The Sexual Cycle of Female Domesticated Mammals.

THE OVARIAN CHANGES AND THE PERIODICITY OF OESTRUM IN CATTLE, SHEEP, GOATS, PIGS, AND HORSES.

(Observations on Animals in Central Europe and South Africa.)

By Professor Dr. MAX KUPFER, of the Federal Technical College, Zurich, Switzerland.

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CONTENTS.

INTRODUCTION.

THIS short article has been written with the object of giving a condensed account of the results of recent investigations on female reproductive organs and observations on the sexual life of domestic animals. It includes the results of experiments conducted with representatives of the equines (donkeys, horses and their hybrids), during a stay of one year's duration at the Veterinary Research Laboratories, Onderstepoort, Pretoria.

The publication is intended as a preliminary and fragmentary announcement for general information, and not as a detailed monograph. Parts of the contents have been published before, although in the present article the manner of presentation is different (discussion of general problems with the aid of diagrammatic plates). The new results (ovarian changes and oestrum in donkeys and horses, as well as some smaller mammals in South Africa) will be published in greater detail with full illustrations as soon as the great volume of material has been worked up. The present opportunity has been used to give a general account, partly because of its scientific interest, partly because of its practical importance, especially for animal breeders.

In the past *ruminants* have usually been selected for investigations of this kind, and an opportunity to discuss the corresponding conditions in *equines* presents itself here for the first time.

Great credit is due to Sir Arnold Theiler, the Director of Veterinary Education and Research of the Union of South Africa, who launched these experiments which were intended to fill a gap in our knowledge. Having realized the biological importance of this work Sir Arnold Theiler obtained the permission of the Union Government to expend the funds necessary for these somewhat costly investigations and then applied his entire energy to ensure their successful completion. The writer wishes to express his deep gratitude to Sir Arnold for the valuable advice which his vast experience enabled him to offer at all stages of the experiments.

(a) *The Significance of the Ovaries.*

Before discussing our actual topic, it is necessary to make a few remarks about those organs, whose structure, functions and mechanism we have to know, in order to understand the findings recorded below.

The ovaries have a twofold significance.

The Ovaries as Producers of Germ-cells.

The ovaries yield those germs whose cell-descendants form the basis of life and all living tissues. These organs therefore ensure the

propagation of the species through their activities. In their capacity as centres for the production of germinal matter they claim the attention not only of the scientist, but also of the practical breeder.

The Ovaries as Internal Secretory Glands.

We know also that the ovaries produce certain chemical stimulants, which act on definite organs and systems of organs in such profound manner that not merely the development and formation, but even the function of the organs or tissues are constantly being influenced by those products. This fact has been proved beyond doubt in recent years by means of scientific experiments (removal of both ovaries, trans- or implantation in organisms the glands of which had been removed or reduced).

Experience has taught us that the so-called *secondary sexual characters*, those somatic attributes which characterize the sex of the individual, are largely controlled by the internal secretions of the germinal glands. In cases where the internal secretory function of the glands becomes impaired or stops altogether, the animal may lose his sexual characters partly or entirely.

(b) *Remarks on the Structure of the Female Germinal Glands.*

Corresponding with its twofold function as a producer of germ-cells and hormones, the ovary has two different elements in its cellular structure. These are closely related to each other topographically and genetically. During certain phases in the development of the ovary the internal secretory elements are included in the tissues surrounding the ova; later on they appear as a separate structure. In studying the morphological picture of the ovary, it is necessary therefore not only to observe the production of ova, but also to bear in mind the question whether the internal secretory elements are able to produce hormones.

The Ovum.

The most important of all the elements which compose the egg-producing apparatus of the ovary is, of course, the egg (ovum) itself. It is well known that the ova at an early stage in the development of the ovary, lose their connection with the cell epithelium which covers the surface of the germinal gland, and wander into the stroma of the ovarian tissue.

The " Anlage " of the Graafian follicle.

The ovum together with epithelial components, also derived from the epithelial covering of the germ gland, form the " Anlage " of the Graafian follicle. This is a closed vesicle filled with liquid, in whose wall the ovum is embedded. When the follicle is mature the ovum is liberated and reaches a portion of the oviduct where it is met by the spermatozoon and fertilization takes place.

(c) *Remarks on the changes in the Ovary.*

Rupture of the Follicle.

In order to make it possible for the ovum to leave the closed Graafian follicle, the following process takes place: the follicle ruptures at one point, its wall is torn, and the liquid in which the ovum floated after its detachment from the wall of the follicle, is squeezed under pressure into the funnel of the oviduct. In this way the ovum reaches the descending portion of the genital canal, where it may meet the male reproductive cell.

Transformation of the ruptured follicle into a corpus luteum.

After the rupture of the follicle and the liberation of the ovum, perhaps even before this, the wall cells of the follicle transform themselves into an organ, which has no direct connection with the process of reproduction, but appears to have an internal secretory function. This organ is now known as "yellow body" (*corpus luteum*) or "follicular gland." The yellow body is simply the product of the differentiation of the Graafian follicle, which, in its turn, was intended to provide protection and nourishment for the ovum.

Significance of the component parts of the Graafian follicle.

It is evident, from what has just been said, that the cells forming the inner wall of the follicle has, according to the modern conception, a twofold function.

As long as the follicle is closed and retains the ovum, the follicular wall cells have without doubt essentially a nutritive function; they act as intermediaries in transferring nourishment from the surrounding ovarian tissue to the ovum.

After the transformation of the follicle into a yellow body, or perhaps even earlier, these cells take on an internal secretory function.

(d) *Remarks on the changes which the* corpus luteum *undergoes.*

Conditions necessary for the formation of corpora lutea.

The first essential for the formation of a true yellow body is the rupture of a Graafian follicle, as was shown above. For the completion of this act two other processes are necessary, the maturation of the ovum and the maturation of the follicle.

The changes which the corpora lutea *undergo.*

Any changes which the ovaries undergo affect the follicles in the first place; they mature and rupture, and the ruptured follicle is transformed into a yellow body. The yellow bodies, in their turn, are subjected to changes whereby, on the one hand, evolutionary (developmental) and, on the other, involutionary (reductional) changes are noted.

Development and reduction of the corpora lutea.

The yellow bodies attain their full development and then their tissues are reduced in such a way that involutionary processes are constantly at work in them after they had reached their full development.

(e) *The significance of the periodic changes in the ovary and of the regulation of this process, for the practitioner (breeder) and the scientist.*

It is of the greatest importance to know exactly how these various changes in the ovaries follow each other, and, more especially, to have a clear conception about processes regulating the chronological sequence of these acts.

The value of this knowledge is apparent: *The breeder* can become acquainted with the exact times, when the egg is liberated from the ovary, and in this way he can arrange the mating of his animals, so that, while the sires are not unnecessarily taxed, he obtains the best chances of achieving conception.

By studying the mechanism of the ovarian changes, *the scientist* gets a better insight into the special functions of the female germinal glands. He also has to watch the further development and changes of the " yellow body," which may, through its internal secretion, influence tissues, organs, or whole systems of organs. The ovaries are component parts of such a system. Cyclical changes which take place in the gonads also influence the remaining sections of the genital apparatus, the entire genital tract with the genital organs, internal and external. The processes in the other portions of the genital apparatus may take place at the same time or before or after those occurring in the ovaries.

An investigation into the changes undergone by the ovaries has, in order to be complete, to extend itself to the other portions of the genital apparatus, both internal and external organs, more especially the latter since they can conveniently be observed. Whenever processes taking place inside the body of the animal are examined, the changes in the external genital apparatus should be recorded, because the two sets of changes stand in relation to each other.

(f) *Psychological phenomena.*

The changes which appear in the genital apparatus are often coupled with manifestations of a psychological nature, such as changes in the mode of living or in the habits of the animals. These changes often enable us to draw conclusions about the occurrence of internal processes; so that our attention, even though it was originally focussed on an internal organ, is bound to be diverted to the external sexual apparatus. It is therefore possible for an investigator to form fairly accurate pictures of the internal processes by observing the external changes in the animal.

The externally visible phenomena, which are partly of a morphological, partly of a psychological character, belong to the group of symptoms which characterise the *oestrum* or " heat." It should be noted, however, that a number of changes in the genital apparatus (ovulation, changes in the uterine mucous membrane, etc.) also form an essential part of the oestrum.

In the following pages our observations on living animals in regard to the appearance and disappearance of oestrum will be detailed and an attempt will be made to bring these data into correlation with the findings at the post mortem examination of the animals.

These few general remarks may serve as an introduction to our short paper. We shall now attempt to give a concise account of the ovarian changes and sexual cycles as observed by us in the course of time in a series of domesticated mammals. The main stress will be laid on the morphological and chronological factors.

I. *The behaviour of the ovary of cattle during normal or disturbed sexual functions* (*Conditions in Central Europe*).

A. *The behaviour of the germinal gland during normal sexual functions.*

(a) *General.*

First of all the essential facts regarding the ovarian conditions and the oestral periods of *cattle* will be discussed. The cow has been chosen as the first representative of our domestic animals, because its

ovarian conditions are simple and clear when compared with the conditions in other mammals, and because the relatively large size of the organs render them suitable objects for demonstrating both the details of the organs themselves and their relations to surrounding organs. In the discussions which follow the cow may be regarded as the type.

Our descriptions refer to Swiss cattle. Unfortunately our relatively short stay in South Africa did not allow us to extend our investigations to the cattle of this warm country. However, casual observations would seem to justify the conclusion that the cattle in South Africa conform roughly to the same type of organogenesis and follow the same periodicity in organic functions as the cattle of Switzerland and Central Europe. Nevertheless it would be advisable to study the sexual conditions of South African cattle throughout a whole year. It might then be possible to show that the influence of domestication was not the only factor determining the processes and appearances in the genital apparatus (although even in the South African latitudes domestication obviously plays an important rôle), but that the ovarian changes are undoubtedly also regulated by a number of other factors, especially climatological, telluric and nutritional conditions.

(b) *Anatomical structure of the ovary.*

The outward appearance of a sexually mature bovine ovary, which measures about 3.5-4 cm. in length, 2.5-3 cm. in breadth, and 1.5 c.m. in thickness, is tuberous and the uneven surface is characterised by numerous more or less prominent protuberances. These protuberances are due, partly to vesicular elevations of the surface of the ovary, and partly to compact reddish, yellow, or yellowish brown papillary masses of tissue, which stand out against the mass of the colourless or grey tissue of the rest of the organ.

The vesicles or Graafian follicles are cavities of various sizes filled with a slightly yellowish fluid (liquor folliculi). In a section the follicles are more numerous in the marginal zone, although several may occur in the deeper central zone. The follicular wall is composed of several layers of cells, of which one cell, the female reproductive cell or egg cell, is recognizable by its greater size and characteristic nucleus. As remarked above, the follicles may be regarded as temporary depots of the egg cells.

(c) *Physiological functions of the ovary.*

(c) 1. *Puberty and adult state.*

The ovary only reaches its full development at a comparatively late stage in the development of the individual. It only reaches this state in the sexually mature animal. Heifers in Central Europe reach maturity at the age of 18 months. Before this age the ovary is in a state of incomplete development, both as regards its architectonic structure and as regards its functional potentialities.

(c) 2. *Follicular changes.*

(c) 2^1. *Expansion of the follicle.*

The Graafian follicles, as well as the egg cells they contain, are continually undergoing changes. The individual follicles expand and grow larger, thus coming into contact with the surface of the ovary.

During this process of expansion the follicles push aside the matria of the ovary and when in close contact with the serous covering, form the protuberances described above.

(c) 2^2. *Rupture of the follicle.*

If the egg cell is to perform its mission, i.e. if it is to form the beginning of a new individual of its species, it has to escape from its capsule, the follicle, where it found protection and nourishment. The liberation of the ovum which only then becomes possible when the follicle ruptures, takes place when certain conditions are fulfilled.

(c) 2^3. *Transformation of the ruptured follicle into a* corpus luteum.

After the follicle has ruptured and liberated the egg cell, it becomes converted into a compact mass of tissue. When this has reached its full size, it appears as a yellowish brown protuberance which, together with the follicles give the surface of the ovary its irregular shape. The "yellow body" which is thus formed from a ruptured follicle, reaches its maximal development in the ovary, and then tends to undergo a reduction in volume, which process is always accompanied by colour changes of the tissue.

(c) 3. *Periodicity of the ovarian changes.*

An interesting result of our investigations is the fact that the rupture of a follicle (liberation of an ovum), the evolution and involution of a corpus luteum are strictly periodic processes. The rupture of mature follicles occurs at definite and regular intervals. The period required for the corpus luteum to reach its full development can be measured by a definite number of days. The exact stage at which involution of the corpus luteum sets in is also fixed.

Normally, rupture of a Graafian follicle takes place regularly every three weeks. Every 21 days an egg-cell, capable of producing a new individual, is liberated from the ovary (ovulation).

Ovulation is followed by the development and the reduction of a corpus luteum, processes which are rendered possible only by the rupture of a mature follicle. The development and reduction of the corpus luteum also occur at definite intervals.

We know that 9-11 days are required for the full development of the corpus luteum. At the end of this period (counting from the rupture of the follicle) the reduction of the tissue begins, so that at the time when a new follicle is ready to burst, the old corpus luteum has reached a definite stage in its involution.

(d) *External manifestations accompanying the changes taking place in the ovary* (*Oestrum*).

Every breeder of cattle in Central Europe knows that every non-pregnant heifer or cow normally comes into oestrum ("heat") after regular intervals of time.

