Cf. figure 11.

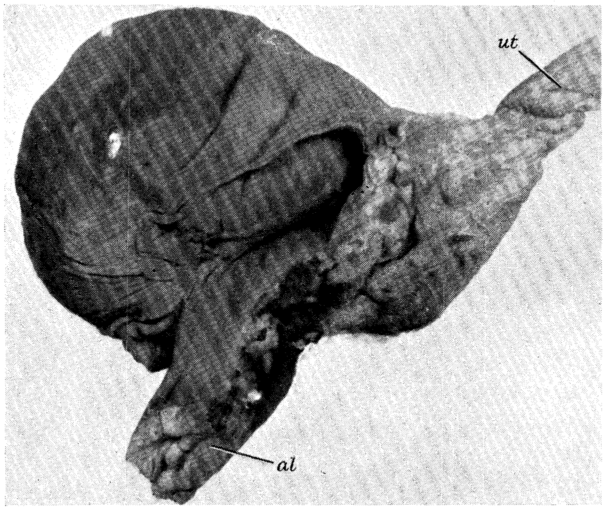
FIGURE 20. Portion of the periphery of a foetal ovary (E 84). (Magn. *a*, × 22·5; *b*, × 280.) One of the larger follicles is shown in (*a*). It was polyovular and contained four oocytes, three of which can be seen in the photograph. (*b*) shows the vacuolated condition of the cytoplasm of the interstitial cells. These cells are probably past their maximum development and beginning to regress.

FIGURE 21. Portion of the periphery of the ovary shown in figure 12, at higher magnification. (Magn. × 9.)

FIGURE 22. Part of a section through the ovary of E 119, which was a little older than E 134, the ovaries of which are shown in figures 12 and 21. (Magn. × 250.) The section shows stages in the de-differentiation of hypertrophied interstitial cells. Some are still large, with many vacuoles in the cytoplasm, while in others the vacuoles have disappeared and the cells are merging into the general stromal tissue of the ovary.

FIGURE 23. L.P. photomicrographs, at the same magnification, of portions of one (*a*) of the active corpora lutea of E 138, near mid-pregnancy, and (*b*), the corpus luteum *C* of E 130, a lactating animal interpreted as passing through a series of oestrous cycles prior to fertile mating and pregnancy.

FIGURE 24. Photomicrographs, at a higher magnification, of the corpora lutea shown in figure 23, (*a*) and (*b*).



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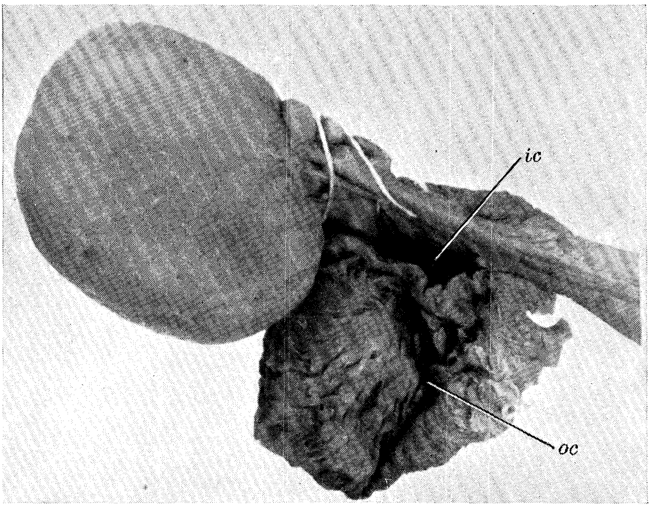
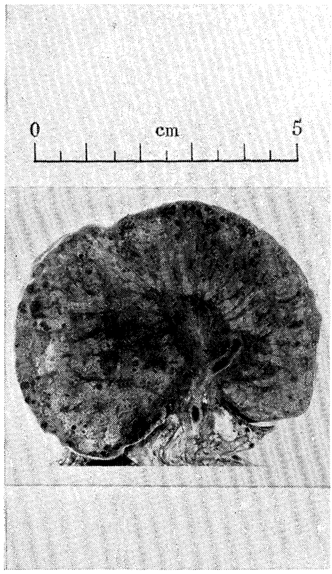


9*b*



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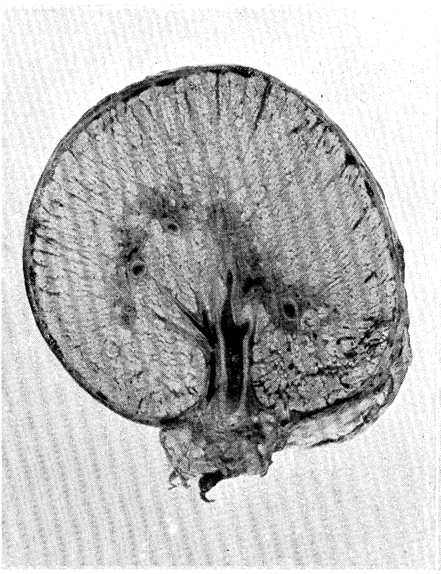

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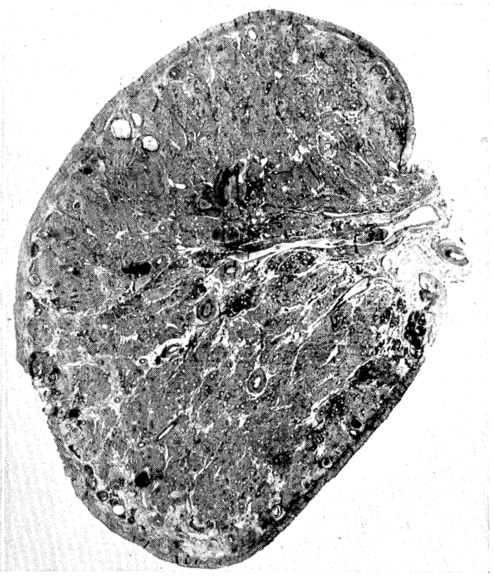

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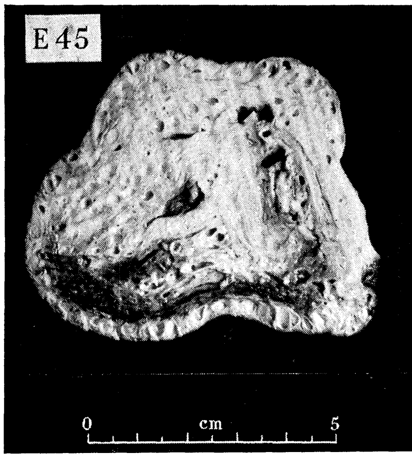

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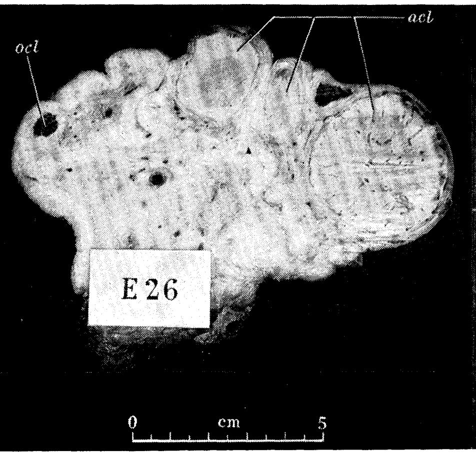

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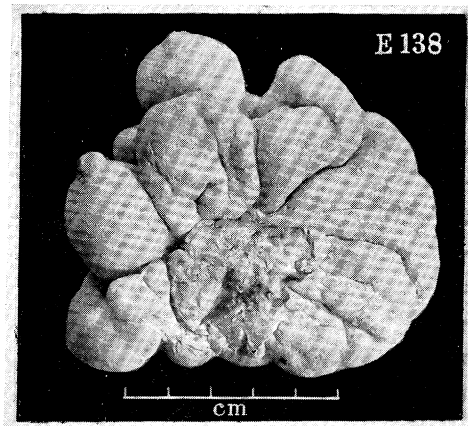
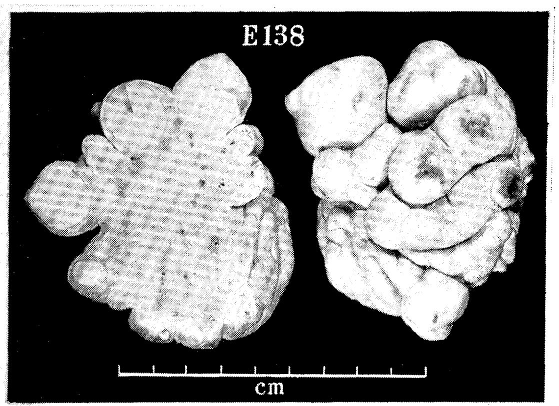
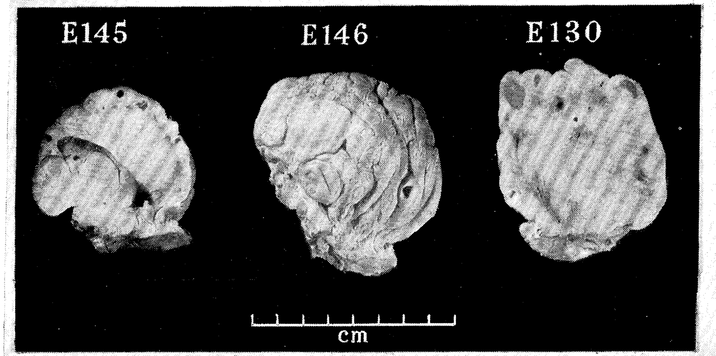


16*a*



16*b*



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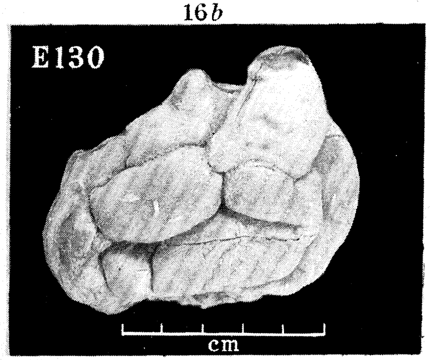

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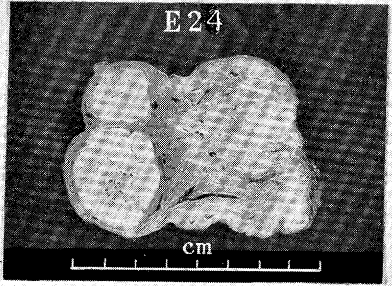

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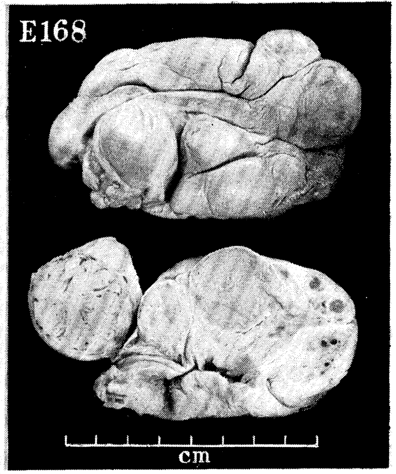

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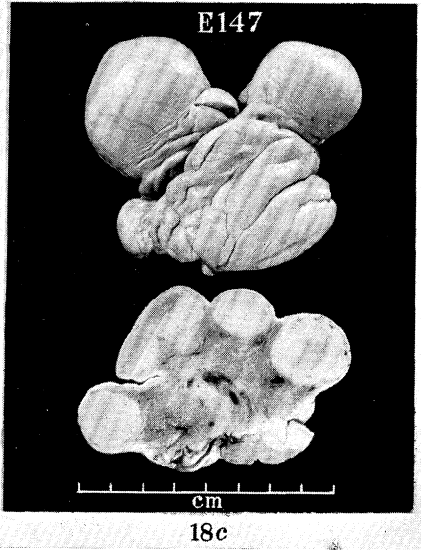
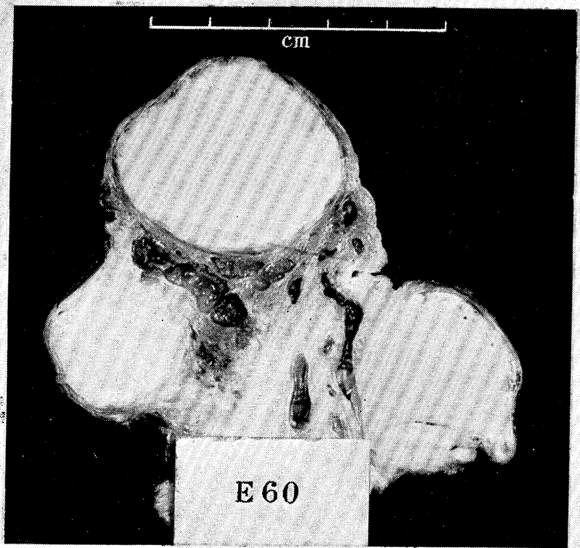
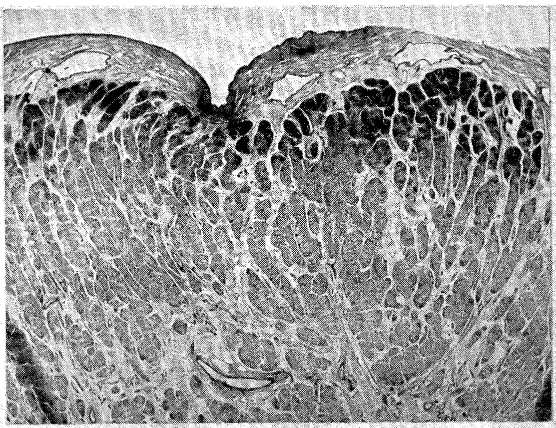


18*c*



18*d*



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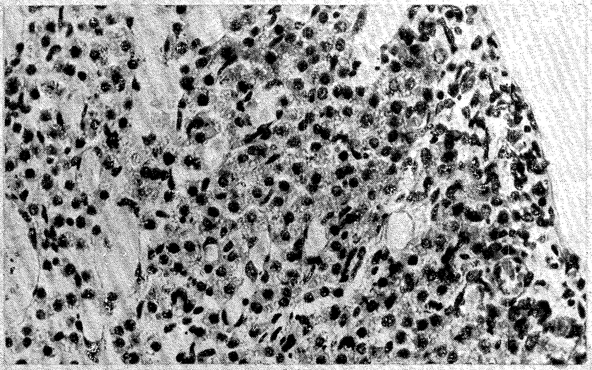
20*a*