(d) 1. *Symptoms of Oestrum.*

Oestrum is recognizable by the peculiar behaviour of the animals showing sexual desire, and by the changes which appear in the external genital organs, namely swelling of the vulva, reddening of the mucous membrane of the vagina, and a mucous or bloody or

blood-stained slimy discharge from the vagina. Sometimes the psychical phenomena predominate, sometimes the anatomical-morphological changes in the external genitals are more prominent.

(d) 2. *Periodicity of oestrum and the relation between oestrum on the one hand, and ovulation and ovarian changes on the other.*

The symptoms of oestrum vary from animal to animal, and may assume a different character according to the peculiarities of the animal.

Normally oestrum recurs every three weeks. Now our investigations have shown that these more or less clearly recognizable signs of oestrum coincide in point of time with the changes in the ovary described above, especially with the rupture of mature follicles in the ovary, i.e. with ovulation. During oestrum a mature follicle ruptures and liberates a mature ovum, and in consequence thereof the evolution and involution of a corpus luteum takes place.

The outward signs of oestrum may serve as a guide to the internal changes taking place in the ovary, but can only be relied upon to do so if we are thoroughly acquainted with the living animal and able to interpret its behaviour both under normal and abnormal conditions. For at times the psychological and anatomical signs of heat are not very conspicuous. The danger is therefore that the symptoms of heat may be overlooked and wrong conclusions drawn as to the condition of the ovaries; particularly in cases of "quiet" heat where the signs of oestrum are not well marked, but the ovaries may still act normally in the production of ova.

B. *The behaviour of the germinal gland during disturbed sexual functions.*

(a) *General.*

The changes which take place with great regularity in the ovaries of the non-pregnant, sexually mature, domestic cow or heifer, can be interrupted by a variety of causes.

The following factors may be responsible for such interruption:—

1. Influence of continuous functioning of the ovaries on the normal cycle.
2. Suppression of the normal cycle owing to pregnancy.
3. Suppression of the normal cycle due to the action of poisons (food poisons, bacterial toxins, parasites, etc.).
4. Suppression of the normal cycle due to stimulation of the uterus.
5. Suppression of the normal cycle due to anatomical changes in individual component parts of the uterus or in other organs.

(b) *The various causes of interruption of the normal ovarian cycle.*

(b) 1. *The influence of continuous functioning of the ovaries on the normal cycle.*

After a certain number of times the normal cycle of changes in the ovaries may show aberrations, may be suppressed, or may undergo an alteration in character These deviations from the normal are due to the fact that the continuous functioning of the organ renders it incapable of producing mature follicles in the normal time and thus also the liberation of egg cells capable of further development, and the formation of corpora lutea are interfered with.

(b) 2. *Interruption of the normal cycle owing to pregnancy.*

When the liberated egg begins to germinate and the animal is in a state of pregnancy, the normal cycle of ovarian changes stops. In such cases the corpus luteum usually persists at the stage of full development, and involution only begins after parturition, i.e. when pregnancy has ended. During pregnancy maturation of new follicles does not take place and hence ovulation is suppressed.

(b) 3. *Suppression of the normal cycle due to the action of poisons.*

Poisons circulating in the blood stream may bring about irregularities in, suppression of, or alterations in the normal cycle. Such poisons may be derived from the food or taken in with the food, or may be of bacterial origin, or derived from animal parasites. Hence it is not surprising to find that animals which suffer or have recovered from infectious diseases frequently show structural changes in the ovaries. Irregularities in the nutrition, circulation or metabolism may also be responsible for the suppression of the normal ovarian changes.

(b) 4. *Suppression of the normal cycle due to stimuli acting on the uterus and other systems of organs.*

Certain stimuli acting on the uterus or parts thereof may bring about suppression or irregularities of the normal periodicity of ovarian changes. Such stimuli may be set up by substances like mucus, pus, watery exudates due to catarrh of the mucous membrane of the uterus, or even solid bodies, such as dead foetuses or foetal membranes, or gases.

(b) 5. *Suppression of the normal cycle due to anatomical changes in individual component parts of the uterus or in other organs.*

In considering the causes of the alterations in the periodic cycle, one must also bear in mind anatomical changes in the component parts of the uterus or in other systems of organs not connected with the generative system. Changes in the uterine blood supply, or in the genital canal may be responsible for the suppression of the cycle.

(c) *The effect of disturbances in the periodic cycle on the structure of the ovary.*

The normal cycle may be disturbed at any phase of the ovarian changes. This may happen before the rupture of the Graafian follicle; or after ovulation, in which case the conditions governing the development and involution of the corpus luteum which arises from the ruptured follicle, may be directly influenced. In the former case abnormalities of the follicle (degeneration, formation of cysts) are observed, in the latter abnormalities of the corpus luteum.

But in both cases the disturbing influence usually affects both ovaries; thus, for example, if there are abnormal conditions in a Graafian follicle or a corpus luteum of the left ovary, the corresponding part of the right ovary will be found to be affected in the same way. Left and right ovaries are usually subject to the same disturbing influences simultaneously.

(d) *Symptoms which can be diagnosed externally and which may stand in relation to internal changes or may point to disturbances in sexual functions.*

Whenever the normal cyclic changes in the ovaries are disturbed, the external behaviour of the animals also shows disturbances or changes. The irregularity of the internal processes in the ovary is often reflected in externally visible irregularities, for instance, in irregularities in the oestrum or in altered habits of the particular animal. Admittedly much closer observation is required to detect alterations in the normal habits and behaviour of the animal than to recognize more or less conspicuous changes in the ovaries. Hence keen observation is necessary, and great care must be exercised if a correct estimate of the value of an affected animal for breeding purposes is to be arrived at.

Several outward signs point to irregularities of the periodic ovarian processes, to disturbances of the normal cycle, to changes in the ovaries, to interruption of ovulation and consequent loss of fertility. Such signs include the following: Irregularity in the appearance of oestrum [delayed oestrum, interruption of oestrum, complete absence of oestral symptoms, oestrum at frequent short intervals, permanent oestrum (" nymphomania," " bulling ")] irregularity in the intensity of the oestral symptoms [oestrum with suppressed symptoms (quiet oestrum), oestrum with exaggerated symptoms]. Similarly the external genital organs may vary in appearance when compared with a normal oestrum; for instance, there may be a permanent mucous discharge from the vagina, or the os uteri may remain open. Among the symptoms that indicate changes of the internal genital organs, such as uterine changes or, especially, deformities of the ovaries, should be mentioned the slackening of the sacro-suatic ligaments and the falling-in of the fleshy parts of the croup and rump along the edges of the sacrum to the base of the tail.

II. *The behaviour of the ovary of sheep during normal sexual functions. (Observations in Europe and South Africa.)*

In the foregoing pages we have given a short sketch of the ovarian condition of European cattle during normal and disturbed sexual functions. We shall now attempt to outline briefly the morphology and the cyclic changes of the ovaries of sheep.

It is unnecessary for the purpose of a morphological description to distinguish between the representatives of the various countries. All the ovaries show a similar structure and can scarcely be distinguished.

(a) *Description of the morphology.*

(a) 1. *General.*

The ovary of the ewe has essentially the same structure as that of the cow. It is, however, much smaller, corresponding with the smaller size of the animal. In the sheep, too, the follicles project beyond the surface of the ovary. In the same way the corpora lutea grow towards the surface of the ovary; during the early stage of their

development they appear, in the shape of buttons or papillae on the surface, whereas the fully developed corpora lutea look more like plugs driven into the ovarian tissue. The stages of differentiation of the corpora lutea in the ovaries of sheep can always be recognized without difficulty. The reddish or flesh-coloured differentiating tissue stands in marked contrast with the surrounding pale tissue of the ovary. On the other hand, it may be difficult to recognize the stages of involution in the metamorphosis of the corpora lutea. The reason for this is that, owing to the gradual reduction and disappearance of the follicular glandular tissue, the yellow body may scarcely project beyond the surface of the ovary. If, in addition to this the tissue of the yellow body has changed to yellow or yellowish white, its detection may become very difficult or even impossible. At a certain stage of its involution the tissue of the corpus luteum has a deep brown colour, and it is seen on the surface of the ovary surrounded by a pigmented zone. At the post-mortem examination therefore it is possible to form an idea of the function of the organ by examining externally the process of differentiation in the ovary.

(a) 2. *Rupture of the follicle and development of the corpus luteum.*

Before rupturing, the mature follicle projects beyond the surface of the ovary in the shape of a thin walled protuberance. On magnification small capillaries are seen in the wall of the vesicle.

When the follicle has ruptured, a red circular wall is formed along the ruptured margin of the vesicle. This wall increases in thickness and so the opening becomes smaller and smaller. Soon the thickened wall takes on the shape of a reddish papilla, which forms the distal part of a new corpus luteum. The corpus luteum continues its growth along the wall of the ruptured follicle and now resembles a plug. In this shape it reaches its full development and then occupies a considerable portion of the ovary.

(a) 3. *Involution of the corpus luteum.*

After reaching its full development the corpus luteum starts on its regressive metamorphosis, during which the tissue is reduced and shows characteristic changes of colour. On the surface of the ovary a reduction in size of the protruding plug can be observed, and in a section through the ovary the area occupied by the yellow body can be seen to have decreased in size.

(a) 4. *Fate of the reduced corpus luteum.*

At the time when the processes described above start afresh and a new follicle ruptures, the old corpus luteum, which has passed through its evolutionary and involutionary period, has become an insignificant pale yellow mass of tissue. The reduction continues during the repetition of the cycle until nothing but a small nodule of tissue with a typical brown colour remains. This remnant persists in the ovary and may be seen on the surface of the ovary as a brown speck, which marks a previous ovulation.

(b) *Periodicity of the ovarian changes in sheep.*

(b) 1. *General.*

In regard to the periodicity of the ovarian changes in sheep, our latest investigations and observations have shown that the different breeds in the different countries behave very differently.

(b) 2. *Special.*

(b) 2^1. *Observations in sheep in Central Europe (Swiss, Steirer, and Bergamask sheep).*

1^1. *Periodicity of the ovarian changes.*

In domestic sheep in Central Europe the rupture of the follicle (ovulation) takes place at regular intervals. Two successive ovulations are separated by a space of about three weeks. It will be seen therefore that this short cycle of 21 days is exactly the same as that of the cow, in which case also a follicle ruptures every 21st day.

During this period of 21 days, which is marked at either end by an ovulation, the ruptured follicle is transformed into a corpus luteum in the same way as in the cow; it gradually reaches the stage of full development and is then reduced. Commencing with the first ovulation we can observe a certain stage of reduction on the 21st day when the second mature follicle will rupture and pour its contents into the oviduct.

The reduction of the first corpus luteum is by no means complete on the 21st day when the second ovulation occurs. It then enters on its second stage of reduction and is still visible as a dark brown or almost black pigmented spot in the ovary, long after the period of 21 days.

In the European sheep mentioned above, ovulation (rupture of the follicle and liberation of the egg cell) takes place throughout the year. We may observe it at all seasons. The process is not confined to one portion of the year.

1^2. *Periodicity of the oestrum.*

When we considered our observations on the ovaries of the above-mentioned sheep from an anatomical and morphological point of view, the question arose whether from indirect observations of a more biological nature there is anything to explain the behaviour of the ovaries in non-pregnant sheep. Regarding this we have only a few scattered and conflicting references on the occurrence of oestrum in the case of sheep. Nevertheless we found it important to become acquainted with these references as the investigation of ovarial phenomena could offer us useful information in so far as experience with cattle and pigs has taught us that ovulation and oestrum usually occur at the same time. Thus the time of oestrum may serve with certain reservations as a guide to the changes which take place in the ovary during that period. When we compared the views of scientific workers, in 1923, in the occurrence of oestrum in non-pregnant sheep, it was observed that these views varied greatly (compare attached table). Some observers believe that the oestral phenomena have a definite seasonal incidence; that a period of the year exists in which oestral phenomena are not evident, to be followed by a season in

which ovarial activity takes place. These observations were made on foreign breeds of sheep. Other observers whose observations were mostly confined to the breeds of sheep kept in Germany, Italy and Switzerland held different views. According to them oestral phenomena occur regularly and continuously throughout the year without a seasonal intermission, the oestral periods following on a regular interovulation period of three weeks. Observations on the ovaries of Swiss, Steirer and Bergamasker sheep have shown that for the majority of sheep in Central Europe a short three-weekly continuous oestral cycle must be accepted.

Literary References on the Occurrence of the Oestrum in Different Breeds of Sheep.

A.

Oestrum with a Definite Seasonal Incidence.

Breed of Sheep.	Oestrum.	Literary Information.
Indian sheep, e.g. *Ovis vignei* in Punjab	One oestral season yearly (September)	Blandford, 1891.
Ovis poli..... *Ovis burrhel.* *Ovis argali*	One oestral season.....	Prjewalsky, 1876.
Ovis musimon..... *Ovis vignei.* *Ovis ammon.* *Ovis canadensis* (All wild breeds.)	Oestrum yearly, during one oestral period	Lydekker, 1898.
Ovis canadensis.....	First half of November, oestrum	Lydekker, 1898.
Barbary wild sheep—*Ovis tragelaphus* (in Zoological Society Gardens, Regent Park, London	One oestral season.....	Heape, 1900.
Half breeds between Cheviots (Leicesters) Scotch Blackfaced (Scotch Highland sheep)	October or November, Oestrum	F. H. A. Marshall, 1901.
Scotch Blackfaced, half-breeds between Cheviots and Border Leicesters; Cheviots and Blackfaced Leicesters and Blackfaced	October or November Oestrum. Oestrum then twice in succession (dioestral), occasionally a third time (with Blackfaced kept in Lowlands) and oestral season extends over 15 to 18 days	F. H. A. Marshall, 1904.
Scotch Highland Sheep kept in the Lowlands	One oestral season with oestra which repeat themselves several times	
Dorsets.....	Two oestra yearly.....	F. H. A. Marshall, 1904.
Dorset Horn sheep on Isle of Wight	Oestral season from autumn to spring, regular oestra with non-pregnant animals	
Hampshire Down sheep...	Sometimes two oestral seasons yearly	F. H. A. Marshall, 1904.
Limestone breed of some districts of Westmoreland and Derbyshire	One oestral season in September	F. H. A. Marshall, 1904.

B.

Oestrum extends over the whole Year.

Breed of Sheep.	Oestrum.	Literary Information.
Australian Merinos in New South Wales	Oestra throughout the whole year	Walace, 1891.
1.....	Oestra during whole year. Periodically only under favourable nutritional conditions. Repetition of oestra in intervals of 1 to 3 weeks space.	V. Telschow, 1911.
Certain Merino sheep.....	Oestra periodically during whole year	F. H. A. Marshall.
1.....	Oestra throughout the year at intervals of 3 (possibly 2) weeks. Because of habitual use of autumn oestrum latter is more marked	R. Schmaltz, 1921.
1.....	Oestra spread over whole year (originally limited to one resp. two "Dioestral" seasonal periods)	O. Zietzschmann, 1923.

1^3. *Addendum*: *The Morphology of the ovaries in cases of twin-pregnancy.*

Since cases of twin-pregnancy are of common occurrence in sheep, we frequently find two follicles maturing at the same time in an ovary or in the ovaries. These follicles rupture at the same time, or within a few hours or one day of each other. When two follicles mature at the same time, they may be situated in one and the same ovary, or one each in the two ovaries. Their situation is of no consequence to the process which follows. In cases where both ovaries are involved the evolution and involution of the corpora lutea also keep pace with each other, so that the one corpus luteum always shows the same developmental stage as the other. We see here, as in other cases of double or multiple development of corpora lutea (for instance in the ovaries of pigs), an example of harmonious development of an organ, which finds its expression in the convergent function of the two components of a paired organ. The periodicity of the left ovary corresponds with the periodicity of the right ovary. The changes on the right and left side are co-ordinated both in a morphological and functional sense.

It may be added here that the same applies to the ovaries of the cow, but, of course, in the case of cattle maturation of two follicles and development of two corpora lutea, i.e. cases of twin-pregnancy, are rare.

(b) 2^2. *Observations on two South African breeds of sheep (Persian and Merino).*

2. (a) *Persian woolled sheep.*

These observations include 35 sheep. The investigations were started with 20 sheep to which 15 were added after about a month. Most of the animals had changed their first and second incisors, but

all had changed their first incisors. Apart from a few cases of pregnancy, all the animals were mature, non-pregnant and perfectly healthy.

In order to study the oestrum in these ewes, 4 rams, which were afterwards increased to 5 and then to 10, were used. Every morning the rams were mixed with the ewes for a period of about half an hour, in a stone-walled kraal, and observed from a distance. Cloth " aprons " were tied round the rams so as to prevent copulation. If no symptoms of heat were noticeable in the ewes or the rams, the latter were frequently admitted to the former for a second time but without their aprons, in order to control the first observations.

The investigations began on the 25th of April and were continued until the beginning of January of the following year. In bad weather the observations were carried out in a covered corrugated iron shed, which opened on one side into a stone kraal.

2. (a)[1]. *Periodicity of the oestrum.*

In the Persian woolled sheep it was found that oestrum appeared seasonally. At the beginning of the investigations, i.e. at the end of April, oestrum showed itself regularly and very distinctly. Also during May oestrum periods were observed in regular sequence. All the rams, without exception, indicated this by the impetuous way they chased the females and by their sexual desire. Some of the ewes still showed oestrum in the first half of June, as was distinctly indicated by the rams. During the latter half of June only very few ewes showed signs of heat. And then followed a complete cessation of oestrum, which lasted throughout the months of July, August, September, October, November and December. Unfortunately we had to leave the farm at the beginning of January so that we were unable to obtain corresponding data for the months of January, February and March.

Towards the end of April, during May and in the first half of June, oestrum appeared in the individual animals with extreme regularity. The symptoms of heat during every oestral period are apparent for two days. Throughout these two days the ewe is being chased by the rams, which try to " cover " her. On the third day these symptoms have disappeared; the rams take no further notice of the ewe; the oestrum has passed.

These oestral periods of two days' duration appear regularly and with definite intervals. Between the second day of the first oestrum and the first day of the following there is usually an interval of 17 days.

2. (a)[2]. *Periodicity of ovarian changes.*

In order to obtain a picture of the internal changes in the ovaries which accompany the external sexual manifestations of the animals, post-mortem examinations were made from time to time throughout the course of the investigations. As a result of these examinations it was found that ovulation actually takes place during these regularly recurring oestral periods (end of April, May, first half of June and occasionally also the second half of June), in some cases on the first day, but in most cases on the second day of oestrum. In a few cases ruptured follicles were also observed in the ovary at Christmas time, however, none of the rams had detected the oestrum. These ovulations would, in nature, not have led to pregnancy. Apart

from these latter isolated cases, no ruptured follicle and no fresh corpus luteum could be detected at the post-mortem examinations during the period July to December. As far as reproduction is concerned, the ovary is inactive during this time, since the liberation of ova, which alone is of importance for reproduction remains in abeyance. The maturation of the follicles is very much retarded.

A review of the results obtained during our investigations, which lasted 9 months, seems to justify the conclusion that Persian woolled sheep in South Africa differ from the sheep we examined in Central Europe (Switzerland, Northern Italy) inasmuch as the former show a seasonal oestral and ovulation cycle. The sexual functions which are expressed as oestrum and ovulation are confined to a definite period of the year in South African sheep. The rest of the year may be regarded as a resting period and is not actively concerned in the reproduction of the race.

It would appear that in sheep in the Central European latitude domestication has brought about an extension of the oestral and ovulation season so that it now includes the whole year, whereas the Persian sheep has in a sense retained its wild state in spite of the fact that it has long been used as a domestic animal. The short period of sexual activity may be an adaptation to the conditions necessary for rearing the offspring. At the end of the summer or the beginning of the South African winter oestrum and ovulation appear, according to our observations, in the Persian sheep. The gestation period would therefore end in the spring, when the warm weather was at hand. After the lactation period the lambs would be able to find sufficient nourishment in the open veld where they would now roam with the flock day and night.

The interval between two ovulations is shorter by a few days in South Africa than in Central Europe. This may be connected with the climatic conditions in the hotter country. It is certainly advisable to have the heat and ovulation cycle as short as possible during the active season, so as to have a greater chance of conception taking place.

2. (b) *The Merino sheep.*

In order to supplement our observations on Persian sheep, investigations were also conducted with a number of Merino sheep. Twenty young sexually mature animals were obtained for the purpose. Before the experiment commenced these sheep were kept with others of the same age and breed, and served merely as controls in another experiment. They were then kept separately from the 17th August, 1925, until the middle of January of the following year and were examined daily in respect of sexual manifestations by means of a dozen Merino rams with aprons tied round them.

Another 14 Merino ewes of suitable age were obtained for post-mortem examination during the various stages. These sheep were kept with the other lot and brought in contact with the rams every day; they were brought under observation several times a day. Owing to certain difficulties in obtaining suitable animals, these sheep were only brought into the experiment on the 24th of August. The observations were again continued until the termination of our stay in South Africa, i.e. till the middle of January, 1926.

The total number of Merinos in the experiment was therefore 34, (20 animals for observation and 14 for post-mortem examination).

2. (b)[1] *Periodicity of ovarian changes.*

Our investigations showed that no oestrum appeared between the 17th August (24th August for the second lot) and the end of December. The ewes were completely indifferent towards the rams, and the rams never took the slightest interest in the ewes. Soon after the commencement of the observations we came to the conclusion that both the female and the male animals were in a period of absolute sexual inactivity. We were therefore able, without undue risk, to remove the aprons of the rams and allow them, whilst under observation, to mix with the ewes in a natural way. These rams were known to the farmers as being sexually very active and we had occasion to observe them in that state some months previously during our investigations with Persian sheep. However, in the course of the period mentioned at the beginning of this section, we never saw any symptoms in these animals which could be interpreted as manifestations of heat.

It was only at the beginning of January that a change occurred and a few animals began to show the first characteristic symptoms of oestrum. Unfortunately our investigations were then terminated by our departure from South Africa.

2. (b)[2] *Periodicity of oestrum.*

The several post-mortem examinations made during the period the Merinos were under observation (middle of August, 1925, until the middle of January of the following year) corroborated completely the results obtained from the observations of the living animals. During this period none of the animals, slaughtered at random, showed any ovarian changes which could be taken to indicate a reproductive activity. We never saw a freshly ruptured follicle nor a corpus luteum in its evolutionary or its early involutionary stage, but we did see slowly maturing follicles. Our observations on the differentiation of the follicles enable us to state that during the period August (latter half), September, October, November, December, the only active process in the ovary is a slow maturation of follicles, and that there is no rupture of follicles nor development or reduction of fresh corpora lutea. These latter processes must be confined to the period from January till June (perhaps even July); we were actually able to observe a few isolated cases of ovulation towards the latter half of January. That ovulation does occur during April and May is certain, since parturition was observed during the latter part of September.

We may conclude, therefore, that, in South Africa, the Merino sheep, too, have a seasonal ovarian cycle. The ovaries are active during the first half of the year (the South African late summer and the beginning of winter); during the second half of the year (South African spring and summer) they are inactive; ovulation with the liberation of egg cells does not occur, development and reduction of corpora lutea are not observed, neither do the animals, male or female, show any sign of oestrum.

There is no doubt that in the Merino sheep under our observation the ovarian functions were not continuous. Changes in the ovaries did not take place at short intervals throughout the year. Again ovulation and oestrum are confined to a definite portion of the year. Between two active periods there is a long period of complete inactivity and rest of several months' duration.

In this case, too, the animals seem to have adapted themselves in respect of their ovarian functions to the climatic conditions. Ovulation and the important sexual function take place in the early months of the calendar year; consequently the gestation period falls in the South African winter and parturition occurs in spring or early summer, so that the young are able to reap the benefits offered by nature, during their lactation period and the initial portion of their independent existence.

Comparing now the results obtained in Central Europe with those in South Africa, it may be stated that South African sheep have a seasonal periodicity of oestrum and ovulation, with concentration of the productive functions of the ovary (ovulation) in one particular part of the year; whereas the sheep in Central Europe (Switzerland) have a continuous cycle without insertion of an inactive season. This latter condition must be regarded as result of domestication on the natural functions of the organs with artificial increase or productivity. The former condition represents a conservative behaviour of the organic functions. Although these animals have been under the influence of domestication for a long time, their mode of life still corresponds very much with that in the wild state. They have adapted themselves to their new conditions in such a way that the preservation of the species is best served.

III. *The behaviour of the ovary of goats during normal sexual functions. (Observations in Europe and South Africa.)*

After the description of the ovarian cycle of cattle and sheep the corresponding conditions in *goats*, illustrated in Plate No. III, will be readily understood.

General Morphology and periodicity of the ovarian changes in goats.

1. *Observations on Swiss goats (white goat of the plains, cross between Appenzeller and Saanen goat, ibex-coloured goat).*

Our first studies on the reproductive organs of goats were made with the various Swiss breeds. We examined the sexual organs of goats of the Swiss plains, crosses between Appenzeller and Saanen goats, and also a few ibex-coloured mountain goats.

The female germinal glands are considerably larger than those of sheep. Externally they show, in the same way as the sheep ovaries, the various differentiations very clearly; formation of follicles and corpora lutea.

If we examine a large number of cases at different times of the year we can observe a series of different stages of follicular development, on the surface of the ovaries. As soon as the follicles have reached a certain stage in their development, they protrude beyond the surface of the ovary. The mature follicle has the appearance of a fairly large clear vesicle in the wall of which, before rupturing, a fine net of capillaries is visible. Whenever a follicle has this appearance we know that it is mature and on the point of rupturing.

The progressive stages of development of the corpora lutea can be recognized by their reddish or flesh colour. The distal portion protrudes in the shape of a papilla or plug beyond the surface of the

ovary, and the point where the follicle ruptured and where the corpus luteum was formed can for a long time after ovulation be recognized externally as a crater-shaped depression in the yellow body. If sections are made through corpora lutea at different stages of development, the continuous change of colour of the tissue can be observed throughout the formation of the follicle-gland (compare the coloured sections of the different stages of organogenesis in the diagram, Plate III).

After reaching its full development the corpus luteum starts its reduction. The stages of this regressive metamorphosis can be recognized by the yellow tissue. The further the reduction of the corpus luteum has progressed, the less does it protrude beyond the surface of the ovary. This reduction can also be observed very clearly in sections by the decrease in size of the area occupied by the yellow body.

Shortly before the rupturing of a new follicle the corpus luteum (which originated from a Graafian follicle and started its development at the time of ovulation) has been reduced to a very inconspicuous mass of tissue, which it is often difficult to find in the ovary because of its milky-yellowish colour and its situation in the stroma.