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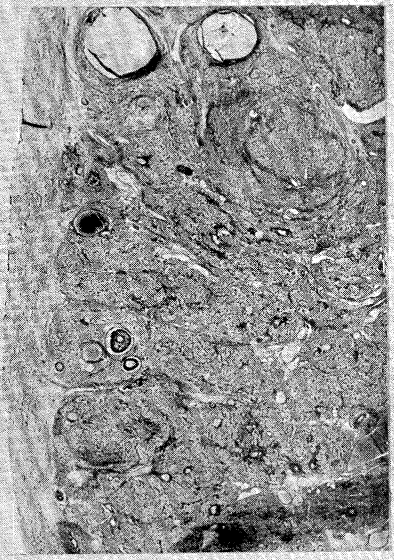

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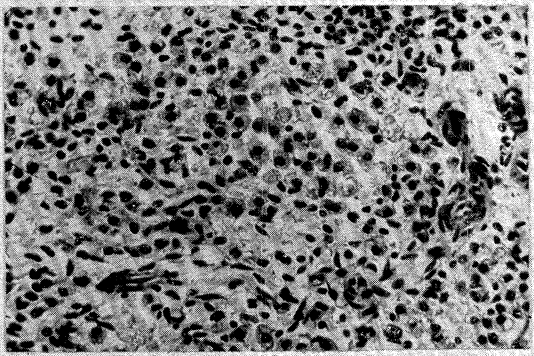

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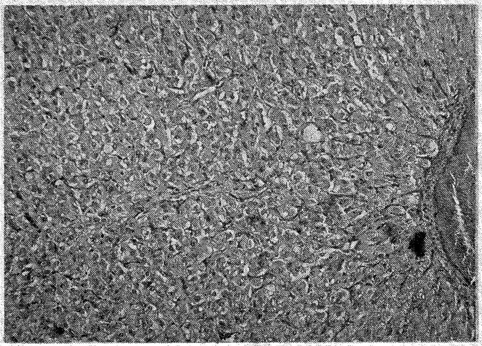

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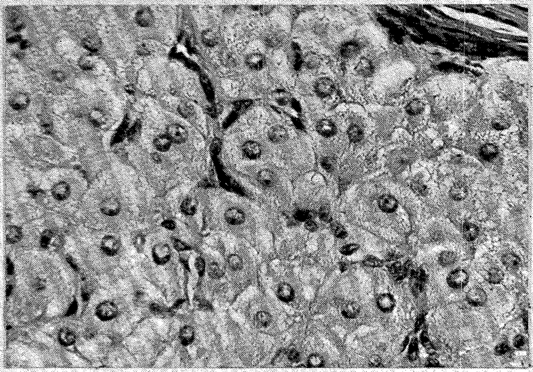

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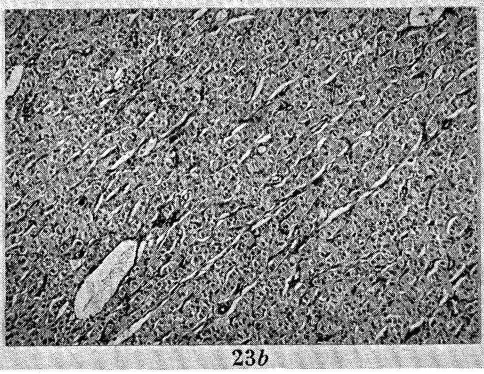

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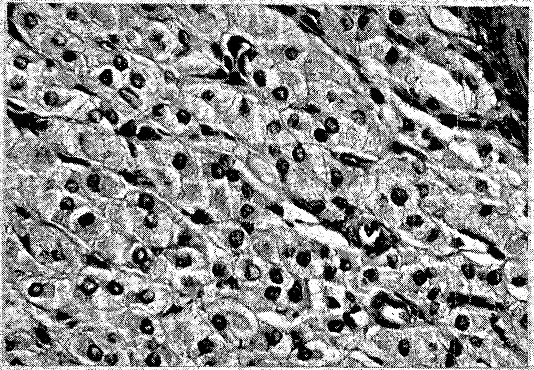

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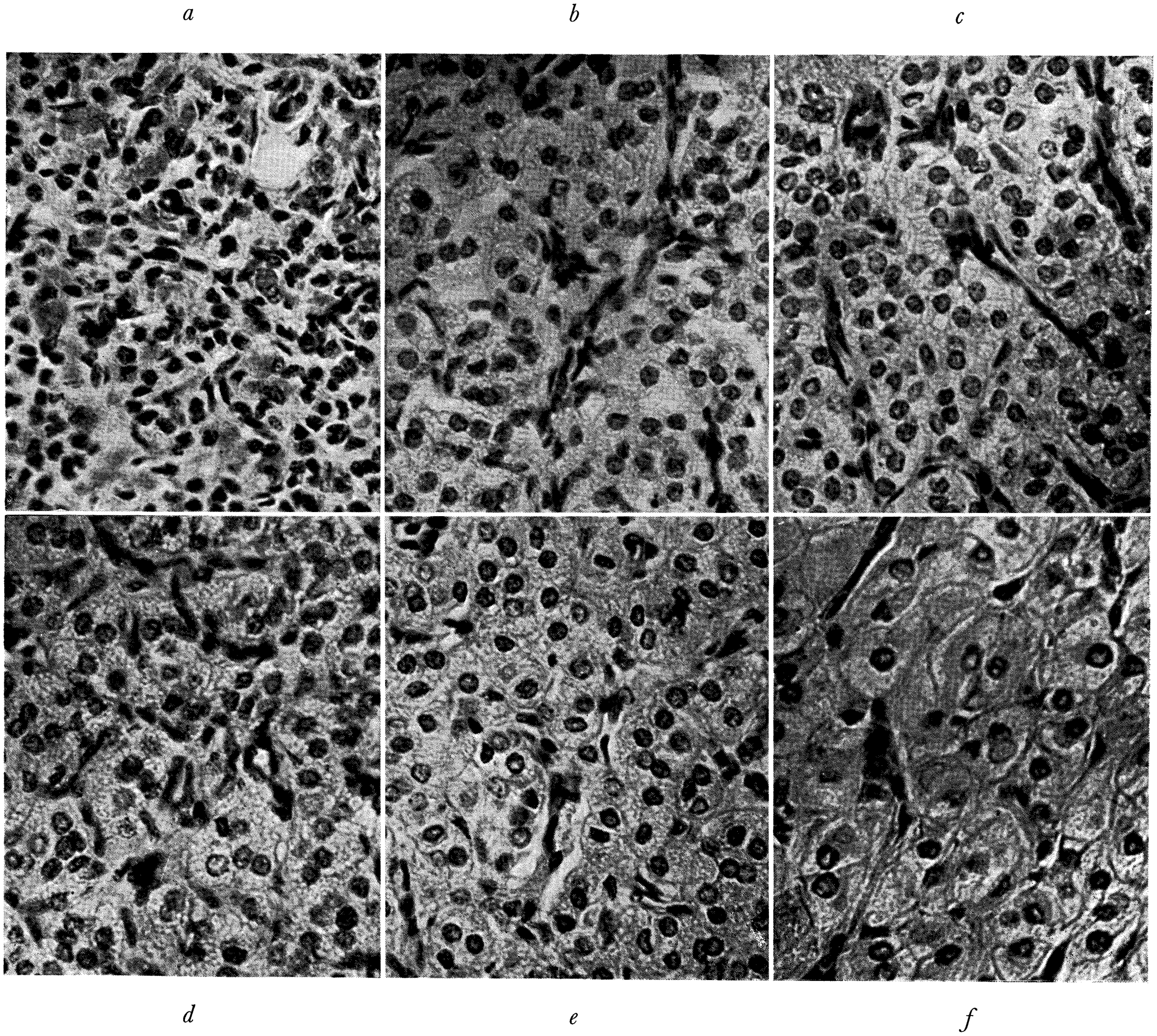

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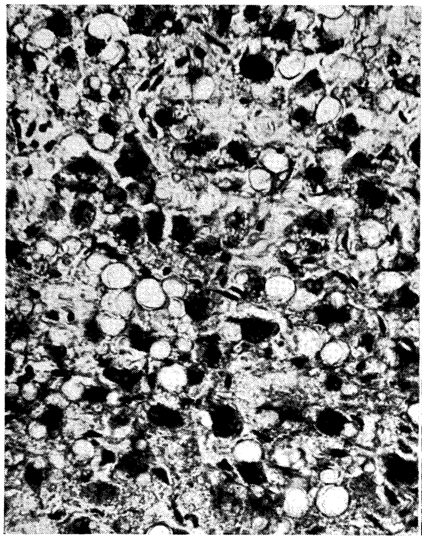

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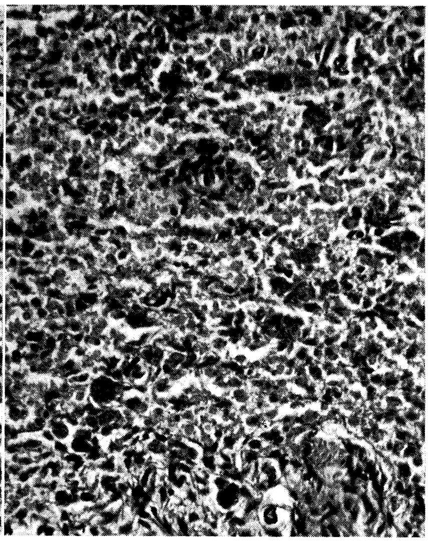

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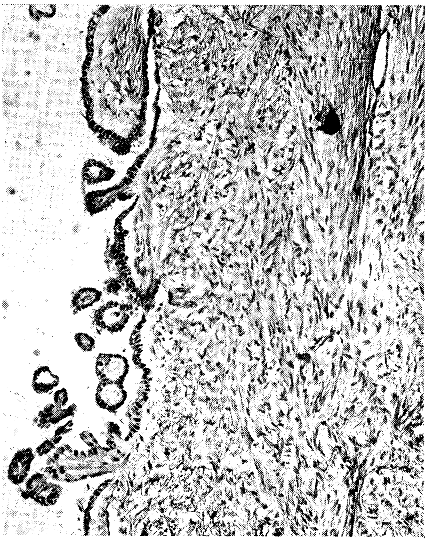

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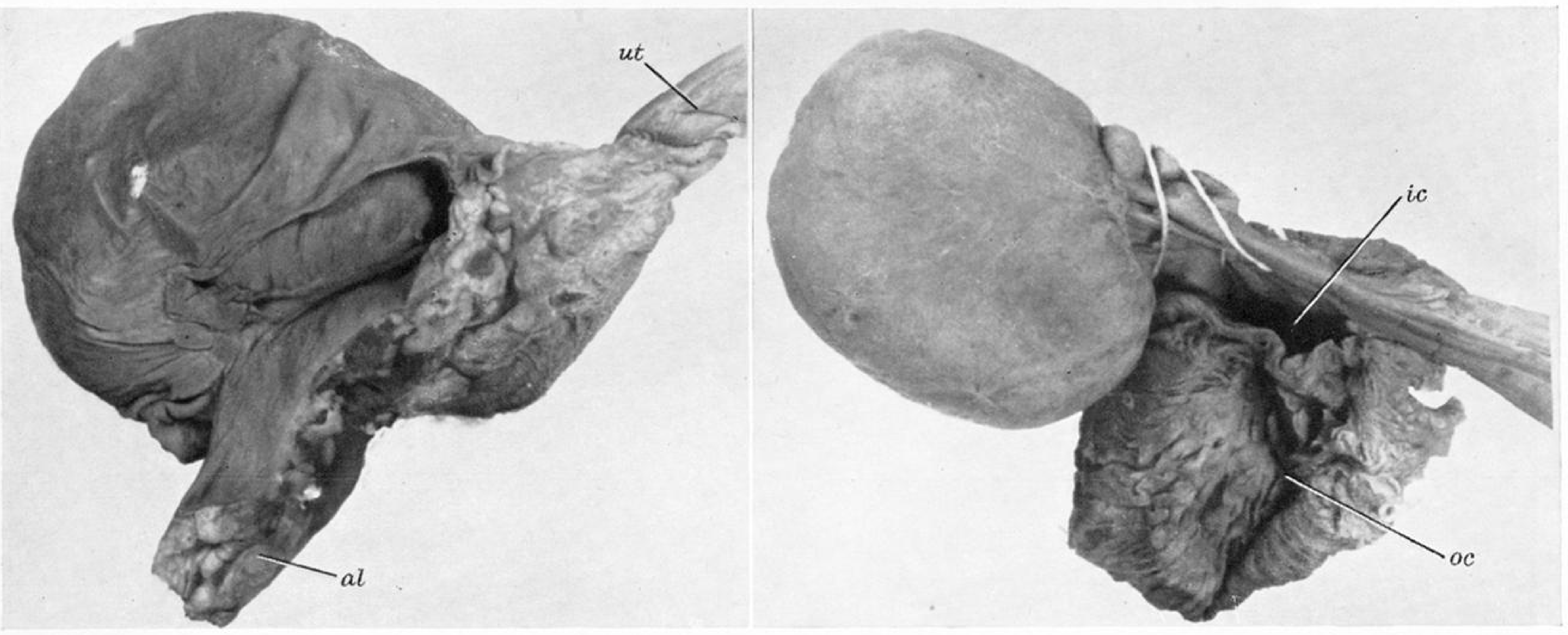
PLATE 8

FIGURE 25. Photomicrographs, at the same magnification and with the photographic conditions as similar as possible, of portions of the six corpora lutea of E 130. The sections, 10μ thick, were mounted on a single slide to ensure similar staining. The corpus luteum *C* at (*a*) is markedly newer than the others, and *A* at (*f*) is markedly older, while the remaining four are intermediate in condition and indistinguishable from each other.

FIGURE 26. Portion of a corpus luteum of E 3, about 6 months post-coitum. The luteal tissue is in an advanced state of fatty degeneration. The fat vacuoles show as empty spaces in this photograph of a section cleared in toluene.

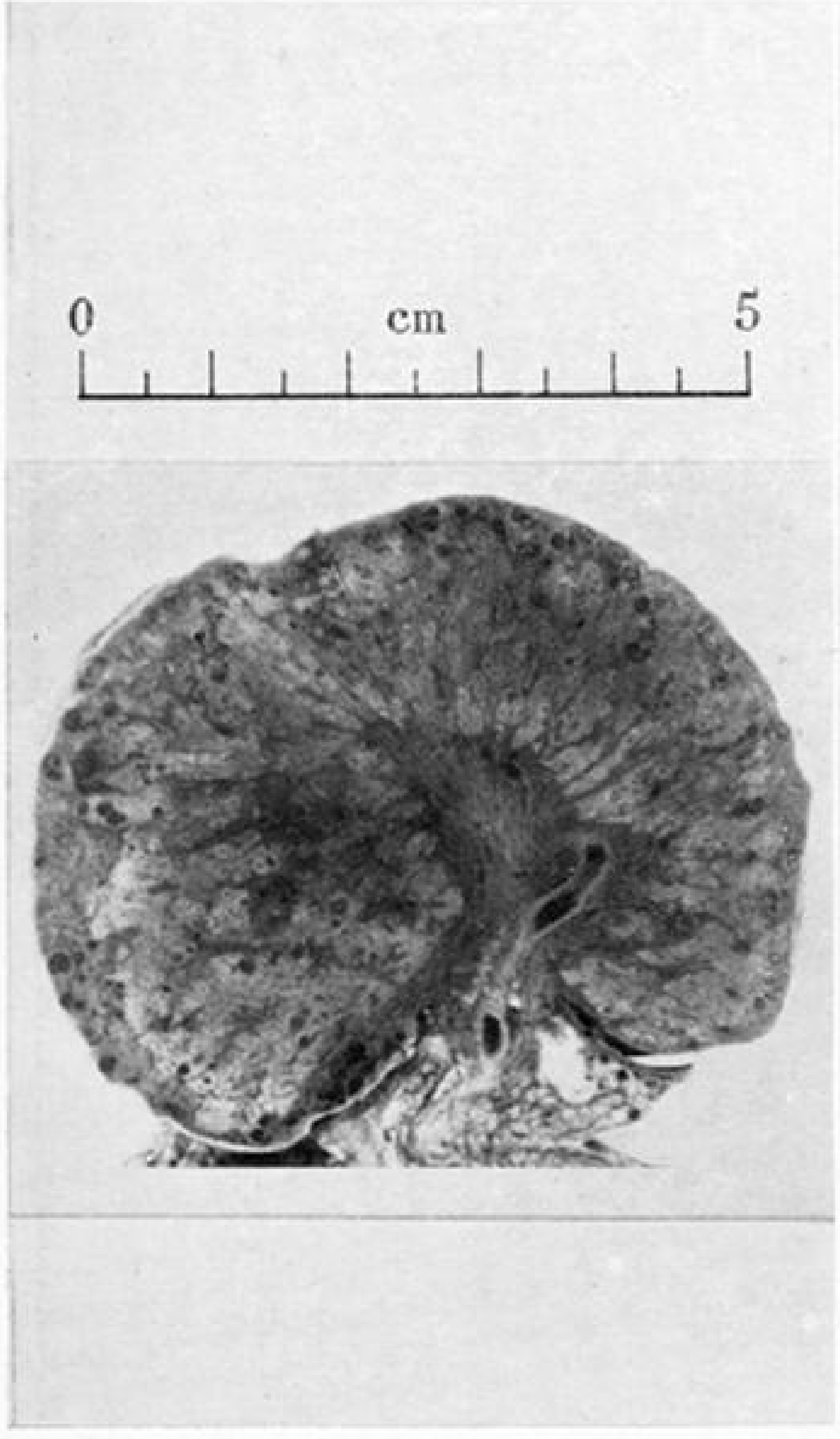
FIGURE 27. The site of an old corpus luteum. Although plainly visible as a dark brown patch in the cut surface of the ovary when examined macroscopically (cf. figures 14, 15), it is almost indistinguishable from the surrounding stroma in a stained section.

FIGURE 28. Portion of the periphery of the ovary of E 138, near mid-pregnancy, to show subsurface crypts and papillose projections which increase the area of the germinal epithelium.



9*a*

9*b*



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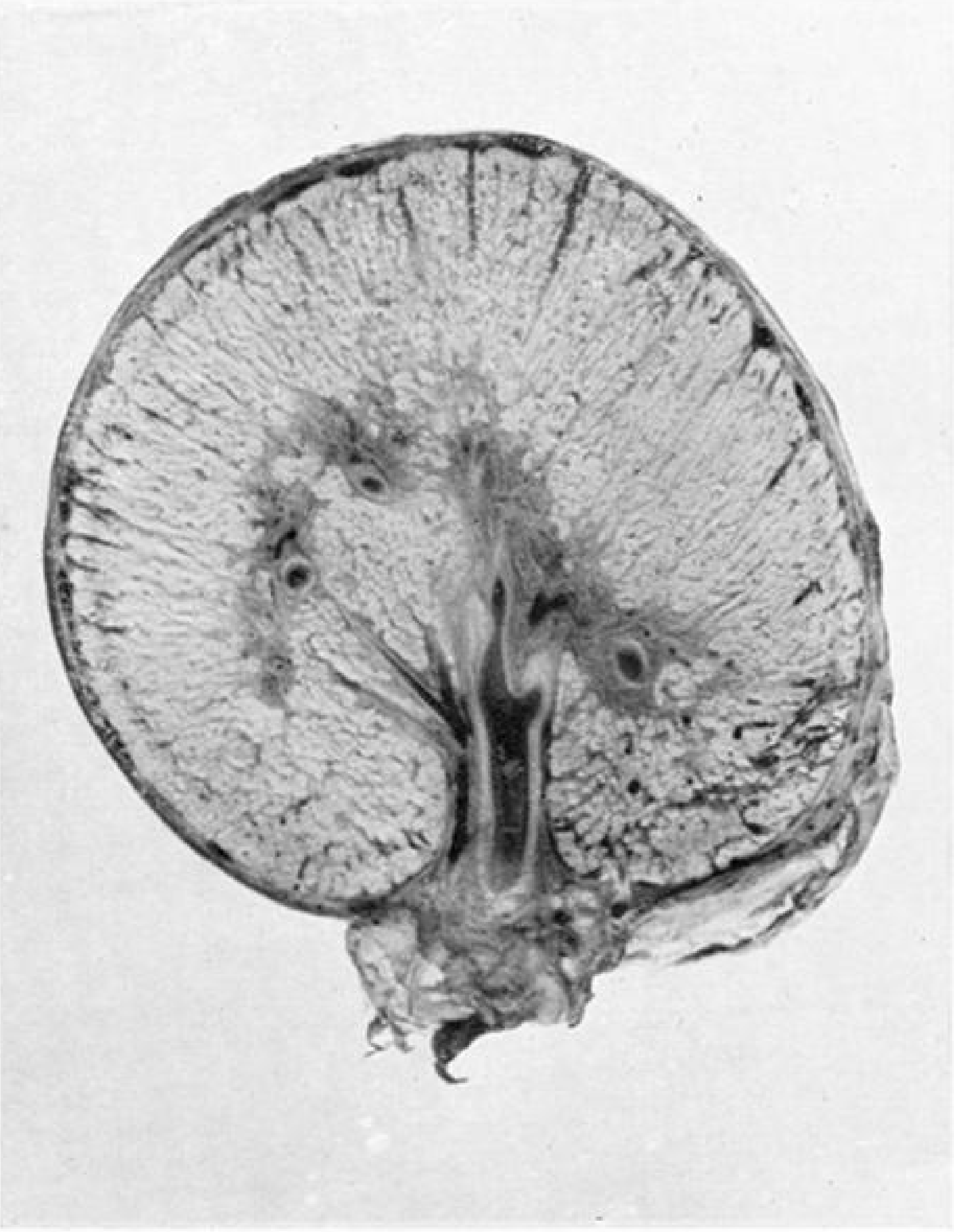

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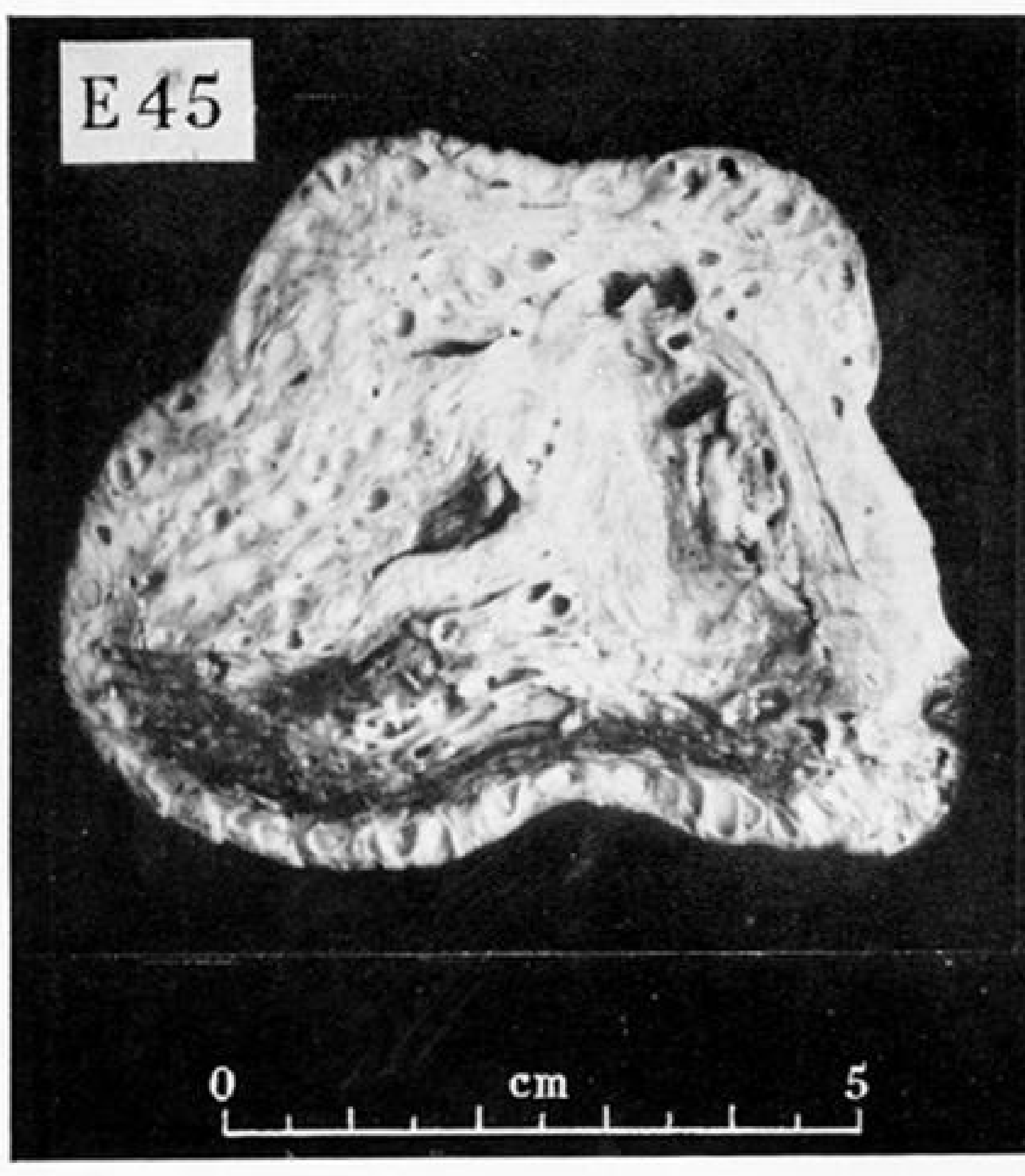

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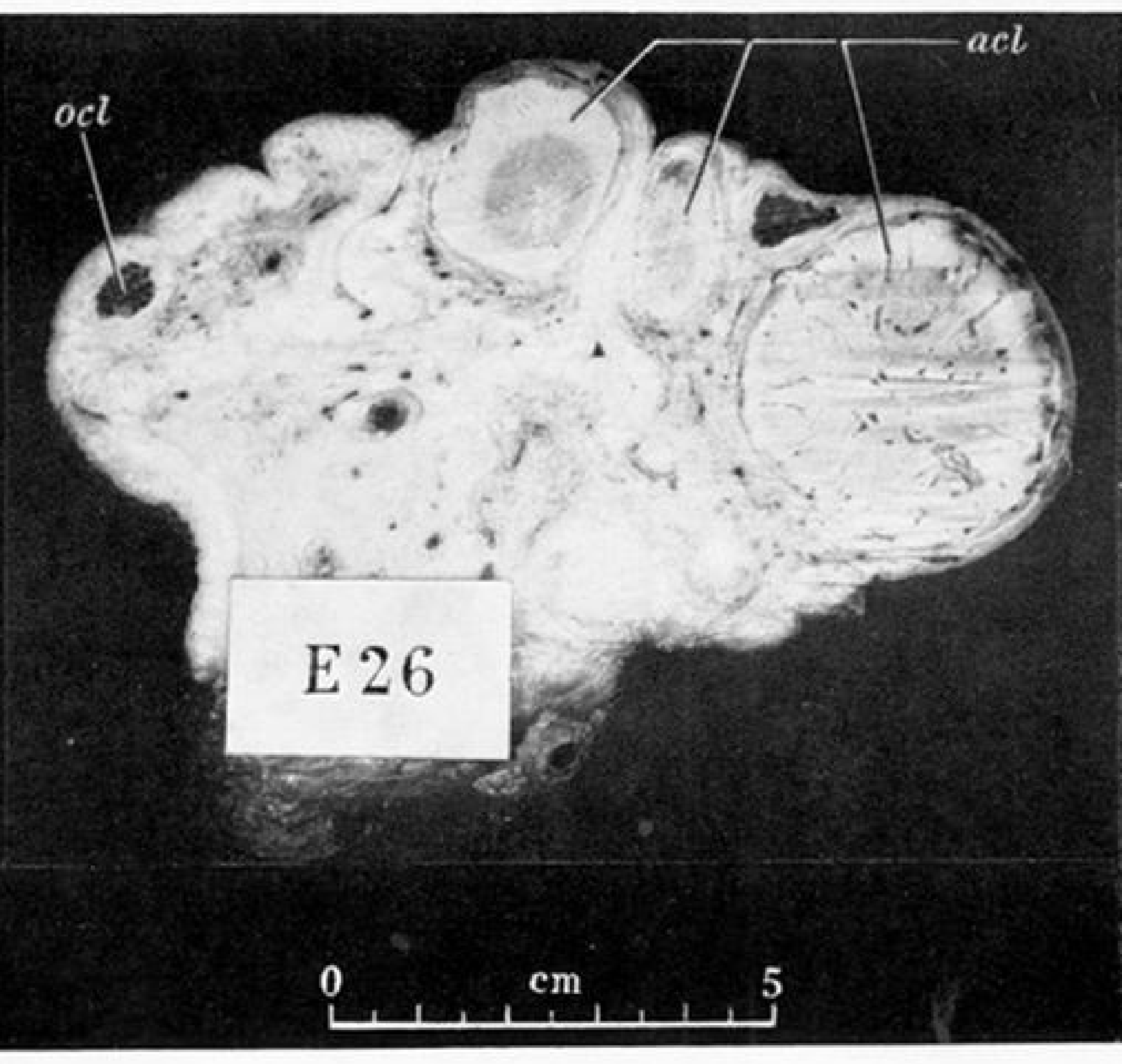