As is the case of the ovaries of cattle and sheep, the changes in one ovary of the goat always take place in harmony with the changes in the other. Thus, if the differentiation of the corpus luteum in one ovary has reached a certain stage, the differentiation of a follicle in the other ovary will be in another definite stage; or, if two corpora lutea develop together it is immaterial whether they are situated in the same ovary or in both ovaries, since their stages of development will always be distinctly defined. The same applies to the development of the follicles.

In regard to the periodicity of the ovarian changes the investigations have yielded the following results.

In the cyclic progression of sexual changes (ovulation, formation, development and reduction of corpora lutea, rupture of follicles) there is no continuity throughout the year. The cycles do not follow each other continuously. Ovulation is confined to a particular season of the year; during the remainder of the year there is no ovulation.

The season of vigorous organic functoning when ovulation takes place, is the latter half of the calendar year. The inactive season during which no follicles rupture and no eggs are liberated, comprises the first half of the year.

Naturally the two seasons merge into each other gradually.

Ovulation was definitely observed during the months of October, November and December. There can be no doubt that ova are liberated during these months. The season may extend into the adjoining months under certain circumstances, for instance the influence of domestication. On the one hand the earlier months may be included in the active season, on the other, the months following those mentioned above.

The important process during the active season is ovulation. Consequently we find in the ovaries during this season ruptured follicles, corpora lutea in the first or later stages of their development and others in the process of reduction.

During the active season ovulation occurs repeatedly and regularly. Examination of the organs has shown that several (2, 3 or more) ovulations appear during the season.

The ovulations recur at regular intervals, namely, every 3 weeks. As in the case of cattle, sheep and, as we shall see, also pigs, a Graafian follicle ruptures every third week and empties its contents, the liquor folliculi with an ovum. Every three weeks a corpus luteum is being formed which reach a definite stage of reduction at the next ovulation and then continues its regressive process during the following inter-ovulation period.

The investigations have proved definitely that the cycle can be repeated several times in one and the same organ. During this season we can observe regularly in older animals a number of corpora lutea, the evolutionary or involutionary stages of which fit into the diagrammatic cycle of their differentiation and correspond to the intervals between various ovulations. The corpora lutea of previous ovulation periods have been reduced just as far as must be expected according to the degree of maturation of the new follicles or the stage development or reduction of the yellow bodies of the later ovulation periods. In every case we have to deal with recent structures.

In the breeds of goats which we examined, the period of ovulations is followed by a season of reduced ovarian activity. Ovulation is entirely suppressed during this time. Whereas the genesis of corpora lutea was repeated at short intervals during the active season (ovulation season), the formation of yellow bodies and the short sexual cycles are absent during the inactive period. During this period of rest the only processes going on in the ovaries are the further reduction of the corpus luteum of the last ovulation and the much retarded maturation of a Graafian follicle. The reduction of this corpus luteum takes place during an interovulation period, just as during the normal cycle in the active period. But whereas a new Graafian follicle matures and ruptures after the usual period of 21 days during the active period no ovulation takes place during the period of retarded corpus luteum reduction. The reduction of the corpus luteum is continued, as in the active season, during a further interovulation period, but at the end of the usual period of 21 days the next ovulation of a mature follicle does not occur, but is delayed and only takes place much later at the end of the inactive season. This ovulation then marks the beginning of another active season.

In the same way the maturation of the Graafian follicle continues right through the inactive season until the beginning of the ovulation period. Whenever the maturation falls in the inactive season its duration is prolonged both relatively and absolutely.

The entire period of reduced ovarian activity, which, as stated above, may occupy months, begins at the conclusion of the regularly recurring short cycles, and ends at the recommencement of regular typical short cycles.

These conclusions were arrived at after a careful investigation of a series of ovaries of goats at different seasons of the year. The examination of organs during that year gave the following results:—

1. Ovaries with a series of corpora lutea in different stages of development (freshly ruptured Graafian follicles, corpora lutea at the beginning of their development, corpora lutea at full development, and corpora lutea at various phases of reduction).
2. Ovaries with yellow bodies all of which were in stages of reduction (no freshly ruptured follicles, no corpora lutea at the beginning or at the height of their development) and with a very slowly maturing Graafian follicle.

From a certain period in the course of the investigations the former organs were to be found, from another period, the latter.

These results enabled us to draw the conclusions described above.

We find in the female Swiss goats which we examined, conditions which may be described as a seasonal periodicity of the reproductive functions. This mode of ovarian functions is probably the rule amongst wild animals, where the productive functions (ovulation, liberation of the egg cell) are confined to a definite portion of the year.

We have already indicated the possibility of attempting, by means of selection and domestication, to extend the period of cyclical ovarian processes, so that in course of time the process would be continuous and ovulation would occur right through the year. It would appear that some breeds of goats already show such secondary conditions in their sexual functions.

At present we wish to emphasize the fact that, in the sexual functions of the goat, a long period of rest alternates with a period of ovarian activity.

2. *Observations on South African goats.*

2. (a) *The Boer goat.*

Having had an opportunity of studying the ovarian changes in goats in Switzerland and Central Europe, we were greatly tempted during our stay in South Africa to extend our observations to the breeds of goats in that country. This we were able to do. Boer goats and Angoras were examined as thoroughly as that portion of our time, which was not occupied with our major investigations, would allow.

The examination again consisted of regular, daily observations of the living animals, which were carried out systematically at various times of the day, and of post-mortem examinations.

The investigation was commenced on the 8th July, 1925, with 20 female Boer goats, of which it was known that the majority had not mixed with rams. We succeeded in obtaining sexually mature, non-pregnant animals.

These 20 animals were kept under observation from 8th July, 1925, till 15th January, 1926. From time to time one of the goats was selected and slaughtered for the purpose of checking the processes going on in the ovaries.

For the study of oestrum and the detection of sexual periods, two old rams and a younger ram were used. These were admitted individually to the female herd. In this way we were able to control results obtained with the first ram, with the second and third. In almost every case the results agreed. If the first ram detected oestrum in a female, the second and the third ram found the same animal independently. If, on the other hand, the first ram found no female in oestrum, the second and third rams could be admitted to the herd without the protective "apron," since no covering was to be feared.

These animals were somewhat shy at the beginning of the investigations which were conducted from an appropriate distance. The assistants, too, remained at a corresponding distance from the animals.

In regard to the appearance of oestrum it was found that a number of goats was actually on heat when the investigation commenced, at the beginning of July. Oestrum appeared in several animals on the same day. The oestrum which usually lasted 2 or 3

days, recurred regularly during July and a part of August. The interval between two periods was 19, 20, or 21 days, counting only the days that were free of oestrum. Thus if the oestral period "A" ended after 2 or 3 days, the day following the last day of the oestrum would be called "the first day of the interval" and the last day before the beginning of the next period "B" would be called "the last day (19th, 20th, or 21st) of the oestrum-free interval." Hence the new oestrum must be expected 20, 21 or 22 days after the last day of the preceding oestrum.

Towards the latter half of August the regularly recurring oestral periods began to cease. After the 26th August no oestrum was observed, not even in animals which previously showed regular periods. At the beginning of this inactive period the rams took some interest in the ewes and tried to find animals on heat in the usual way by nosing the genitals. However, after a while even this interest disappeared and the rams, too, became sexually completely inactive. These rams, which only a week previously had chased the ewes impetuously, now stood amongst the females absolutely calmly. This condition of complete absence of oestrum in the females with loss of sexual activity in the males continued through the months of September, October, November, December, and the first half of January, i.e. until the time that we left South Africa.

In regard to *ovulation* the observation was again made in the Boer goat that the appearance of oestrum coincided with ovulation. At the time when symptoms of oestrum were clearly visible in the female animals, the post-mortem examination showed ruptured follicles, newly formed corpora lutea or follicular glands in the first phase of reduction. Goats killed during July and the beginning of August showed signs of ovulation in the ovaries. Ovulation usually takes place on the second, sometimes on the first, and in exceptional cases, on the third day of oestrum. During the active season ovulations follow each other at the same regular intervals as the oestral periods, whereas during the inactive season, ovulation does not take place. Post-mortems carried out during September, October, November and December failed to reveal any signs of productive activity in the ovaries of Boer goats. The morphological condition of the ovaries clearly indicated their inactivity: although it should be pointed out that the inactivity is relative and not absolute, since new follicles actually undergo maturation at a very slow rate, of course, for the next oestral and ovulation season.

From the above statements we conclude that the Boer goat has a seasonal ovarian cycle. A period of ovarian activity alternates with an inactive period. The former comprises, according to our own observations, the months of July and August. If, however, we take into account the fact that parturition takes place in September, we have to include the months of April, May and June. It is even probable that the season may begin in February. Towards the end of the South African summer and throughout the South African winter ova are liberated in the ovaries of Boer goats. These ovulations are repeated during the active season, at intervals of about 3 weeks. In the spring and summer the ovulations (and consequently the formation and development of corpora lutea) remain in abeyance: it is during this season that the kids are born.

This regulation of the oestral and ovulation periods is again adapted to natural conditions for the preservation of these animals.

Birth takes place at a time when the conditions for the nutrition of the lactating mother are favourable; and similarly the conditions at a later date when the young has become independent are suitable.

The functioning of the sexual organs of the Boer goat follows a type which is familiar to us in wild animals—although it has never been accurately studied. Seasonal reduction and confinement of ovulation and oestrum to a portion of the year, during which the changes of reproduction are used to the full (by means of repeated short ovarian cycles), concentrate births during a season best suited for the development of the young. Instead of continuity in the sequence of cycles, we have interruption, instead of having the ovarian functions (rupture of follicles, ovulation, evolution and involution of corpora lutea) spread over the entire year, we find them concentrated in one season, followed by a period of rest during which no important changes take place in the ovaries.

2. (b) *The Angora goat.*

In order to make our studies on the ovarian changes in South African goats as complete as possible, Sir Arnold Theiler placed 20 Angora goats at our disposal. These were bought in Cape Colony and sent to the Government experimental farm in the Free State. It was stipulated that these ewes should be 1½ to 2 years old, so that they should have just reached sexual maturity, and it was found that they fulfilled these conditions. The agents gave us the assurance that the animals had been kept separately and had not mixed with rams.

The same method of examining the ovarian changes in the living animal was followed as in the case of previous groups. Full-grown sexually mature rams were admitted to the ewes under strict supervision, at certain times of the day, and careful observations made. For this purpose we had two strong, very aggressive Angora goats and a male Boer goat.

In the first series of experiments the rams were covered with an apron and admitted singly one after the other to the ewes. In the second series the males were admitted in the same order but without protection. Thus the ewes were tested at least six times a day by a ram for signs of oestrum; and in this way any results obtained with a ram with an apron could be controlled with the same ram without the apron. The Boer goat ram was bought from a native living on the farm, who knew very well the aggressive nature of the animal in the presence of ewes on heat.

Apart from these daily observations, which were also caried out in bad weather in a covered-in shed, a number of post-mortem examinations were made in the course of the investigations. This unfortunately reduced the number of animals under observation, but, on the other hand, gave us valuable information about the internal condition of the organs. The combined method alone can give us a reliable estimate of the value of our observations, since, as will be shown later, the external behaviour of the animal does not, under all circumstances, give us a true reflection of the changes going on in the internal organs.

For various reasons the investigations could only commence on the 22nd August, 1925. They were continued during the following months and terminated at the end of our stay in South Africa at the

middle of January, 1926. Unfortunately, therefore, the investigations could not be extended over a year, not even over half a year. If, in spite of this, we venture to publish our observations in this preliminary report, it is done because we believe that even the smallest contribution may be of value for subsequent investigators, and also because we are convinced that our results, taken in conjunction with the results obtained with Boer goats, do enable us to draw some valuable conclusions concerning the ovarian functions of these animals (Angora goats).

Throughout the whole period from the end of August, 1925, till the middle of January, 1926, no signs of oestrum were observed in these animals. The female animal remained indifferent towards the males. During oestrum goat ewes usually turn towards the ram and fan or twist their tails. The vulva appears swolen and reddened, and sometimes a secretion flows from the vagina. None of these symptoms could be observed in our ewes during the months September, October, November, and December, neither did the rams show any interest in the female herd. Every day we observed the same picture; complete indifference amongst the animals of both sexes, and total absence of any symptoms which could be regarded as indicating an existing or approaching oestrum.

The appearance of the ovaries at the post-mortems conducted during this period was in complete accord with the daily systematic observations on the living animals.

None of the ovaries examined during September. October, November and December showed freshly ruptured follicles, nor were freshly formed corpora lutea or such in recent stages of reduction, to be observed in the ovaries.

Also in regard to the differentiation of follicles the ovaries displayed a monotonous picture: whichever animal was slaughtered the stage of differentiation at any given time always corresponded with a slowly progressing maturation of the Graafian follicles. Throughout the whole period of sexual inactivity the ovarian functions were confined to the maturation of follicles. Since this period is a long one, it follows that the maturation process must be very slow. As a rule the final stage of maturation is only reached at the end of the season, and the follicle does not rupture earlier. Hence, during this period of rest, developmental processes which may give rise to corpora lutea, remain in abeyance, since the rupture of a follicle is the first condition necessary for the formation of a normal yellow body.

Accordingly ovulation and oestrum must take place at a time other than that during which our observations were carried out, i.e. between January and the end of August. Parturition was observed during the month of October and it would seem probable that ovulation and oestrum occur during the months of April, May, and, perhaps, June. May seems to be the favourite month for this function. Naturally this period is subject to variation within certain limits and the various influences which appear in the different years, may shift it sometimes to this month, sometimes to another.

It is probable that ovulation takes place repeatedly during the active period and that ova are liberated regularly at short intervals. Accordingly, it may be presumed that short periods of heat, probably of two days' duration, follow each other at short intervals.

The ovarian periodicity in the Angora goat is, therefore, as in the Boer goat, seasonal. An active period, at the beginning of the

calendar year, alternates with an inactive period, which certainly embraces the latter half of the year and includes the South African spring and summer.

Another observation should be mentioned here which suppotrs the view that during the South African summer the productivity of both ovaries is completely suppressed and that therefore oestrum does not appear. It may be argued that the animals under our observation had not attained full sexual maturity and that this was the reason why they showed neither oestrum nor ovulation; however, this doubt can be removed. A number of animals gave birth to lambs in October. If now a continuous active season actually did exist, we would expect these ewes to have come on heat towards the end of November or, at the latest, in December or January. However, at the post-mortem examination of these animals we found nothing but slowly maturing follicles (apart from the reduced corpora lutea from the gestation period), but no fresh corpora lutea, or mature follicles. We may conclude, therefore, that the period mentioned was actually an inactive season.

Let us now compare again briefly the results obtained from our systematic investigations of goats. The results obtained in Central Europe agree in so far with those obtained in South Africa as the cyclic changes in the ovaries, the ovulation and the oestral periods are concerned; these are not continuous throughout the year, but are confined to one season. An active season alternates with an inactive or unproductive season, when ovulation and, consequently, the formation of corpora lutea, does not occur.

Of great interest is the observation that, corresponding with the differences in climatological conditions in the two countries at the same time of the calendar year, the ovarian functions take place at different times of the year. In goats in the Swiss midlands, for instance, the active season falls in the second half of the calendar year, whereas in South Africa, it is in the first half of the year. Accordingly births take place at the beginning of the year in Switzerland and towards the end of the year in South Africa. However, in both cases birth occurs at a season which is best suited for the existence of the young; in Central Europe it is during the spring that lambs are born and in South Africa during the European late summer or autumn which corresponds with the South African spring.

IV. *The behaviour of the ovary of pigs during normal sexual functions (observations in Europe and South Africa).*

(a) *General Morphological conditions; morphological anatomical series; ovarian changes in the pig (evolution and involution of the* corpora lutea; *differentiation of the follicles).*

Even a superficial examination of the ovaries of the pig reveals a peculiar morphological condition.

On account of the presence of several Graafian follicles and the simultaneous formation of a number of corpora lutea (corresponding with the multiparity of the animal) the ovary has the appearance of a bunch of grapes.

In order to get acquainted with the changes taking place during the ovarian cycle it is advisable to begin with the examination of a series of ovaries of young, sexually mature, non-pregnant sows. These organs will illustrate the process very well.

Both left and the right ovary (see Diagram IV, Fig. a), show a number of mature follicles (Gr. Fo. mt) whose apices protrude beyond the surface of the ovary.

The follicular wall, which is stretched by the pressure of the liquor folliculi, is covered by a very fine net of capillaries.

In addition to these mature follicles, both ovaries show a few ruptured follicles, in which the point of rupture is still visible.

Apart from these mature, intact and the ruptured follicles, and those which are being transformed into corpora lutea, the ovary in our illustration shows a number of follicular glands, which, as we shall see, have passed their maximal development and have now reached a certain stage in their reduction. These reduced corpora lutea, which appear as compact spherical masses of tissue on the surface of the ovary, are conspicuous by their yellow colour.

Soon the newly ruptured follicles, whose walls grow thicker and which, through ovulation, have been transformed into corpora lutea, take on a berry-like appearance on the ovaries.

The corpora lutea increase in size and circumference. Soon the follicular glands (Co. Lut.) have reached their full development.

As the differentiation proceeds, the tissue alters its colour; the cherry red colour which was present at the beginning of the development changes to a whitish flesh-coloured hue.

After reaching its full development the corpus luteum begins its reduction. Macroscopically, a reduction in size of the follicular gland, a gradual degeneration of the capillaries which supply the gland, and a progressive, change of colour of the follicular tissue which becomes more and more yellowish, are the changes which can be observed.

At the time when the yellow bodies (which originated in as many ruptured follicles) have reached their full development, we see numerous small vesicles in the ovary. These rapidly increase in size at the same rate as the reduction of the yellow bodies proceeds. A number of these follicles reach maturity. Usually as many as will rupture at ovulation.

When the yellow bodies have reached a definite stage in their regressive metamorphosis, the new follicles, which have now reached maturity, rupture. This marks a new ovulation in the ovary. With the rupture of the new follicles, an interovulation period, that period which is bounded by two ovulations, has come to an end.

The reduction of the old corpora lutea, which at the time of the new ovulation had reached a fairly advanced stage, proceeds still further and is accompanied by a further decrease in size of the corpora lutea. Thus the regressive metamorphosis of the corpora lutea in the pig, too, extends beyond an interovulation period, and is continued during the next interovulation period.

At the end of this second period the reduction has proceeded so far, that the corpora lutea are usually no longer visible externally. Yet, as shown above, we are able to follow macroscopically the development and reduction of a corpus luteum from a ruptured follicle through two interovulation periods.

(b) *Periodicity of the ovarian changes in pigs.*

After discussing the morphological conditions of the organs, we have to consider the important question, how long the intervals are, after which the cyclical processes in the ovary are repeated.

(b) 1. *Observations on pigs from Switzerland and Northern Italy.*

1[1]. *Conditions in non-pregnant, sexually mature pigs.*

In order to elucidate the chronological sequence of the ovarian changes just described, we, first of all, studied the relation between oestrum and the above processes in the ovaries of pigs. For this purpose it was necessary either to observe the animals carefully every day, or to have an accurate history of the animals from the breeder. On account of the prevalence of Foot and Mouth disease in Switzerland, it was not possible for us at that time to keep pigs for scientific purposes. Neither were we able to obtain many reliable accounts about the appearance and sequence of oestrum in pigs. Nevertheless a fair number of trustworthy breeders and estate managers expressed the conviction, based on their experience, that the pig has a three-weekly cycle. Our personal experience taught us that the mature follicles in the ovary of the pig actually rupture at the time of oestrum, and we were able to deduce that an interovulation period in the domestic Swiss pig (Swiss country pig) comprised 21 days.

Further investigation showed that the ovarian cycle is continued throughout the year; however, the number of regular cycles is smaller than in the cow or ewe. Post-mortem examinations have shown that after a certain number of interovulation periods, there is no longer a regular cycle.

1[2]. *Conditions in pregnant sexually mature pigs.*

The findings in cases of pregnancy have been particularly interesting.

The number of corpora lutea and the number of eggs which presumably have been liberated, does not agree with the number of foetuses reaching maturity. The latter number is usually the smaller of the two. Whereas the average total number of follicles which rupture at the time of ovulation in the left and right ovary, is 16, only about half that number (on an average 8) embryos develop. Actually about double the number of follicles rupture during oestrum, compared with the number of young born. It is safe to assume that twice as many eggs are expressed from the ovaries as embryos develop in the uterus. We may conclude that only a portion, in many cases half, in some only a small fraction of the relatively large number of ova which reach the uterus at ovulation, are fertilized. It may be pointed out that there is a surplus production of sexual cells not only on the part of the male, but that also the gonads of the female show a tendency to produce an excess of germ cells.

(b) 2. *Observations on South African pigs.*

2[1]. *Conditions in non-pregnant sexually mature pigs.*

Our extensive investigations with donkeys and horses occupied so much of our time that, unfortunately, we were unable to devote much attention, during our stay of one year in South Africa, to the conditions in the smaller mammals. Nevertheless we kept a number of animals under daily observation and carried out post-mortem examinations from time to time.

Amongst others we observed the South African country pig, a small type of pig, undoubtedly a cross between various breeds.

These pigs were kept in two enclosures with sufficient shade and every day two suitable boars were admitted for half an hour. To prevent impregnation "aprons" were tied round the boars before they were admitted.

Although we were not able to observe the pigs in South Africa for a whole year, yet we are of opinion that the results we obtained during that relatively short period enable us to assert with a fair degree of certainty that the South African pig has a continuous oestrum and ovulation, in the same way as in the European pig.

Oestrum and ovulation coincide in the South African pig, too. The sows come on heat fairly regularly every 19th day and oestrum lasts for two days. During oestrum the sows are chased by the boars, but this may also happen at a time when there is no sign of oestrum in the females. However, when the sows are not on heat they resent the attention of the boar and try to escape from him, whereas they remain standing during oestrum and allow the boar to mount them. During this act the boar shows characteristic movements of the lower jaw and foamy saliva may flow from his mouth. Whenever there is a change in this behaviour, we may know that the oestrum is coming to an end and a new interovulation period is beginning.

Ovulation may occur in either of the two days of heat. As a rule the follicle ruptures on the second day. Our observations extend over the months of August, September, October, November and December, that is during the South African spring and summer. It is during this period that in sheep and goats oestrum and ovulation began to cease or had ceased.

V. *The behaviour of the ovary of equines during normal sexual functions.*

(*Observations on South African donkeys and comparison with South African horses.*)

The reproductive organs of some of our domestic animals have repeatedly been the subject of investigation during the past years, but the *ovaries of the equines* have always been neglected. This was regrettable as the sexual organs of mares seemed to present conditions of particular importance.

It used to be stated that the ovary of the horse was unique amongst mammalian ovaries. It was supposed to differ from the ovaries of other mammals both morphologically and functionally. The ovary of the horse, so we were told, is characterised by the formation of a so-called ovulation groove, a depression which enables the follicles to emit their contents at a definitely fixed point on the ovary. For this reason the ovary of the horse was supposed to occupy its unique position, since none of the ovaries of the other mammals thus far examined, shows a single, morphologically defined depôt for the temporary collection of the ova as they escape from the ruptured follicles; on the contrary, it has always been found that the mature follicles may rupture at any spot on the ovary and that any spot may serve as a basis for the development, maturation and rupture of a follicle.

In other respects, too, the ovary of the horse presented unsolved problems. As such may be mentioned the sexual cycle and especially the changes in the ovary, the regulation of the reproductive functions, and the appearance and course of oestrum. The question was unsolved

whether the horse behaved in the same way as cattle, sheep (in Europe) and pigs, where the organs undergo cyclical changes at short intervals and the functions are repeated with great regularity; or whether the horse conformed to the seasonal type, where a period of ovarian activity alternates with an inactive and unproductive period.

On account of our ignorance on these points and the absence of systematic observations, it was uncertain at what time of the year ovulations took place and whether these were distributed over the whole year or not. Since in high grade studs it is advisable to tax the sires unduly, service should be arranged according to the functions of the ovary, and hence the solution of the problem formulated above had undoubtedly a great value for the breeder.

Our grateful thanks are due to the Director of Veterinary Education and Research for giving us an opportunity during our one year's stay on the Government farm Bestersput in the Free State, to tackle these problems and attempt their solution by means of observations and investigation.

(a) *Results of investigations with donkeys.*

The following description applies to donkeys whose reproductive organs we examined carefully in the first instance. Later on we also had the opportunity of controlling our results on horses and found on the whole, very similar conditions.

1. *Material.*

More than 260 donkey mares were placed at our disposal for observation, investigation and post-mortem examination.

Apart from the ovarian cycle it was desired to study the development of the female sexual organs, and the animals were specially selected for this purpose.

These animals comprised three main groups.

The *first group* consisted of immature donkey mares which had never shown manifestations of sexual functions but were just below the age of sexual maturity. It was by no means easy to collect these animals, which were to serve for the solution of our main problem. The usual method of keeping animals in South Africa, where the female animals run with the males day and night on the veld, and coitus is seldom observed, made it appear probable that one animal or another might have been covered previously—a suspicion which, unfortunately, proved to be only too well founded in several instances.

The *second group* included animals in more or less advanced stages of pregnancy. These animals were needed to supply the embryological material necessary for the study of the development of the ovary in the intrauterine stages, and also to determine how mares behave during pregnancy in regard to reproductive organs and sexual functions.

The *third group* was intended to supplement the material supplied by the second group. Mares immediately before foaling and mares with foals at foot were included in this group. These animals enabled us to study the condition of the sexual organs at the end of pregnancy and also supplied foetal ovaries immediately prior to and after birth.

2. *Method of investigation.*

All the animals in the three groups were observed daily. At a definite hour they were brought in larger or smaller groups into a fenced-in camp where 14 (and later on 13) donkey stallions were kept. For the rest of the day and night the sexes were kept strictly separate. A full account of the method of observation may be left for a later, more complete, publication. In this brief article we need merely state that special care was taken to register everything that was observed. Numbers were branded distinctly on all the animals, and a separate register was kept for each animal. In addition, comprehensive tables were kept for each group, on which the observations were entered.

These observations on donkeys were continued for nearly a full year. During that period there were only a very few days when the weather was too bad and no observations could be taken.

For the purpose of determining the relation between oestrum and ovarian changes, post-mortems were conducted at various intervals. In this way we were able to examine the ovaries absolutely fresh under the exact conditions and at the exact moment that was desired.

3. *Beginning of sexual maturity.*

Some of the results of our investigation may now be detailed.