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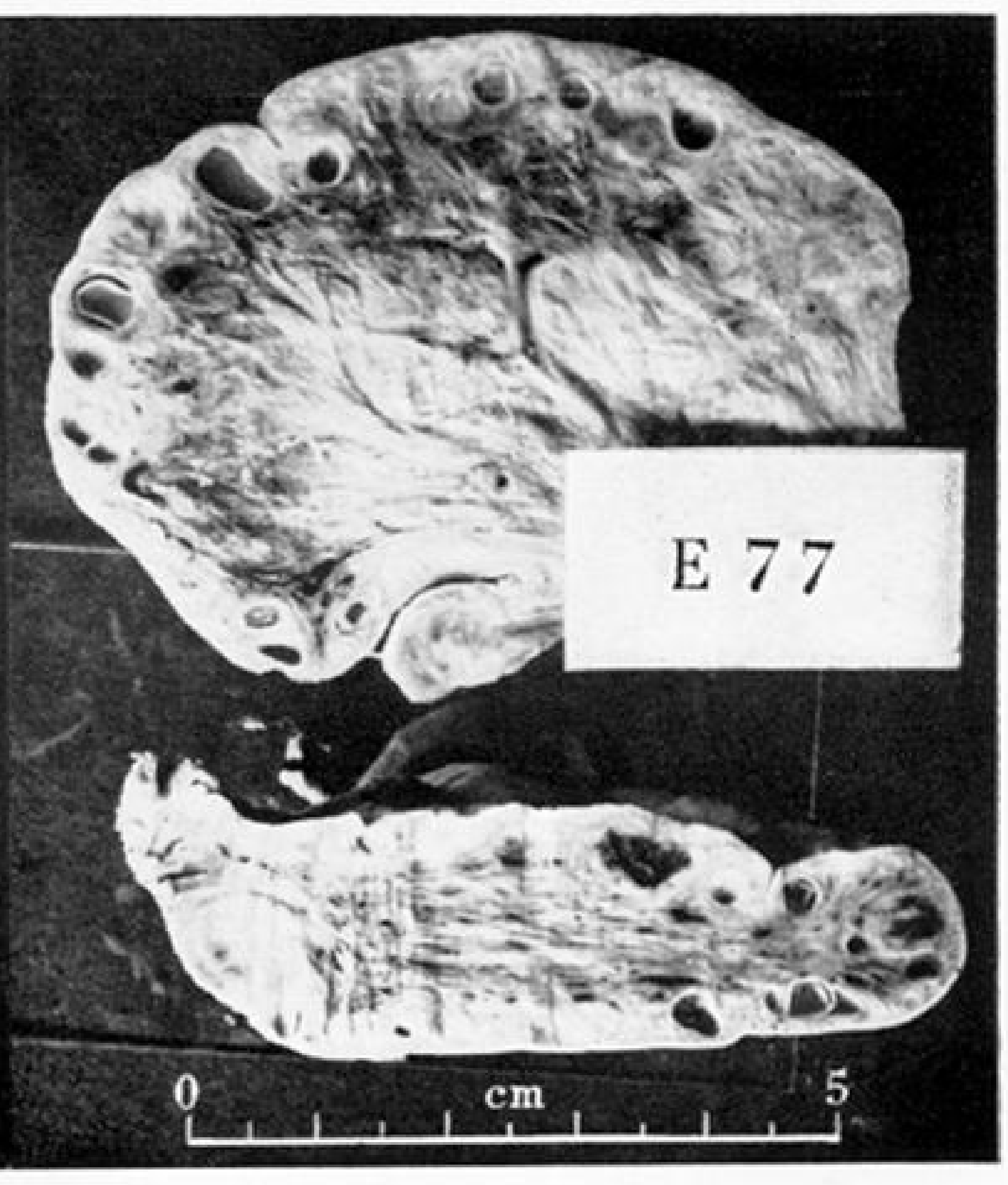

15

PLATE 5

FIGURE 9. The ovaries of a very young calf (E 134): (*a*) the left ovary, with ovarial sac in place, (*b*) the right ovary, with ovarial sac pulled away. This shows how the ovarian ligament appears to be continuous with the uterine horn. The Fallopian tube cannot be distinguished externally. The ovary was withdrawn from the inner compartment *ic*; *oc* is fimbriated outer compartment, *ut* is the tip of the uterine horn, and *al* the anterior ligament.

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FIGURE 14. The cut surface of the ovary of a pregnant animal nearing term (E 26) bisected in the axis of the hilum. Three corpora lutea, which were histologically indistinguishable, (*acl*) and two very old corpora lutea (*ocl*) are seen.

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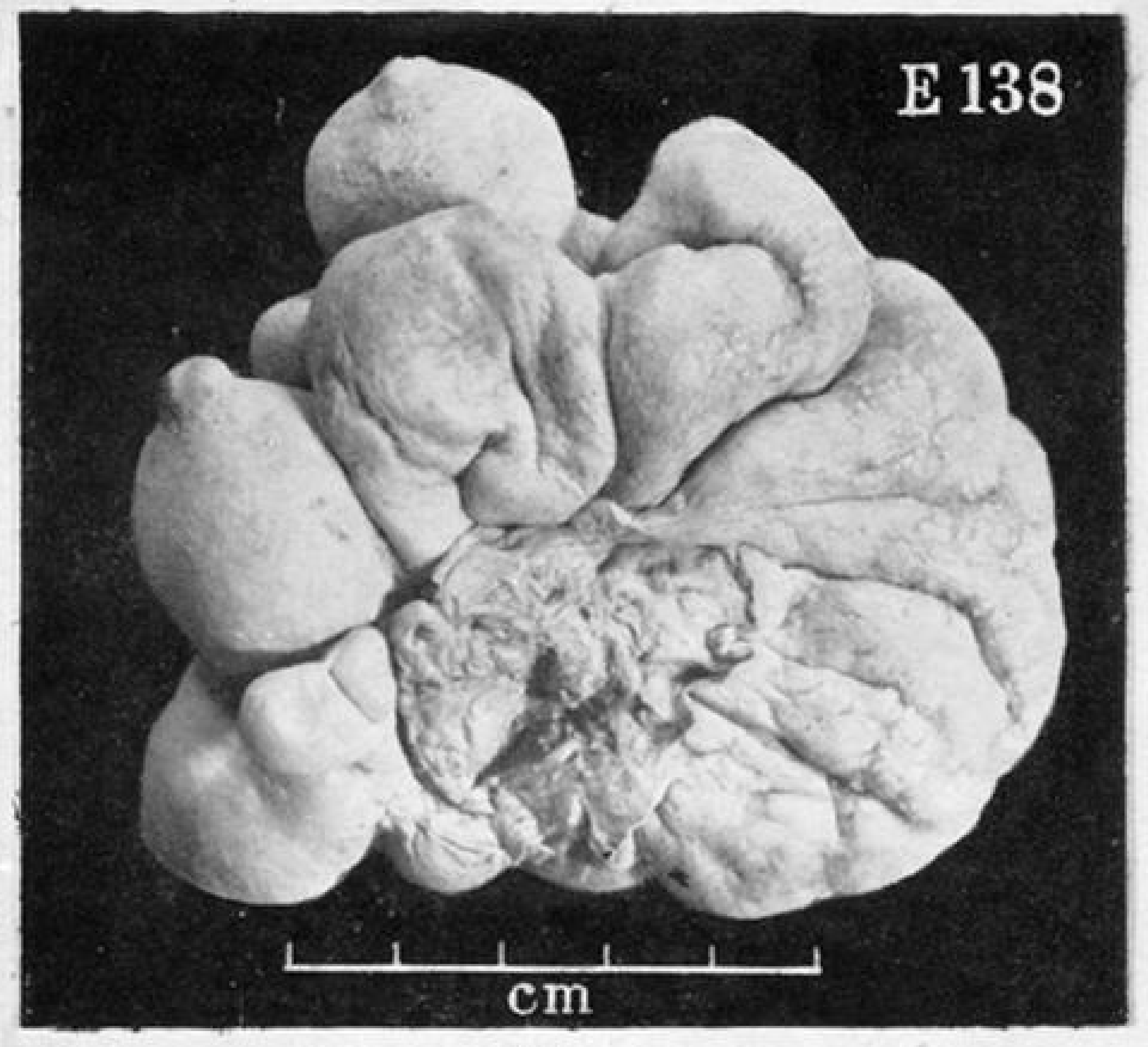

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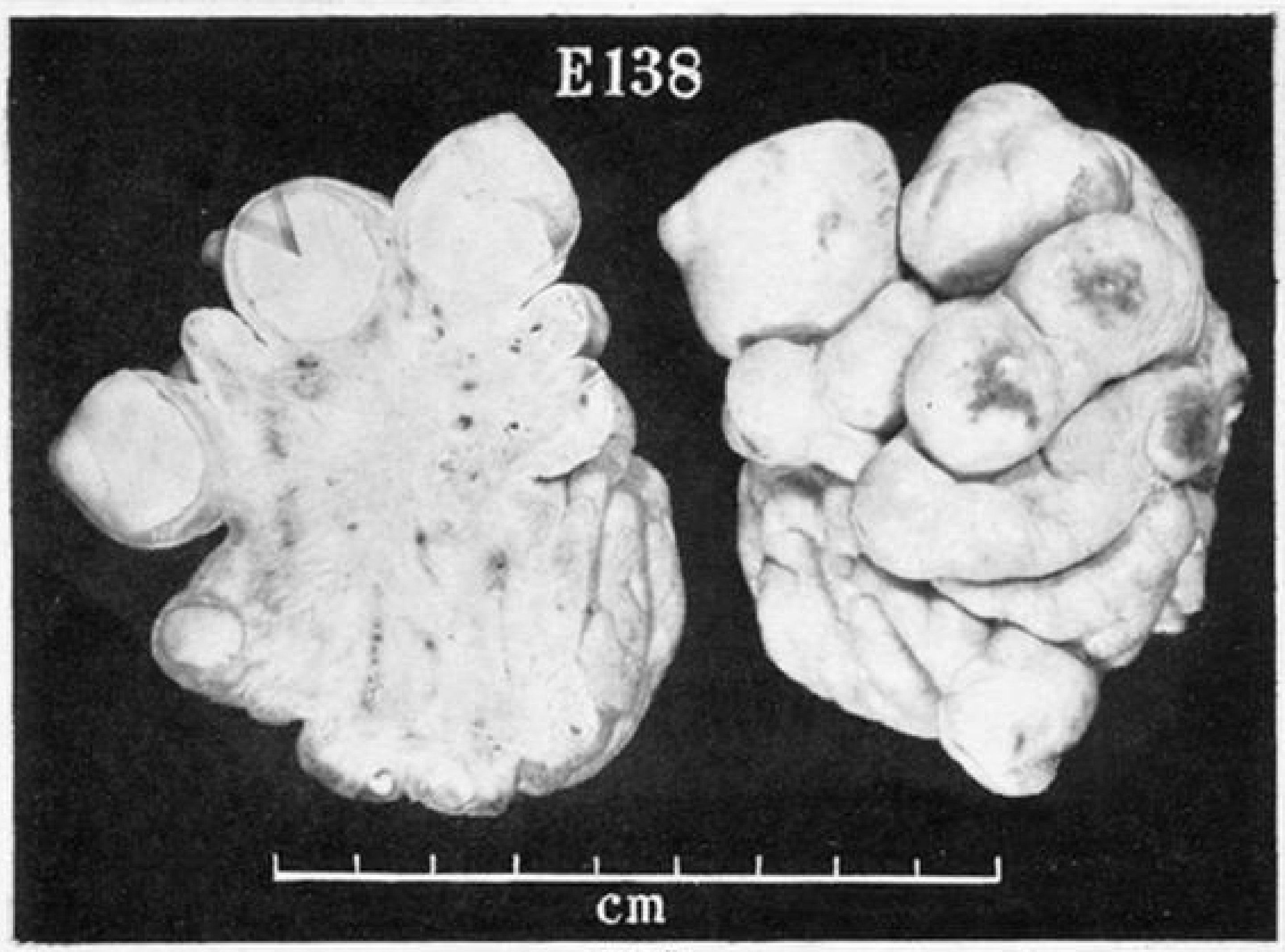

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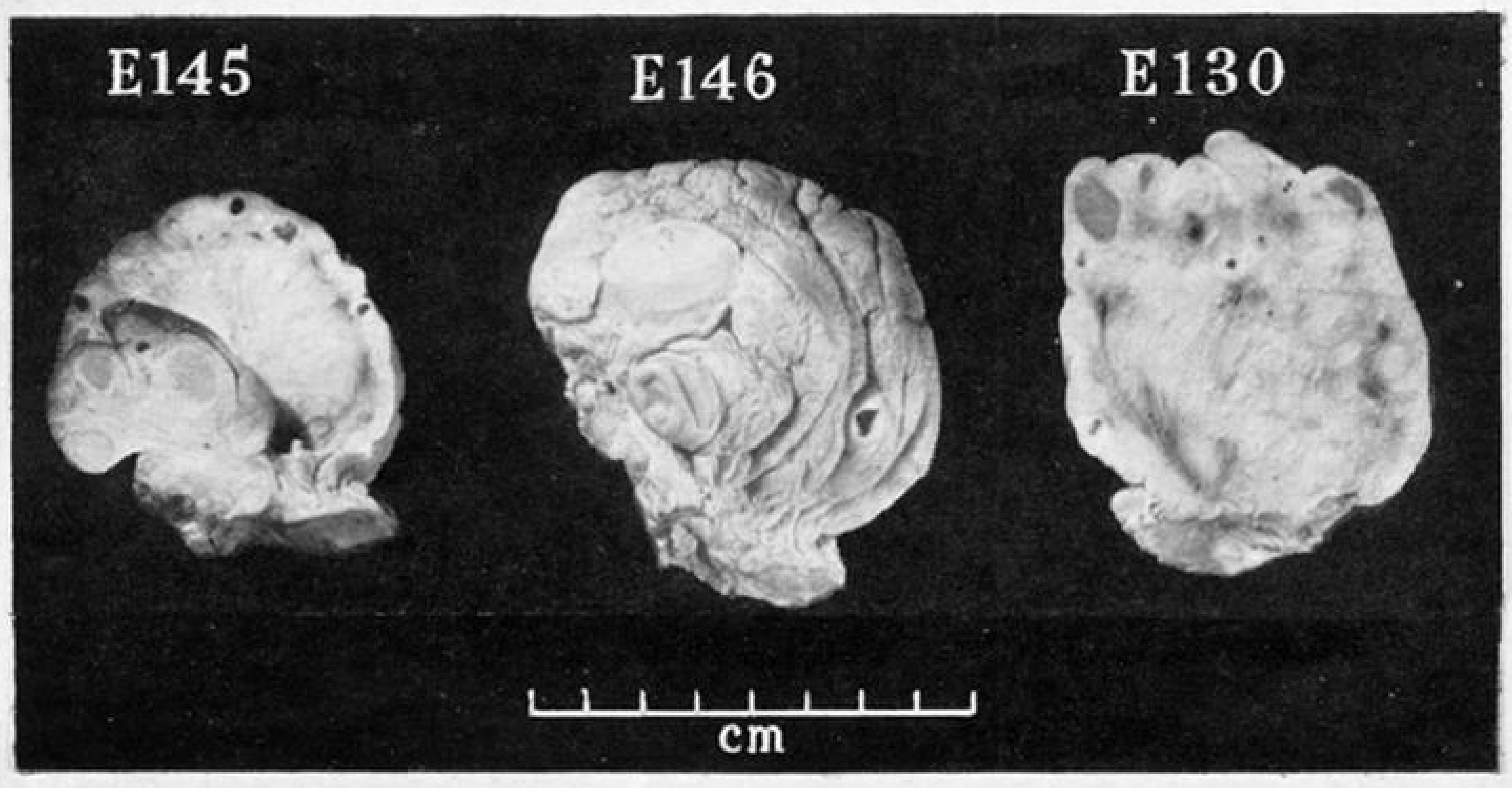

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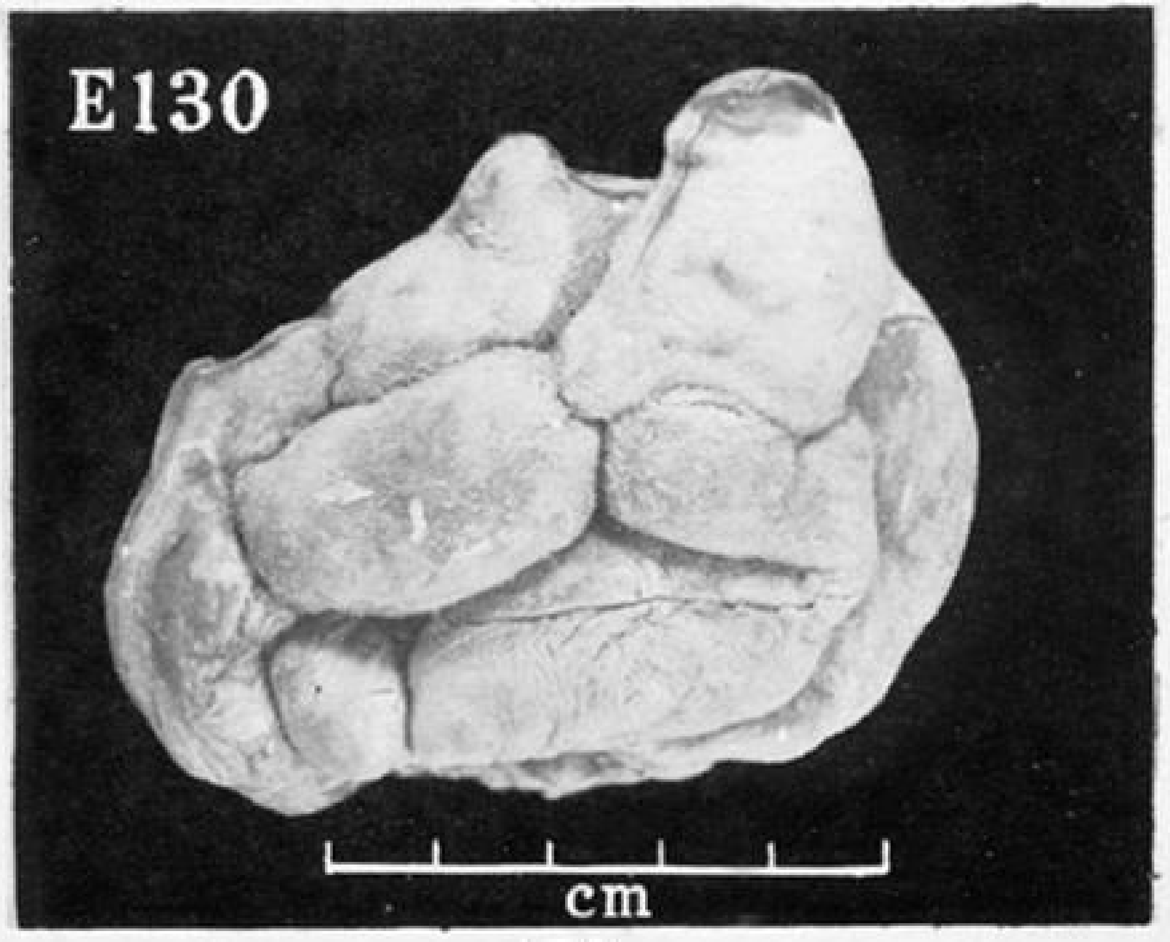

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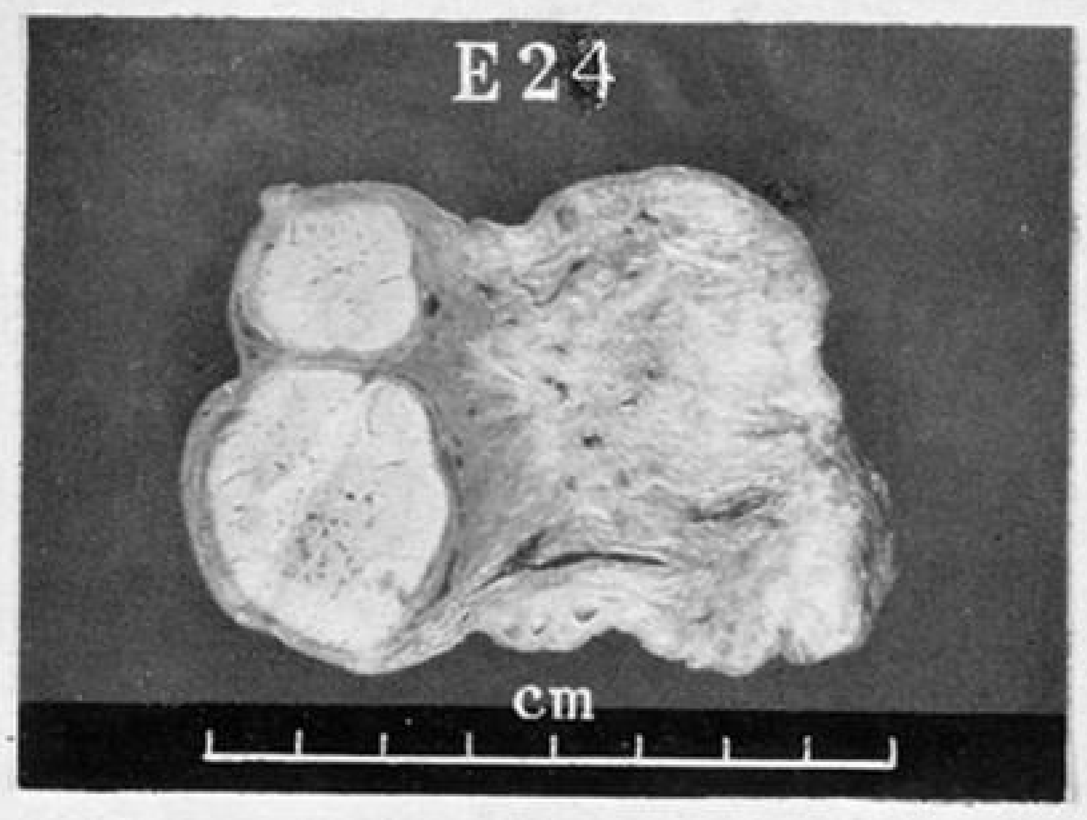

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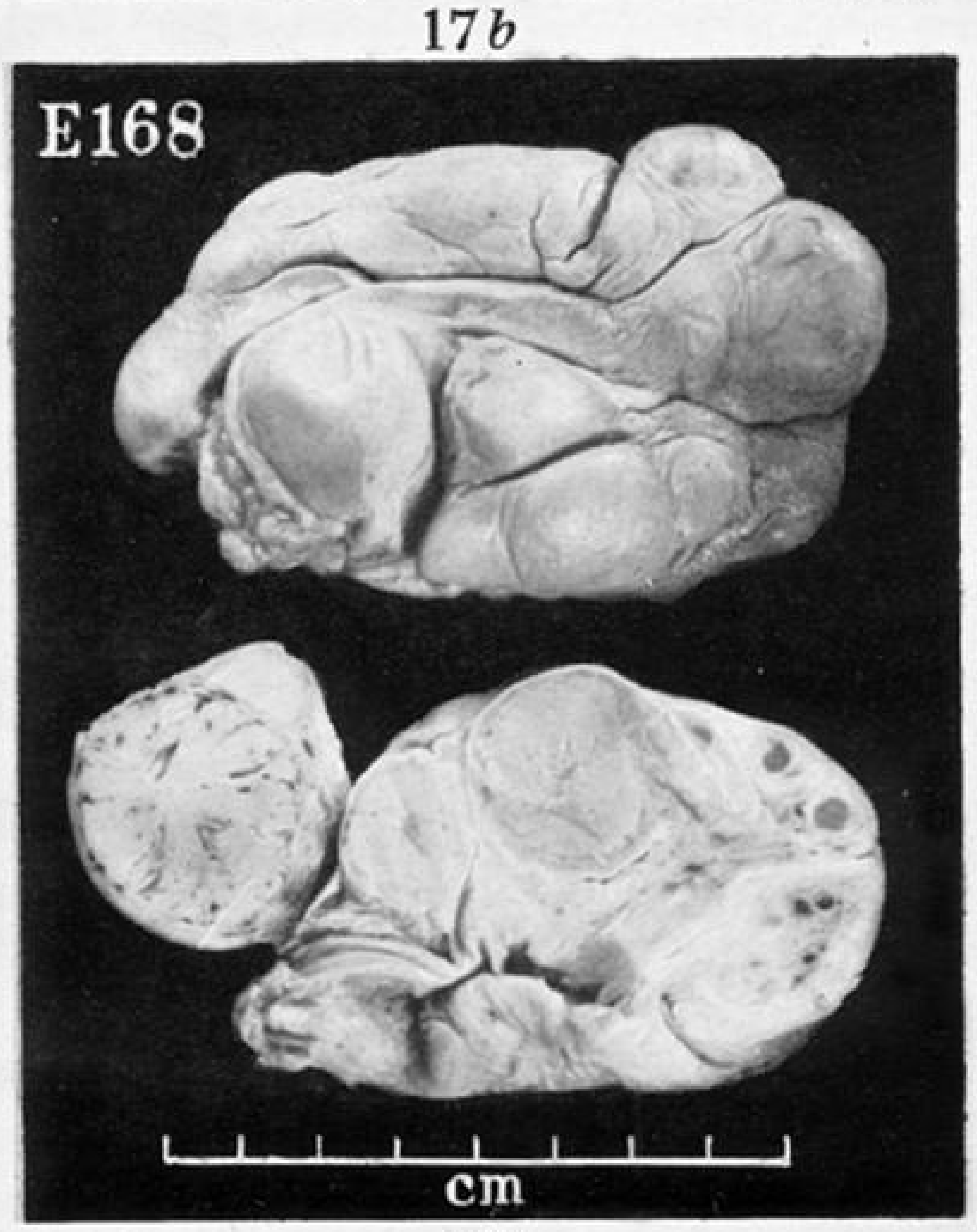