We have found that donkey mares in South Africa may become sexually mature at one year of age, and that one year old animals in many cases, possess functioning, ovulating sex glands. However, since, at that age, the female sexual apparatus, especially the uterus and the external genitals, have not completed their development, the chances for a successful conception are not very great. Frequently the vulva is so narrow that the penis cannot enter the vagina and in this way nature prevents a coitus in these very young animals.

4. *Observations on one year old donkeys.*

4[1]. *Condition of the ovaries.*

The ovaries of one year old animals are fully capable of maturing follicles and allowing them to rupture. The ruptured follicle is gradually transformed into a corpus luteum which reaches its full development and is then reduced. Generally the ovaries of these young animals are smaller than the reproductive organs of older mares, so that the various stages of differentiation (follicles, corpora lutea) also have correspondingly smaller dimensions. Future histological examinations will have to eludicate the process involved in the maturation of the ovum.

4[2]. *External changes.*

Hand in hand with the ovarian changes, certain external symptoms and changes may be observed. In this respect the animals show considerable individual variation.

It is important to note that animals at this early age show symptoms of oestrum remarkably frequently. These symptoms are very pronounced, although the corresponding changes in the ovaries are macroscopically not very distinct. In such cases external oestrum is not always accompanied by an ovulation. Oestrum may appear in one year old donkeys without the rupture of a follicle and the liberation of an ovum. The same observation may also not infrequently

be made, as we shall see, in older animals. These results, as will be shown again later, make it necesary to distinguish two types of oestrum: oestrum without ovulation ("empty" or "incomplete" oestrum) and oestrum with accompanying ovulation ("full" or "complete" oestrum).

The duration of the incomplete oestrum may vary from case to case and from one individual to another. Frequently the incomplete oestrum only lasts one or two days, whereas the true or complete oestrum usually extends over several successive days.

5. *Observations on 2-2½ years old and older donkeys.*

In animals 2-2½ years old the sexual organs have reached their full development and function normally.

5¹. *Morphology of the ovaries.*

The ovaries of donkeys are relatively small compared with those of horses and show a variety of shapes according to the stages of differentiation of the maturing follicles and other structures. Usually they are tuberous or pear-shaped and frequently the surface of the organs show a number of follicles whose apices protrude beyond the surface of the ovaries.

5². *Maturation of the follicles.*

In regard to the maturation of follicles the left ovary may behave differently from the right. A single follicle may be formed and it may reach such dimensions during the process of its maturation that almost the whole ovary appears to be involved in its differentiation. It may also happen that a larger number of folicles mature at the same times that these are situated either in the left or the right or in both ovaries.

Usually only one follicle ruptures; however, at times, but not frequently, it may be observed that two follicles rupture at the same ovulation period.

The interesting observation was made that the follicles are arranged in rows in the ovaries. This can be seen very distinctly in some cases and stands in relation to the fact that there is a particularly active development of follicles at the poles of the ovary. It is specially at the cranial pole where the formation of follicles takes place so that new follicles are continually being rowed on to the old ones. In many cases, it is true, the serial arrangement of follicles cannot be seen later on.

In the ovary of the donkey the fully mature Graafian vesicle shortly before rupturing, has a very considerable size (the same is also the case in the horse). Before rupturing the follicle may have reached so large a volume that it alone is seen in the ovary and the other components of the organ are completely pushed aside or have vanished. The ripe follicle does not always project beyond the free surface of the ovary. Very often, especially before reaching full maturity, it merely touches the free surface. The wall of the follicle is particularly tender and thin at the place where the wall and the covering membrane of the ovary touch. This accounts for the protrusion of the distal parts of the follicle under the internal pressure immediately before rupturing. Generally the superficial follicular wall shows a beautiful network of blood vessels at the time of rupturing.

It is a fact worthy of note that in relatively young animals mature follicles may appear at different points on the ovary and that the rupture of follicles is by no means confined to one special spot, the so-called " ovulation groove."

The results of our investigations with young sexually mature donkeys permit us to say that the ripe follicles do not eject their contents into a groove, but simply rupture on the outside in the same way as the mature follicles of cattle, sheep, goats and pigs. A depôt or central place for the emission of eggs from the follicles does not exist. When the vesicle ruptures its contents are not emptied into a preformed groove but straight on to the free surface of the ovary. Hence the ovaries of donkeys and, apparently, of the equines in general (horses show the same conditions at first), do not, as was believed until now, occupy a unique position among the mammals in regard to the morphological conditions on the surface of the ovary.

Donkeys, undoubtedly also horses and probably the other equines as well, behave in respect of the rupturing and emptying of the follicles, like most mammals: their follicles rupture directly on the free surface of the ovary.

In older donkey mares (and more noticeably even in older horse mares) it can often be observed that the two poles of the ovary show a more intensive growth (owing to the differentiation of tissue) than the central portion. Consequently the polar ends protrude beyond the middle portions and the ovary is bent in the middle. Later on ovulations (rupture of follicles) are only possible in the region of this bend, where the superficial tissue contains little tough connective tissue. However, it should not be forgotten that this depression is simply the result of local growth of ovarian tissue starting at the poles, and that originally follicles could mature and rupture at any part of the ovary. The term " ovulation groove " should therefore *not* be interpreted in the sense that a special groove is formed in the course of the organogenesis of the ovary of equines, for the purpose of collecting temporarily the contents of all follicles which rupture. The " ovulation groove " of the ovary of equines is a purely morphological conception; it is a structure which is formed secondarily by deforming processes in the ovary and does not exist in the young animal. In donkeys (and also in horses at first) an extensive surface is available for the maturation and rupture of follicles. It is due to secondary processes that this area is reduced and that (particularly in horses) only a small surface remains in the ovary for the rupture of follicles.

5^3. *Evolution and Involution of the corpora lutea.*

As soon as the follicle has ruptured an intensely red zone is formed round the place of rupture: this is caused by the flow of blood from the capillaries which are torn with the rupturing of the follicular wall. The periphery of the burst follicle is soon surrounded by a wall of red tissue due to the proliferation of the tissue. Gradually the opening of the ruptured follicle is closed by a further growth of this wall.

After the rupture of the vesicle and the closure of the ovulation-opening, a papilla, which at first is blood red, is formed on the surface of the ovary in the place of the point of rupture. This papilla remains visible for weeks and only disappears when the shrinking corpus

luteum, whose distal end is represented by the papilla, withdraws itself more and more from the surface and becomes deeply embedded in the tissue.

If a section is made through a freshly ruptured follicle, one finds the original follicular wall of the relatively enormous vesicle thickened and inside the Graafian follicle coagulated blood which afterwards is transformed into a gelatinous mass.

This coagulum fills the entire spacious cavity of the single Graafian vesicle and is condensed and reduced through organisation with connective tissue, at the same rate as the proliferation of follicular wall cells (corpora lutea cells) proceeds. The remains of this blood coagulum may be seen in the centre of the corpus luteum long after the rupture of the follicle, when the proliferating tissue has nearly obliterated the spacious cavity of the follicle, and the follicular wall tissue which now represents the yellow body, has lost its red colour and has become yellow.

In a future publication we hope to show how the corpus luteum develops out of the ruptured follicle and how the regressive processes transform the corpus luteum. At present we have to content ourselves with the diagram (Plate VI), which shows the corpus luteum from the moment a follicle ruptures right through all the stages of transformation. We are able to follow here the fate of the corpus luteum of the first interovulation period until it has become a small, inconspicuous, brownish red mass of tissue which has lost its contact with the surface of the ovary and can only be found in a section through the stroma of the ovary.

It is worthy of note that the tissue of the original corpus luteum, after continuous reduction, is withdrawn from the surface of the ovary, with which it loses its connection. In consequence of this we are not able to tell (as we can in the case of cattle where the reduced corpora lutea are permanently recognisable on the surface of the ovary as distinctly pigmented specks), by a superficial inspection of the surface of the ovary, whether the gland has passed through many ovulations or not.

5[4]. *Periodicity of the ovarian changes.*

It is of the greatest interest to enquire about the chronological arrangement of these changes which, in principle, are identical with those we have studied in the ovaries of cattle, sheep, goats and pigs.

In regard to *ovulations* it can be stated that the rupture of follicles and the liberation of mature ova from Graafian follicles, take place during one half of the year only, no such processes occurring during the other half of the year. According to our observations ovulations take place during the months of October (second half), November, December, January, February, March and April (first half). During the months of May, June, July, and August and September ovulations are entirely absent. In the course of a year therefore we can distinguish a period of activity and productivity of the ovarian functions, from a period of inactivity and unproductivity and cessation of functions. Ovulations are confined to a season of 6 or 7 months.

The ovarian cycle is seasonal.

During the active season the donkey mares do not ovulate frequently. The series of ovulations is limited.

Young animals which enter the sexually mature age at the beginning of the season, whose ovaries have not functioned yet, and which, according to our experience, start their ovarian function relatively late in their first season usually ovulate only once during that season.

Older animals, whose organs have been in function during the previous season, generally ovulate once or twice (sometimes three times) during the new active period.

The time for the appearance of the one or two (or three) seasonal ovulations is not definitely fixed. The ovulations may occur right at the beginning of the active season, or towards the end or in the middle of it. Our investigations have revealed the interesting fact that the animals of one group often ovulate collectively; the ovaries of a number of animals may at the same time show ruptured follicles which must have burst within a short period.

If donkey mares ovulate twice (thrice) during the season, the second (third) ovulation follows the first (second) after a considerable pause. The interval between the first and second ovulation is not constant but always comprises several weeks or even months. It is certain that the second ovulation does not follow on the first after a short interval. It is possible that a thorough study of the notes and post-mortem reports bearing on this subject may enable us to draw more accurate conclusions about the duration of the interval; in a future publication this subject will be discussed again.

In case of a single ovulation (such as is usually observed in one year old animals) the rest of the ovulation season is taken up with the transformation of the ruptured follicle into a yellow body and with the processes of reduction of the first corpus luteum (see diagram).

The regressive processes in the tissue of the corpus luteum do not end at the close of the active season, but are continued, at a slower rate, during the following inactive season.

In cases of two ovulations the processes which took place in the first follicle (transformation of the ruptured follicle into a corpus luteum and reduction of the latter to a certain stage) are repeated after an interval; the two corpora lutea of the two interovulation periods are then to be seen side by side in the same ovary or, one each, in the two ovaries.

The inactive season, as indicated above, is occupied with the further reduction of one (or more) yellow bodies. The involutionary processes during the second phase of reduction take a very slow course and occupy several months.

From the above description it is apparent that the whole process of transformation from the ruptured follicle to the yellow body and its reduction, takes a very long time in South African donkeys (and in South African equines—horses—altogether) when compared with other animals. A rapid development and reduction of the corpus luteum, such as is found in a concentrated ovulation cycle with intervals of three weeks only (for instance in cattle where the formation of the yellow body and the first stage of reduction are complete in three weeks) does not take place here.

A possible explanation for this state of affairs may be sought in the following consideration: the enormous changes which the equine ovary undergoes during the maturation of the follicle and again

during the transformation of the ruptured follicle into a corpus luteum, would soon exhaust the productive power of the organ, if they were to be repeated at short intervals. It is only natural therefore that the opportunities for the development of follicles and corpora lutea should be limited.

The ovary of donkeys does not liberate its egg-cells in rapid succession. The emission of ova is seasonal and does not occur frequently during the season (only once, twice or three times). The ova are liberated at comparatively long intervals during the active season. Ovulation is confined to a certain defined time of the year and occurs rather irregularly during this time. South African donkeys (and horses) therefore conform to a different ovarian cycle than, for instance, cattle in which the rapid sequence of ovulations and other periodic processes may be regarded as the result of advanced domestication.

The inactive season gives an opportunity to the yellow body or bodies which was (were) formed during the active season to undergo further reduction. Figures g^1, h^1, i^1, k^1, l^1, in our diagram (Plate VI), illustrate the different phases during the period of reduction. The mass of tissue gradually shrinks down to a small residue owing to the continuous involutionary changes; whilst, at the same time, the colour of the tissue changes from a bright yellow to a dark brown. During reduction in the inactive period the processes take a very slow course. The period, which corresponds with the South African winter, is used by the ovary for the development and maturation of one or more follicles, which are destined to rupture and be transformed in the usual way into corpora lutea during the following active and productive season.

To sum up we may say that ovulation in South African donkeys is not subject to a strictly chronological cycle, but that, nevertheless, a certain system is followed insomuch as an ovulation season of several months' duration, alternates with an inactive season during which ovulation ceases altogether.

The actual and potential energy which is expended in the case of European cattle, sheep and pigs, during the course of the year, in the form of short ovarian cycles, is also, to a great extent, expended in the ovary of donkeys during the one half of the year and is concentrated in a process which includes only a few cycles.

After this brief discussion of the internal processes in the genital apparatus, especially in the ovaries, we must direct attention to the external manifestations of the animals.

5^5. *Observations on the appearance of oestrum.*

Our daily regular observation of the living animals gave us an insight into their sexual life and elucidated the relation between oestrum and ovulation.

5^{5a} *The symptoms of oestrum.*

In donkeys oestrum can very easily be diagnosed as it is characterised by a number of well marked symptoms, of which, however, the one or the other may be masked or altogether absent. When donkey mares on heat are chased by a stallion they will stand still, after their initial flight; the head is lowered the hind legs are placed apart; and they carry out characteristic movements with the lower jaw as if they were cheming. When the stallion approaches, the

swollen labia majora are opened and closed alternately. The animals micturate and at the same time frequently squirt out a slimy or bloodstained mucous discharge from the vagina.