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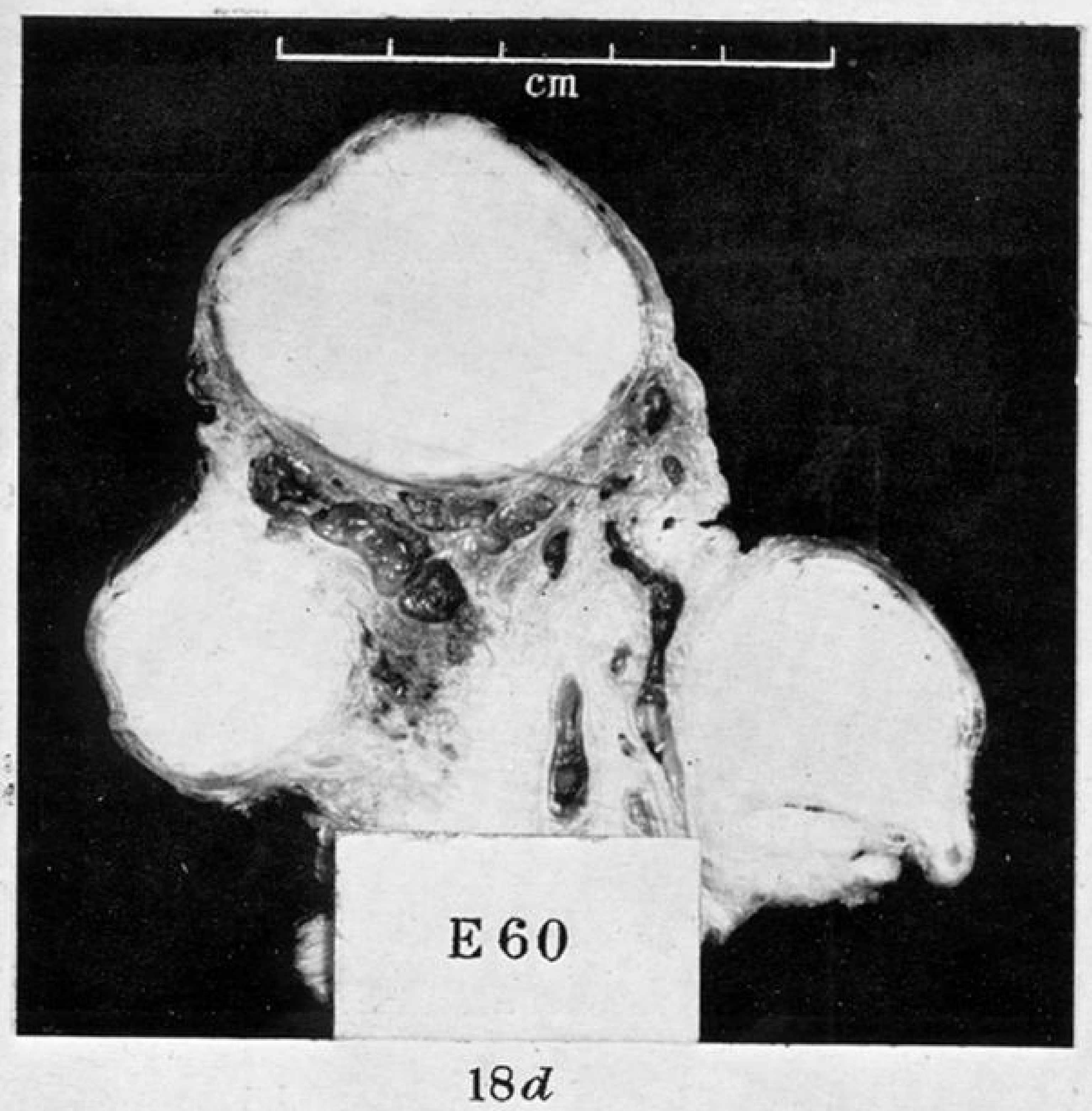
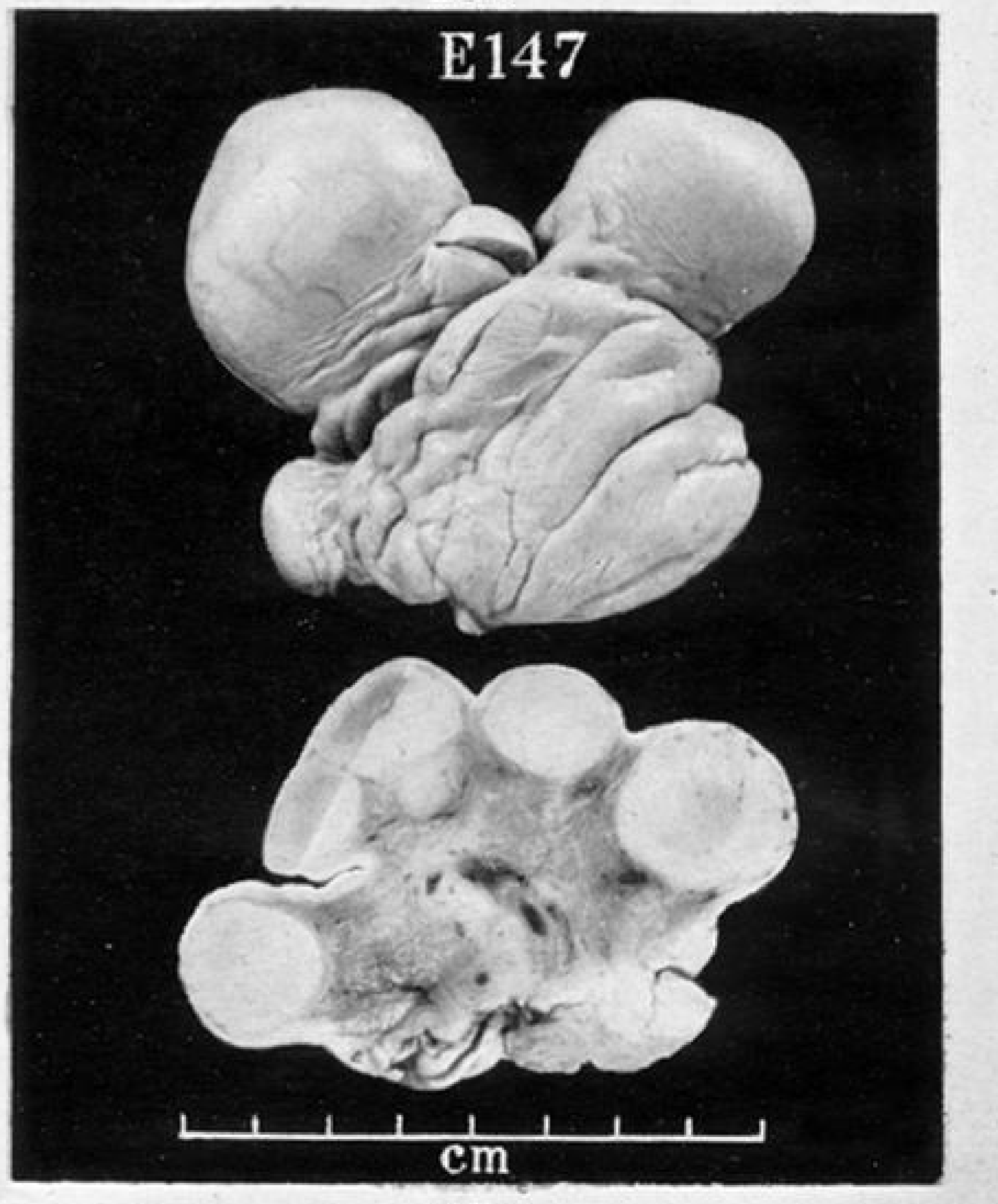


18*d*



18*c*

PLATE 6

FIGURE 16. The ovaries of an animal in mid-pregnancy (E 138): (*a*) medial aspect of right ovary; (*b*) left, cut surface of left ovary; right, lateral aspect of right ovary. Several rupture points are clearly seen. All the corpora lutea shown in the photographs were histologically indistinguishable.

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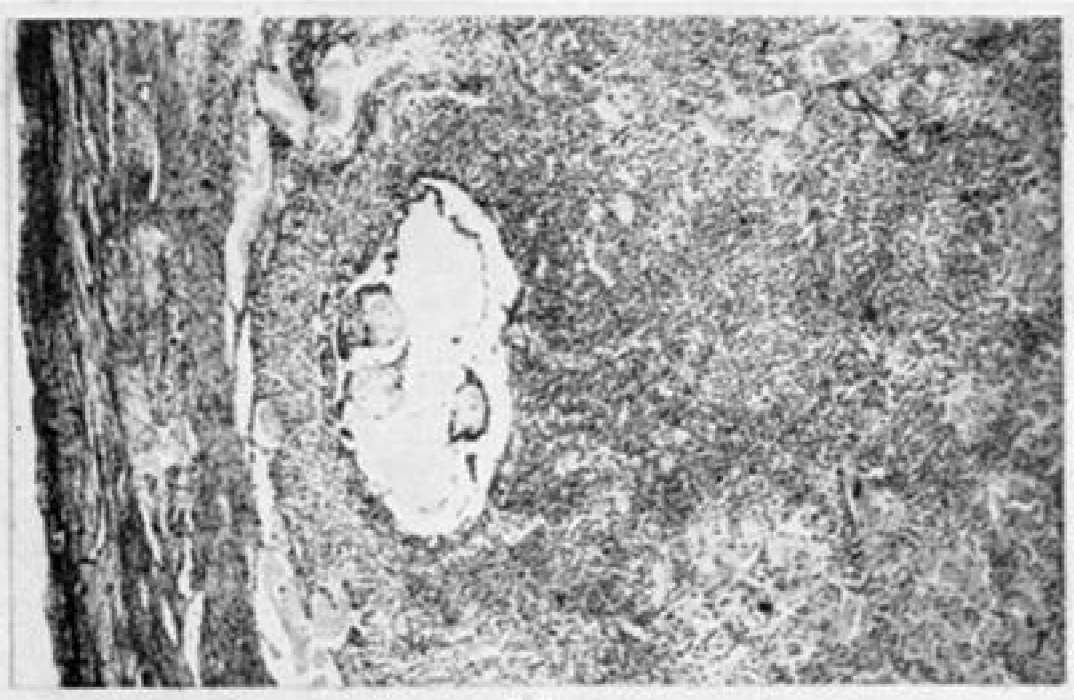
19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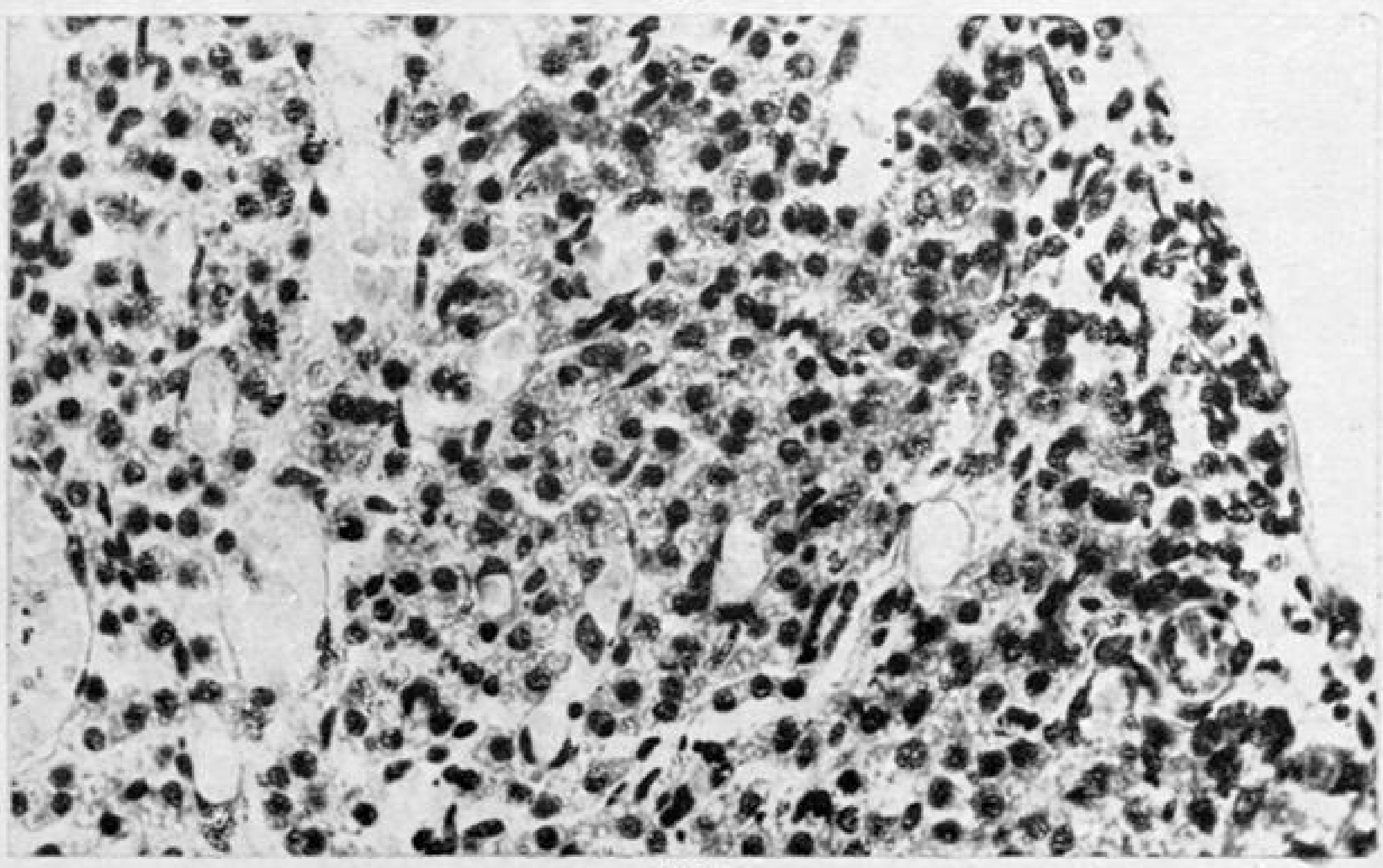
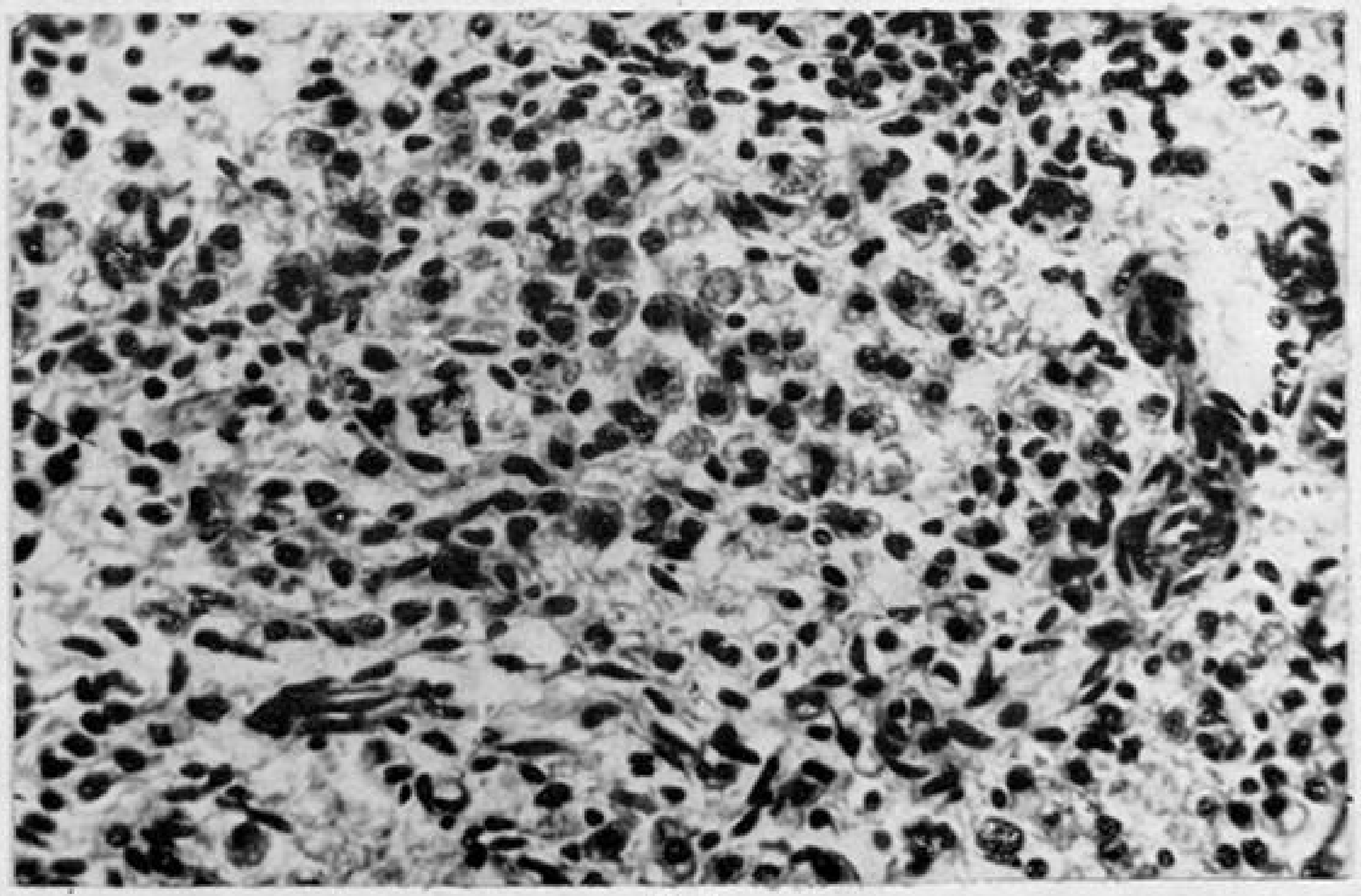