5[5b]. *Seasonal appearance of oestrum.*

Oestrum does not appear at any odd time of the year. Here again we have to distinguish two seasons of the year, during one of which oestrum periods occur, whereas they are absent from the other. We can refer to the one as the oestral season, to the other as the " inactive " or " quiet " or " dead " season. The oestral season includes the months of October, November, December, January, February, March and April, and occurs during the South African summer. The inactive or quiet season embraces the months of May, June, July, August and September and falls in the South African winter.

The ovulation period therefore coincides with the oestral season, and the ovulation-free period of the year with the " inactive " season. No doubt these seasons may vary from year to year. The influence of climate, telluric factors, and nutritional conditions may be responsible for an extension or reduction of either of the seasons by weeks or months. However, it is important that, in regard to oestrum, the year is divided into two seasons which appear constantly, even though they are not absolutely fixed according to days or even months. The one season is characterised by the appearance of oestrum, the other by its entire absence.

During the oestral season oestrum does not appear very frequently in the individual animals, but usually they show more than one heat period during the season. Oestrum does not appear at regular intervals, but may occur at any time during the season. We frequently observe that a number of animals show symptoms of oestrum at the same time.

5[5c]. *Duration of oestrum.*

The duration of a heat period may vary. The symptoms may last for one day only, or for a number of consecutive days. It is not uncommon for animals to show the symptoms for one day, after which several days without any symptoms may follow, and then to manifest oestrum again for a number of days.

5[5d]. *Relation between oestrum and ovulation.*

If now we consider the relation between oestrum and ovulation, we should point out particularly that two types of oestrum should be distinguished in the donkey (and also in the horse): oestrum without ovulation and liberation of an egg-cell, and oestrum accompanied by ovulation and the emission of an ovum by the ovary.

There can be no doubt about this observation. In our main publication we shall cite numerous examples to prove the correctness of our assertion. These examples appeared with all typical manifestations of oestrum and yet no ovulation took place, others again appeared where no oestrum occurred and where the post-mortem examination showed a ruptured follicle or a fresh corpus luteum.

Ovulation may therefore be linked to the symptoms of oestrum or not. Oestrum with ovulation should be regarded as a complete oestrum including both the external symptoms and visible ovarian changes and

ovarian functions. Oestrum without ovulation is an incomplete oestrum as it includes only the external symptoms but not the ovulation and the ovarian functions.

In the case of an incomplete oestrum the group of externally recognisable symptoms is detached from the anatomical-physiological phenomenon of ovulation. And yet we should bear in mind that even when we are unable to recognise ovulation in the ovaries, there may be (and probably are) processes and changes going on in the ovaries and in other parts of the female sexual apparatus, so that even in cases where the rupture of follicles cannot be observed directly, preparatory processes for such rupture may take place.

Our observations make it seem probable that originally only the external oestrum and the symptoms belonging to it appeared, and the process of ovulation which is essential for reproduction, was secondarily added to the whole group of symptoms. The actual symptoms of heat precede the ovarian changes and seem to prepare the way for them. They announce phenomena and prepare processes which culminate in the act of ovulation.

The symptoms of oestrum also include a physiological process which is of decisive importance for the propagation of the animals. We refer to the secretion of a specific odoriferous substance in the genitals of the female, by means of which the donkey stallions are able to detect the mares on heat. This scent attracts the stallions which are then stimulated sexually and begin to chase the females. Those mares which are in oestrum will stand still, as described above and will allow the males, after a short courtship (nosing and licking the flanks) to cover them.

At the beginning of pregnancy the corpus luteum has a dark, flesh coloured appearance; the colour changes during the course of pregnancy and becomes first reddish brown and then dark brown.

If conception has taken place the spacious cavity of the ruptured follicle is soon filled by a compact mass of tissue, the corpus luteum, which is formed from the remains of the ruptured follicle by the thickening and folding of its wall.

The new corpus luteum of the latest ovulation period, the corpus luteum gravidjtatis, is at its greatest at the beginning of pregnancy. Later, when the follicular wall tissue has filled the cavity of the former Graafian follicle by means of cell proliferation, the corpus luteum is no larger.

During pregnancy reduction processes are continually at work on the compact corpus luteum, which, shortly before parturition has shrunk to a very inconspicuous mass of tissue.

Thus the corpus luteum is subject, throughout pregnancy, to a process of reduction which is nearly complete at the end of gestation.

This result does not agree with the previously generally accepted view that the corpus luteum is not reduced during pregnancy, but remains at its full development until the young is born and normal conditions have been restored. This result of ours will have to be taken into consideration whenever the significance of the corpus luteum is discussed. The fact has been established beyond doubt that in the donkey the yellow body is considerably reduced during pregnancy.

A further interesting finding was this that not only the corpus luteum was involved in the regressive changes, but that the other portions of the ovary are also involved and the organ as a whole

reduced in size. The results of this regressive process are apparent on examining the ovary macroscopically at various times during pregnancy. Shortly before the end of pregnancy the two ovaries usually have the shape of long drawn out bands of tissue. The tuberous shape, which was regarded as typical for the ovaries at the beginning of pregnancy, has disappeared. The follicles too have been reduced. At times it is difficult to find the ovaries in the body cavity owing to their narrow ledge-like shape.

Thus the equine ovary gives us an illustration of an involutionary process of an organ. This is particularly interesting as other parts of the female genital apparatus—we need only mention the changes in the uterus—also show the phenomenon of involution.

The involution of the ovaries seems to stand in a reciprocal relation to the involution of the uterus. Whereas the two ovaries are reduced during pregnancy to two small insignificant masses of tissue, the uterus enters on a process of differentiation corresponding to the development of the foetus, so as to be able to fulfil its various new functions (nutritional and protective organ, channel for foetus to pass through).

After parturition the position is changed. The ovaries have to prepare themselves for a new ovulation and are busy forming new follicles and bringing them to maturity. Hence the ovaries are in a state of evolution after parturition. On the other hand, the uterus is being reduced to its normal mass.

The practician (breeder) is particularly interested to know when ovulation appears afresh in mares which have foaled and how soon after parturition oestrum may be observed. Experience has taught us that the reply to these questions is not so simple. We have to distinguish between two groups of cases: Animals which foal towards the end of the oestral season, and animals which foal early in the season or at any rate, during the first two-thirds.

If a mare foals shortly before the end of the season, she may show symptoms of oestrum after a shorter or longer interval, but an ovulation never appears.

If, however, foaling takes place at the beginning or during the first two-thirds of the season, a new ovulation occurs after a varying lapse of time. The time for this new ovulation is not definitely fixed. In the detailed publication this question will be discussed again.

(b) *Results of investigations with horses.*

[*Crosses between South African and German (Oldenburg) Breeds*].

Short account of a few findings in horses.

Sir Arnold Theiler enabled us to control on horses the results we had obtained in donkeys. During our stay in South Africa we observed and examined considerably more than 100 horses and had for this purpose different groups of animals: two year old mares which had never been to a stallion; pregnant mares which were to supply the intra-uterine embryological material; and mares just before foaling which also promised to supply foals.

A detailed description of these investigations will have to be reserved for a later publication. Here we can only mention a few facts of a general nature.

In general we can say that the ovaries of horses are morphologically and physiologically very similar to the ovaries of donkeys. The principles underlying the structure of the ovary of horses and donkeys are the same, but the horse ovary, when fully developed, is a bigger, more massive and tougher organ. Its development will have to be dealt with in the later publication.

The cycle of ovulation and oestrum in the horse follows the same scheme as we have described for the donkey.

In horses too the ovarian function (ovulation) is concentrated on a definite period of the year. *The ovarian cycle is seasonal.*

The ovulation period in horses is practically the same as in donkeys. The South African horses which were examined did *not* show a continuity of successive ovulations throughout the year. Ovulation and oestrum take place during the ovulation- and oestral season which, according to our observations, embrace the months of October, November, December and January, probably also February and March.

For the rest of the year the ovaries of the horse are certainly inactive and unproductive; neither ovulation nor oestrum occurs.

Also in regard to the frequency of ovulation and the number of ovulations during the season, horses appear to behave exactly like donkeys. One, two and sometimes three ovulations take place during the active season.

In view of the fact that in South Africa, horses too are allowed to run free on the veld, we had to take into consideration the possibility that some of our mares might be pregnant. For our observations on ovulation and oestrum we were obliged therefore to take young, two year old mares, which had never shown signs of oestrum and whose ovaries had not functioned previously. These two year old animals showed oestrum for the first time during the oestral season they were under observation and their ovaries liberated their first ova. In all of these animals ovulation occurred only once during the time we were able to observe and examine them (although some of them showed oestrum more than once at varying intervals).

However, in some of the older animals the condition of the ovaries at the post-mortem examination indicated two or possibly three ovulations, since two (or three) corpora lutea were found, one of which could be regarded as quite recent, the other as older but still belonging to the same season.

Again we were able to observe in horses what we had already found in donkeys: frequent appearance of externally recognisable symptoms of heat for a longer or shorter period without, necessarily, the rupture of a follicle (ovulation).

In general it was also found here that an oestrum of one or two days' duration was often " incomplete " in respect of ovulation and sexual manifestations; in this case a series of changes appeared in the sexual apparatus, but ovulation was absent. If on the other hand, the oestrum lasted several days in succession, it was usually a " true " oestrum with accompanying ovulation. (In this connection it should be mentioned that lengthy or even permanent oestrum may also be due to an abnormal condition of the ovaries.)

It has been found in South African horses, as in donkeys, that oestrum and ovulation are not arranged, according to a strictly

chronological scheme. The arrangement seems to be rather arbitrary, although a number of influencing factors may accelerate or retard the course of events.

Everything that has been said about the appearance of an " ovulation groove " in the donkey, also applies to the horse.

In young horses the follicles rupture on the surface of the ovary. The apex of the mature follicle may even protrude beyond the surface of the ovary. At first the favourite spot for the rupture of follicles is situated near the cranial pole of the ovary, where the edge of the fimbriated extremity is attached to the ovary. Here the connective tissue covering the ovary, which is tough elsewhere, is thin. Furthermore follicles are continually being formed at the cranial pole, so that this region of the ovary seems particularly suited for the rupture also from an embryological point of view. There is no such thing as a special groove into which the rupturing follicles deposit their egg-cells.

The differentiation of follicles is not localised at the commencement of ovariogenesis, but takes place all over the surface of the ovary; it is only when the processes to be mentioned below make their appearance in the ovary, that the initial unlimited formation of follicles is concentrated in one portion.

As the animal gets older, the unequal growth at the poles and at the centre of the ovary gets more pronounced. The cranial and caudal poles project more and more above the central portion. Owing to the intensive growth of tissue at the poles. the central parts of the ovary whose surface is particularly suitable for ovulation, get depressed more and more. Probably this area is further retracted from its original level by reduction of the tissue or certain parts thereof. These secondary processes bring about a typical bending of the organ in older animals and lead to a deformation of the ovary. That portion of the ovary where ovulation takes places by preference, is then to be found in a depression surrounded by a wall of ovarian tissue with a thick covering of connective tissue. It then appears as if a special groove is performed in the ovary of the horse for the reception of mature and rupturing follicles. However, the embryology and organogenesis of the ovary of the horse teach us that originally ripe follicles appear over the entire surface, in the same way as has been observed in the donkey. The equine ovary does not, therefore, differ, in principle, from that of other mammals.

(c) *Summary of the most important results obtained with Donkeys and Horses.*

Our investigations have proved that the ovaries of donkeys and horses, in many respects, show very similar conditions both as regards morphology and function. In principle the structural conditions of the ovaries and sexual manifestations are the same in donkey mares and horse mares.

Thus the ovaries of both classes of animals show a differentiation of follicles over the entire surface. Secondary processes lead to a reduction of the ovulation surface, which then appears to be situated in a depression in the centre of the organ; however, in reality, this is due to a deformation of the ovary owing to the excessive growth of the ovarian tissue at the poles.

Originally neither the ovary of donkeys nor that of horses has a predestined area for the maturation of follicles. The so-called

" ovulation groove " in the ovary of the horse cannot be regarded as a specific structure; from the comparative anatomical point of view it has no significance. The " ovulation groove " is a purely morphological conception; physiologically the conditions regulating the emission of the follicular contents on the surface of the ovary remain, in principle, the same as in the ovaries of other mammals, and are not affected by the depression of the ovulation area (ovulation groove). The mature follicle ruptures on the surface of the ovary both in the case of the donkey and the horse.

Secondary growth processes in the ovary of the horse result in the formation of a groove-like depression in old animals.

The appearance of ovulation and other sexual manifestations (oestrum) in donkeys and horses is seasonal. In South African donkeys and horses ovulation and symptoms of oestrum occur only at certain times of the year. This season may be described as the " ovulation- " or " oestral season." For the rest of the year ovulation and symptoms of oestrum are entirely absent; it is an inactive period free from ovulation and oestrum.

According to our experience the ovulation and oestral period includes the months of October, November, December, January, February and March. However, it is probable that this season will vary from year to year, inasmuch as both the beginning and the end of the active season are subject to influences determining the condition of the animals.

During the ovulation and oestral season periods of heat are relatively frequent, but there is no regularity in the appearance of the symptoms. The length of the intervals between successive oestra also varies.

Even the duration of the individual periods of heat is subject to variation. It may happen that the symptoms appear for one day and then disappear again. On the other hand, the symptoms may persist for several days in succession. An oestrum of several days' duration may be preceded by a short oestrum of one or two days.