20*b*


21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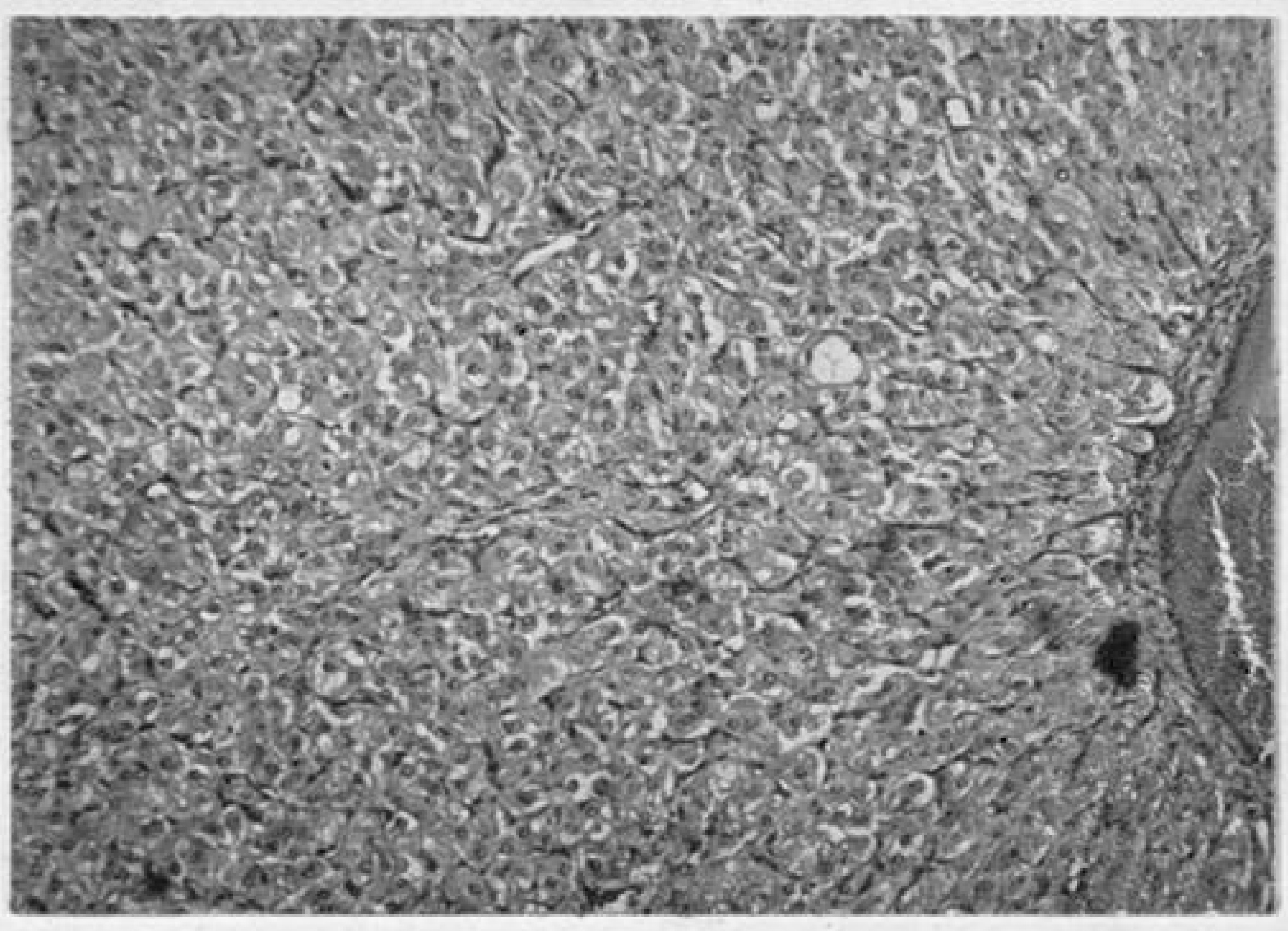
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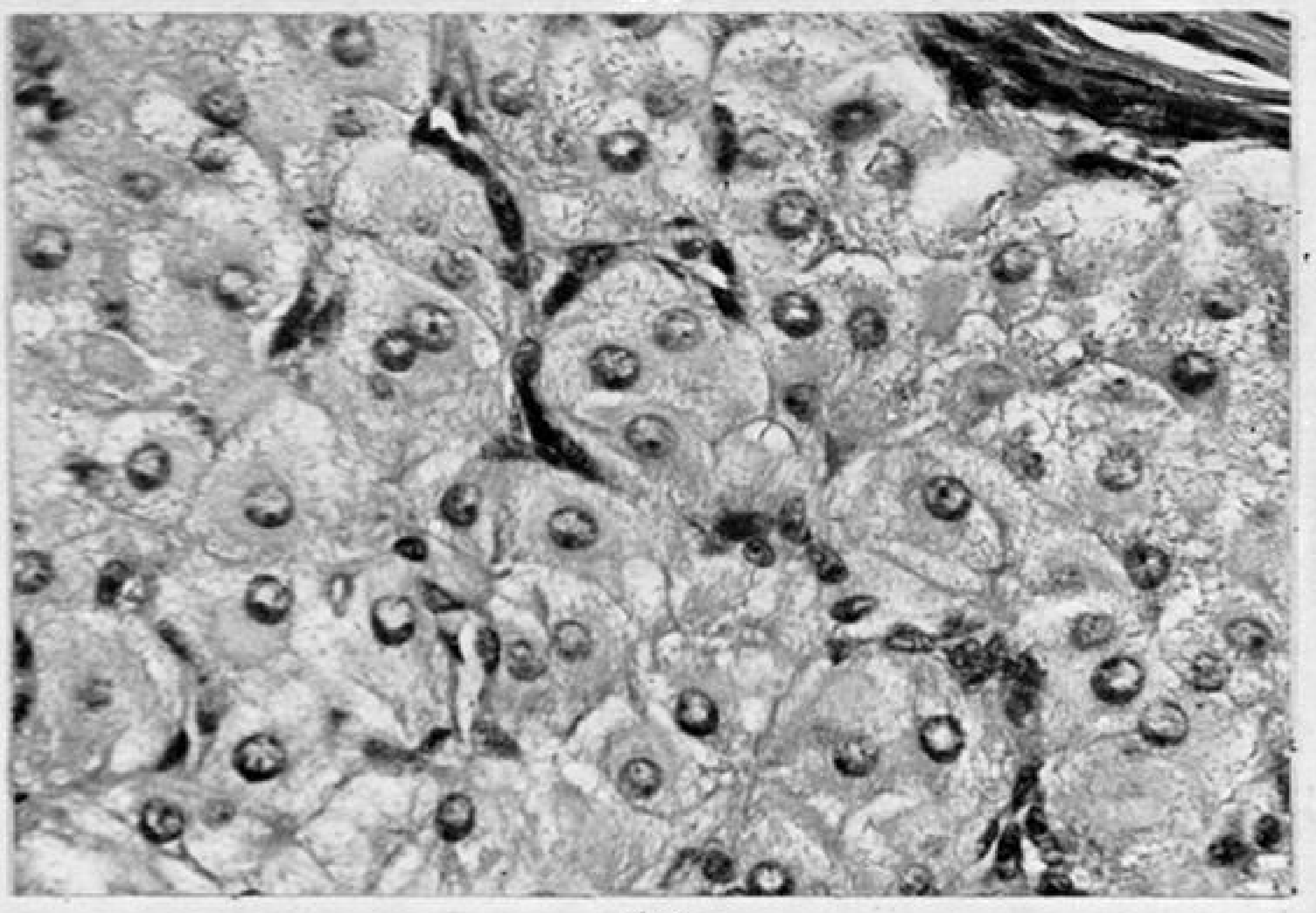

24*a*


23*b*

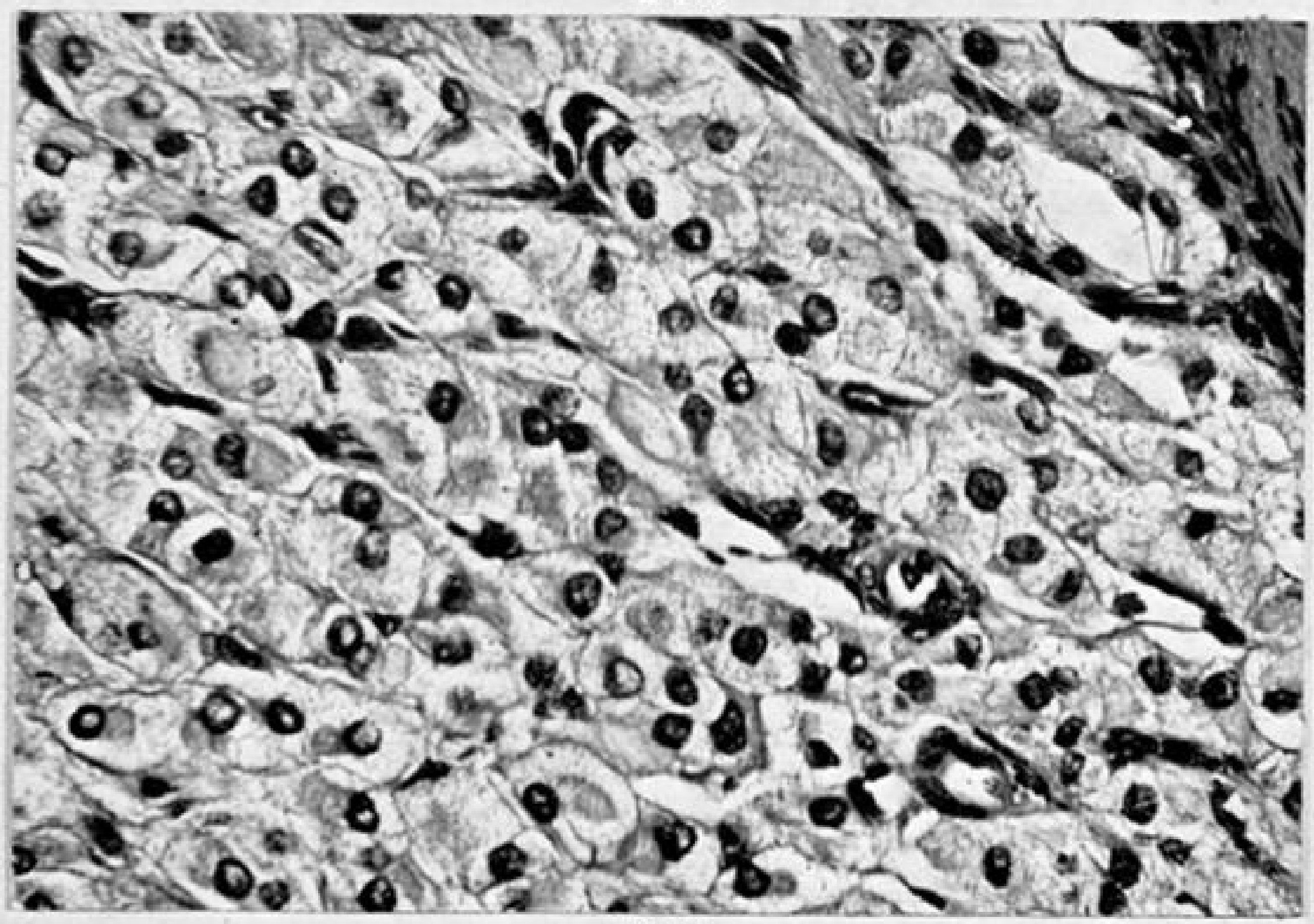

24*b*

PLATE 7

FIGURE 19. Portion of the periphery of a foetal testis (late pregnancy). (Magn. × 4·8.) The section was 12μ in thickness. Many spermatic tubules can be seen, imbedded in blocks of hypertrophied interstitial tissue in a framework of connective tissue. Cf. figure 11.

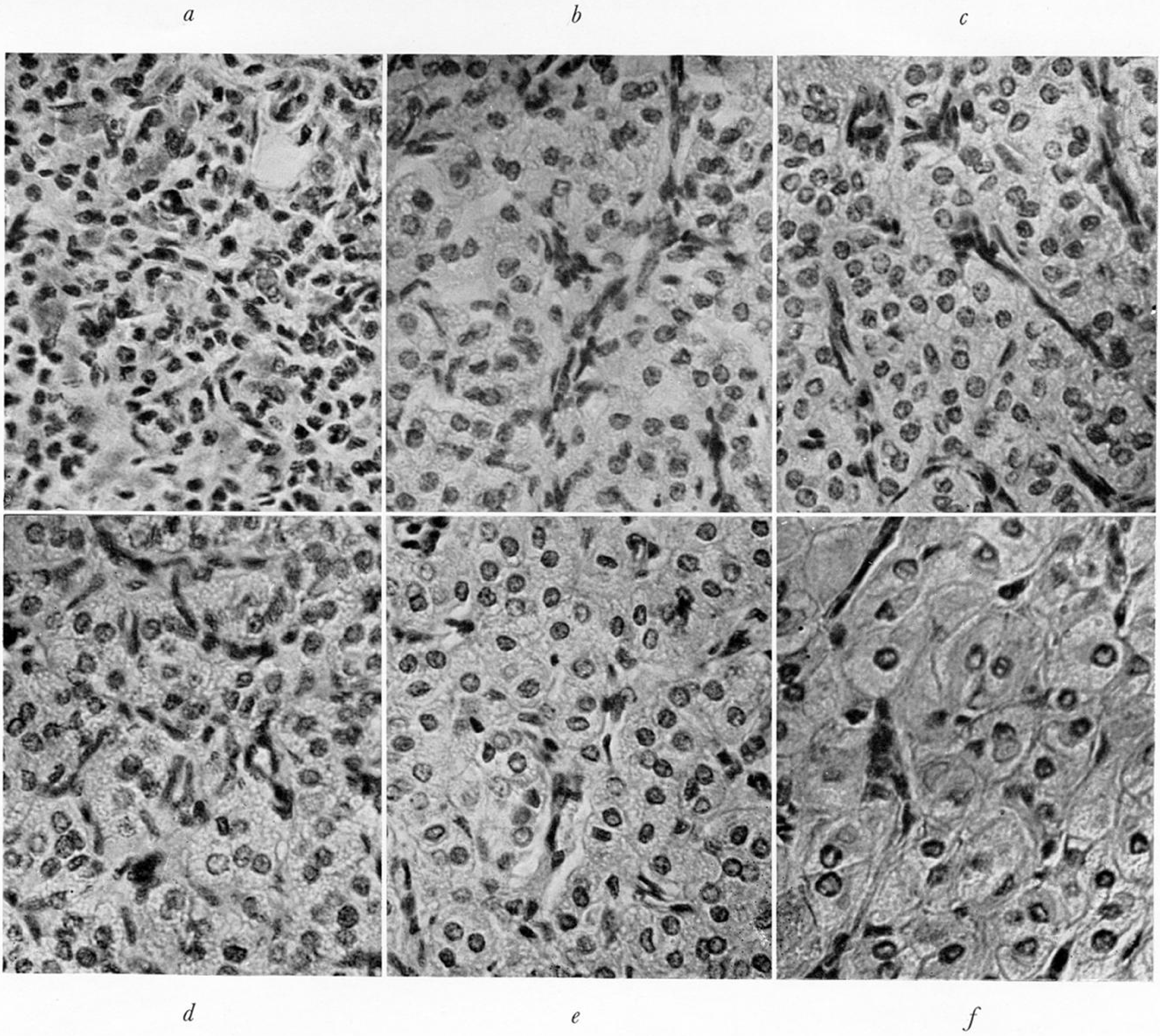
FIGURE 20. Portion of the periphery of a foetal ovary (E 84). (Magn. *a*, × 22·5; *b*, × 280.) One of the larger follicles is shown in (*a*). It was polyovular and contained four oocytes, three of which can be seen in the photograph. (*b*) shows the vacuolated condition of the cytoplasm of the interstitial cells. These cells are probably past their maximum development and beginning to regress.

FIGURE 21. Portion of the periphery of the ovary shown in figure 12, at higher magnification. (Magn. × 9.)

FIGURE 22. Part of a section through the ovary of E 119, which was a little older than E 134, the ovaries of which are shown in figures 12 and 21. (Magn. × 250.) The section shows stages in the de-differentiation of hypertrophied interstitial cells. Some are still large, with many vacuoles in the cytoplasm, while in others the vacuoles have disappeared and the cells are merging into the general stromal tissue of the ovary.

FIGURE 23. L.P. photomicrographs, at the same magnification, of portions of one (*a*) of the active corpora lutea of E 138, near mid-pregnancy, and (*b*), the corpus luteum *C* of E 130, a lactating animal interpreted as passing through a series of oestrous cycles prior to fertile mating and pregnancy.

FIGURE 24. Photomicrographs, at a higher magnification, of the corpora lutea shown in figure 23, (*a*) and (*b*).



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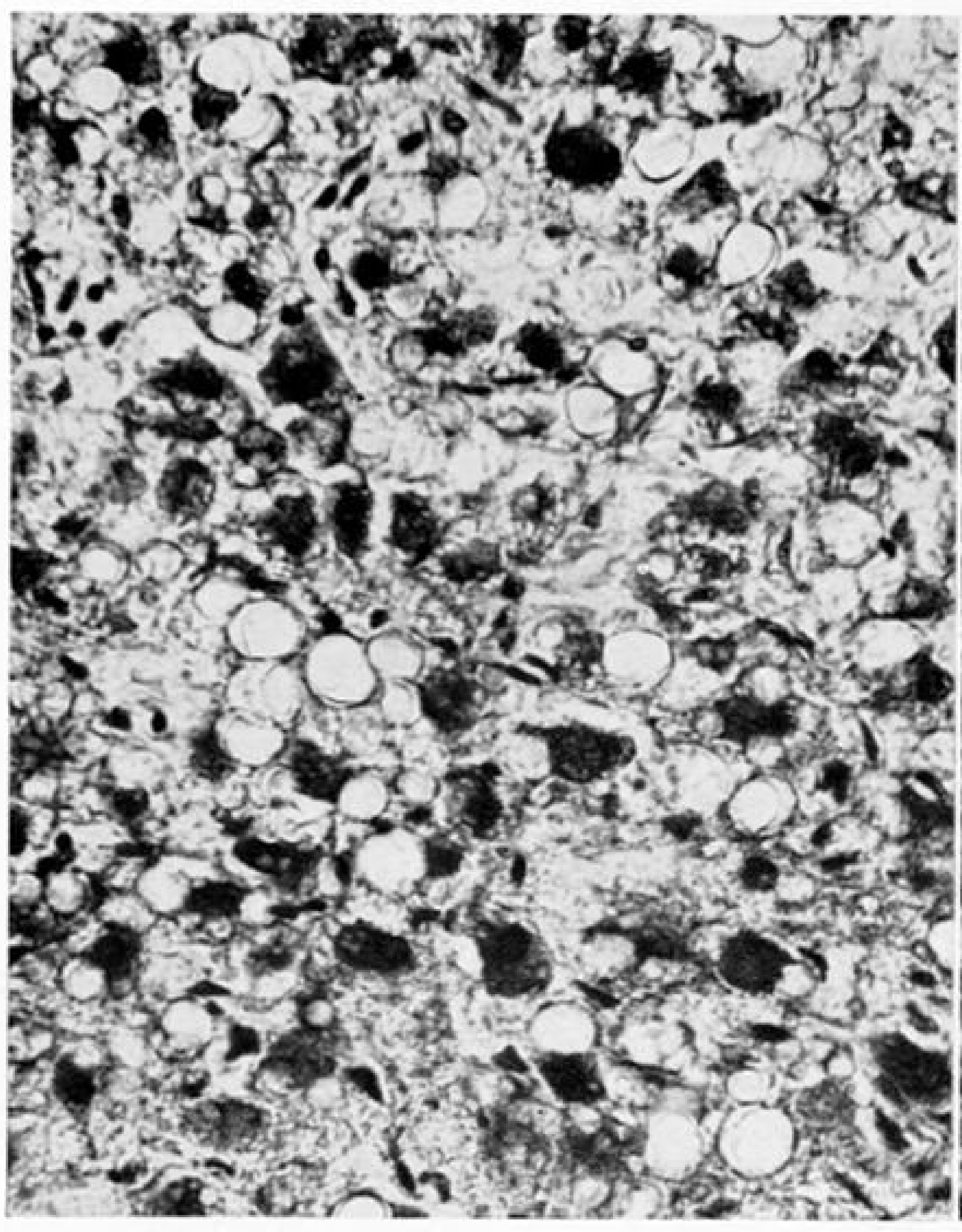
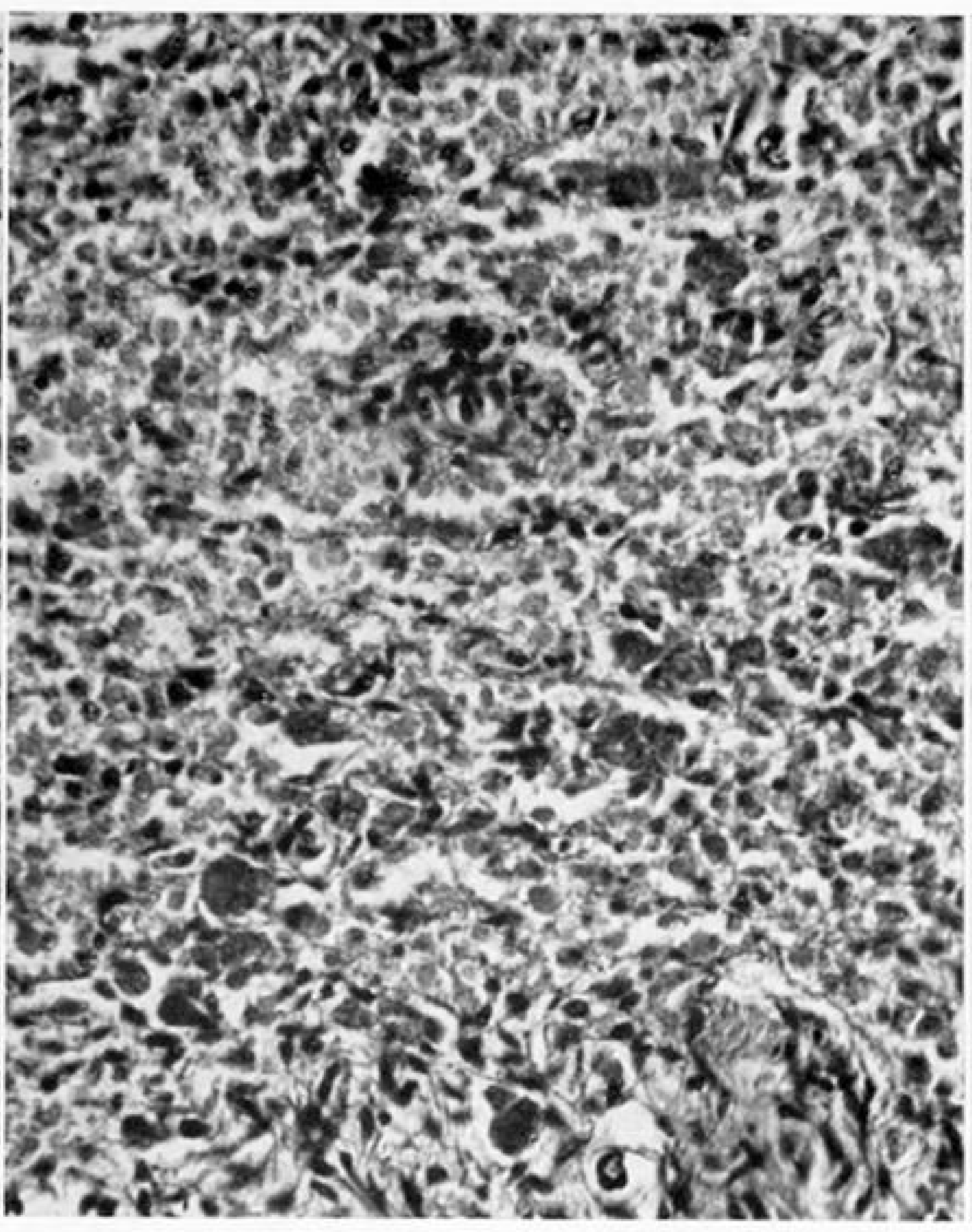


26



27

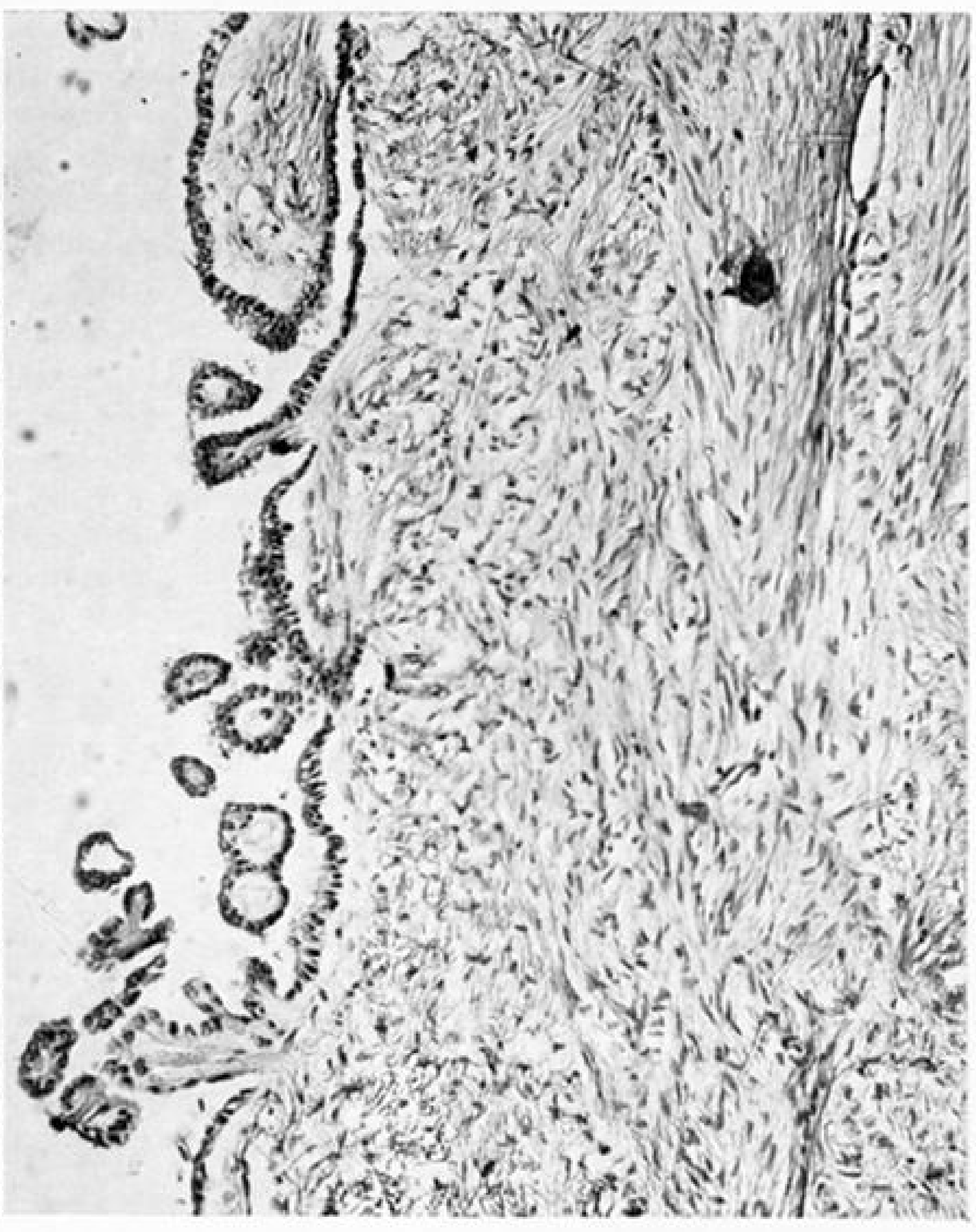


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Plate 8

Figure 25. Photomicrographs, at the same magnification and with the photographic conditions as similar as possible, of portions of the six corpora lutea of E 130. The sections, 10μ thick, were mounted on a single slide to ensure similar staining. The corpus luteum *C* at (*a*) is markedly newer than the others, and *A* at (*f*) is markedly older, while the remaining four are intermediate in condition and indistinguishable from each other.

Figure 26. Portion of a corpus luteum of E 3, about 6 months post-coitum. The luteal tissue is in an advanced state of fatty degeneration. The fat vacuoles show as empty spaces in this photograph of a section cleared in toluene.

Figure 27. The site of an old corpus luteum. Although plainly visible as a dark brown patch in the cut surface of the ovary when examined macroscopically (cf. figures 14, 15), it is almost indistinguishable from the surrounding stroma in a stained section.

Figure 28. Portion of the periphery of the ovary of E 138, near mid-pregnancy, to show subsurface crypts and papillose projections which increase the area of the germinal epithelium.