Ovulation in donkeys and horses takes place only during the oestral season. Ovulation season and oestral season coincide during the same half of the year. During this season the ovaries of donkeys and horses ovulate only a few times (once, twice or three times). The individual ovulations do not appear at definitely regulated times during the season. A fairly long period divides two successive ovulations.

In regard to the relation between ovulation and oestrum our investigations have shown that ovulation does not necessarily occur during every period of heat. It is usually during the oestral periods of several days' duration that ovulation takes place, whereas it is generally absent from the short periods of one day which precede the longer oestra. It should, however, not be inferred that during these latter oestra there are no changes at all in the ovaries or in other parts of the sexual apparatus. On the contrary, it would seem that these periods offer particularly suitable conditions for the initiation or completion of preparatory transformation processes in the ovaries. It is certain that such processes actually occur in other parts of the genital tract also; since even during these short, single-day oestral periods changes can be observed in the external genital organs. Animals showing a short oestrum will attract the males and will stand still to be covered by these.

The short or " empty " oestral periods during which no ovulation occurs, seem to start certain processes which, after a shorter or longer interval, reach their climax at the time of the longer oestrum of several days' duration. During this latter stage, the rupture of the mature follicle, ovulation takes place.

The equines show, therefore, as mentioned before, a seasonal ovarian cycle.

Ovulations do not occur at short regular intervals throughout the year, but are restricted to one period of the year. This concentration of a process, essential for reproduction, must be interpreted as an adaptation to natural conditions of existence for domestic equines in South Africa, and is connected with the " wild " state under which these animals have been allowed to remain by civilized man. The arrangement whereby donkeys and horses in South Africa liberate their ova during the period from October to March, so that conception occurs during these months, is very well suited to the conditions of the country. After a gestation period of about 11 months, parturition takes place at the beginning of the South African spring, which is favourable for lactation. At this time too the cold nights have passed and the new grass ensures the nutrition on the veld not only of the mother, but also of the young in the days to come. This adaptation of ovarian functions to natural conditions can be observed in all those cases where animals are kept in the open in a " wild " state and where domestication has not led to an increased productivity of the ovaries and the reproductive powers. In these cases we find conditions such as have been reported to exist in true wild animals, although the statements have not been proved.

There can be no doubt that the domestication of animals alters their original form of life and habits (which is nothing else but the result of a continuous experiment to ensure the preservation of the species) and force them into a new order of things. Domestication can afford to do this since it is guided by the human mind, which devises ways and means to satisfy the requirements of the animals under the new conditions.

Our investigation has shown, however, that in those cases where the " wild " state is more or less preserved, the regulation of the ovarian functions still conforms to this more natural life.

(d) *Brief notes on observations made on hybrids between donkeys and horses (mules and jennets).*

At the conclusion of our article a few words may be said about our observations on female equine hybrids (mules and jennets).

In spite of great difficulties I was enabled through the generous assistance of Sir Arnold Theiler to examine equine hybrids. For a period of six months (July, 1925, till January, 1926) a number of female mules and jennets were kept on the farm " Bestersput " in the Free State.

These animals were observed every day after having been collected on the veld and brought into a small camp. A number of horse stallions, 13 or 14 donkey stallions and 2 mule stallions were then admitted in succession to the female animals, and a careful record was kept of all sexual manifestations.

At suitable intervals these animals were slaughtered for an examination of the sexual glands and the other portions of the genital apparatus in regard to their morphological behaviour.

It was found that oestrum appears or may appear in the hybrids. Several of the animals showed signs of oestrum once or more than once. The symptoms, which we were able to observe, varied in intensity, but were, in general, less pronounced than in either of the two original strains. It was frequently observed that some symptom or other may be practically absent, or may be very conspicuous.

Female mules and jennets, like donkey and horse mares, show changes in the genitals during oestrum. Usually the vulva is swollen, the mucous membrane of the vagina reddened, there is a mucous or bloody or muco-bloody discharge from the orifice, the vulva opens and closes, the clitoris is swollen, etc.

In general it may be said that mule mares during oestrum show a preference for horse stallions, whereas female jennets prefer donkey stallions. The sexual instinct of the hybrid seems to direct itself to that breed from which its mother sprang (horse in the case of mules, donkey in that of jennets). Similarly horse stallions seem to prefer mule mares, donkey stallions jennet mares.

During oestrum the mule mares behave much more like horse mares than donkey mares, whereas the female jennets resemble donkey mares more in their behaviour.

In regard to the appearance of oestrum our observations have shown that in all probability (unfortunately the observations could not be extended over a whole year) oestrum appears seasonally. An active season alternates with an inactive period.

It is quite certain that oestra do not appear continually right through the year.

During the active season which extends (as in the case of donkeys and horses) over the months of September, October, November, December, January (probably also February, March and April) oestrum may appear once or several times in an animal.

Oestrum may be short or may be of several days' duration.

Usually the beginning of an oestral period is difficult to diagnose, except in those rare cases when the initial symptoms are quite distinct. Similarly it is often very difficult to decide whether an oestrum has ended or is still going on in a mild form.

The male animals (donkey and horse stallions) which gave such valuable service in detecting oestrum in the donkey and horse mares, usually fail in the case of hybrids. Sometimes there was one stallion that would indicate the presence of oestrum in a mare, but then there would be no other stallion to corroborate this result.

Often the hybrid mares had to be left together with the donkey, horse, or mule stallions for a long time before the presence of oestrum would be revealed. It was evident that the presence of the observer was resented by the animals and frequently that may have been a cause why symptoms of oestrum were not shown.

In a few cases coitus took place between the female animals on heat and the males. However, there were always some difficulties; either the stallion was too small and his penis could not reach the vagina of the mare, or the mare was afraid or "shy," and avoided the attacks of the stallion.

Coitus succeeded best when the two animals were driven into the crush of the observation camp. The mare could then be raised, if necessary, and could not run away from the stallion.

Of special interest are the observations on the morphological anatomical changes in the ovaries of equine hybrids, mules and

jennets. Our investigations showed that from a morphological-anatomical point of view the ovaries of these hybrids are very similar to those of the pure strains (horses and donkeys).

In the ovaries of mules and jennets normal Graafian follicles are formed even before they reach sexual maturity. These follicles can be seen distinctly on macroscopical examination of the ovaries; in some of them the apical pole projects beyond the surface of the ovary.

One (or sometimes two) follicles reach maturity. They increase considerably in volume and may protrude beyond the surface of the ovary, in which case a number of capillaries may be seen on the thin covering membrane where the rupture is to take place; or they may just reach the surface of the ovary.

It is certain that an ovulation groove does not exist in the ovaries of mules and jennets. In this respect the ovaries of the hybrids correspond exactly with those of donkeys and horses. The mature follicles which may rupture at different parts of the ovary, empty their contents directly on to the surface of the gland. There is no depressed depôt for the reception of the contents of the rupturing follicles.

There can be no doubt that the mature follicles in the ovaries of mules and jennets actually rupture, and that the ruptured follicle provides the stratum out of which the corpora lutea are formed.

Corpora lutea are formed in the usual way in the ovaries of mules and jennets. We have observed both developing and reduced yellow bodies.

The ovaries of mules and jennets with corpora lutea, fit exactly into the normal series of organs which we were able to construct in the case of donkeys and horses after many post mortem examinations. In no respect did the ovaries of mules and jennets which we were able to examine, and in which the presence of corpora in the course of formation, development or reduction proved that they had functioned, show any departure from the normal in their morphological anatomical appearance. On the contrary, our results support the view that the changes in the ovaries of mules and jennets are accompanied by the normal functions of the organs, and that the ovaries are capable of liberating ova.

Unfortunately the time at our disposal in South Africa did not allow us to amplify our macroscopical observations by means of microscopical examination, which alone could have enlightened us about the minute histological conditions of the ovaries and the germinating capacity of the ovum. We hope to be able to carry out this investigation in the future so as to control and complete our results.

In regard to the relation between oestrum and ovulation, our experience goes to show that the conclusions which we arrived at in the case of donkey and horse mares also apply to their hybrids.

Ovulation (and with it the formation of corpora lutea) occurs, the same as oestrum, seasonally. In South African mule and jennet mares ovulation is confined to one half of the year namely, for certain, in the months of September, October, November, December and January, and probably also in February and March. During the remaining half of the year, ovulation and oestrum do not take place.

Oestral season and ovulation season coincide, and similarly the oestrum-free season and the ovulation-free season of the year.

In the same way that oestrum may appear several times during the active season in mules and jennets, so may ovulation occur more than once in individual animals during the season. This can be inferred from the presence of several reduced corpora lutea derived from follicles which ruptured during the same active season.

In female mules and jennets, as in horse and donkey mares, oestrum may occur without ovulation. These oestra, which we may call " empty oestra " seem to prepare the way for the real oestra with ovulation. There can be no doubt that changes do take place during these empty oestra, in different parts of the genital apparatus and certainly in the ovaries, even though they may not be recognizable macroscopically.

PLATE I.

Explanation.

Diagram to illustrate the organic processes recurring regularly in the ovary of young, sexually mature, non-pregnant cows during an interovulation period (rupture of a follicle, evolution and involution of a corpus luteum, development of mature follicles).

We start from an ovary (Fig. a) in which a mature follicle (Fo.Gr.rpt.) has ruptured and liberated its egg-cell. Following the *continuous* curved line from the ruptured follicle towards the left, the diagram shows how this follicle is gradually transformed into a corpus luteum (Co.lut.I); in Fig. b we see it on the second day after the rupture, in Fig c on the third day, in Fig. d on the 4/5th day, in Fig. e on the 6th day, in Fig. f on the 7th day, and in Fig. g (Co.lut.I) on the 9/11th day (having now reached its full development).

The interrupted line going up from the fully developed corpus luteum in Fig. g (Co.lut.I) connects the consecutive stages in the reduction of the yellow body (Co.lut.Ir). Fig. h shows an ovary with a reduced corpus luteum (Co.lut.Ir) 12 days after the rupture of the follicle.; Fig.i an ovary with a corpus luteum (Co.lut.Ir) 17/19 days after the rupture, and Fig. k illustrates the condition (Co.lut.Ir) after an interval of 20 days since the rupture of the follicle.

Following the interrupted line in a counter-clockwise direction still further, we come to a stage in the reduction (Fig. a, Co.lut.II) which corresponds with the rupture of a new follicle. The corpus luteum has now been reduced to less than one-half of its original volume (see Fig g).

Thus the Figs. a, b, c, d, e, f, g, h, i, k, and again a illustrate the life-history of a ruptured follicle up to the time when a new mature Graafian vesicle ruptures (Fo.Gr.rpt.-Co.lut.I, Co.lut.I, Co.lut.Ir, Co.lut.II in Fig. a).

If the fate of the reduced corpus luteum is to be studied further, we should follow the interrupted line from Fig. a to the left in a counter-clockwise direction. In Figures b-f we see the further stages in the reduction of the yellow body (Co.lut.II) which now does not belong to the latest ovulation period, but to the last but one. Fig. b shows a corpus luteum (Co.lut.II) 21+2=23 days old, Fig. c (Co.lut.II) 21+3=24 days old. Fig. d (Co.lut.II) 21+4/5=25/26 days old. and Fig. e (Co.lut.II) 21+6=27 days old, and Fig. f (Co.lut.II) 21+7=28 days old (counting from the day of rupture of the follicle which gave rise to the corpus luteum). The diagram illustrates the successive and continuous reduction of the corpus luteum.

Following now the *dotted* line from Fo.Gr. in Fig. g upwards, we see a number of ovaries which illustrate the development and maturation of a Graafian follicle (Figs. g, h, i, Fo.Gr., and k, Fo.Gr.mt.). These processes immediately precede every rupture of a new follicle and become, as the diagram shows, very conspicuous in the ovary 9/11 days after the old ovulation (rupture of the follicle Fig. a, Fo.Gr.rpt.=Co.lut.I). The cycle of only one follicle has been depicted so as not to make the diagram too complicated. If several cycles had been included, i.e. if the history of several follicles had been figured as they ruptured in succession after intervals of 21 days, it would have meant continuing in the following figures to include the corpus luteum which in Fig. f, Co.lut.II has already reached an advanced stage of reduction. It

would further have meant indicating the rupture of yet another mature follicle after 21 days which might have occurred in the same or in the other ovary.

The outer circle in the diagram (Figures a′-k′) illustrates by means of longitudinal sections or parts of sections through respective ovaries the progressive development of the corpus luteum I as well as the regressive metamorphosis of the yellow body of the latest interovulation period. Fig. a′ is the longitudinal section through ovary a, Fig. b′ through b, etc. The dotted circle running through Figures a′, b′, c′, . . till k′ and a″, which connects "Fo.Gr.rpt." (Co.lut.I′) with "Co.lut.I′," "Co.lut.I′," with "Co.lut.Ir" (Fig. h′) gives a series of longitudinal sections through corpora lutea belonging to the latest interovulation period (changes in the corpus luteum tissue at various intervals throughout the 21 days). The dotted circle a′, b′, c′, e′, and f′ which (again following it in a counter-clockwise direction) connects all the "Co.lut.II" together, runs through longitudinal sections of corpora lutea of the last but one interovulation period.

PLATE II.

Explanation.

Diagram to illustrate the organic processes occurring in the ovaries of young, sexually mature, non-pregnant sheep (rupture of a follicle, evolution and involution of a corpus luteum, development of mature follicles).

The diagram illustrates the organic changes taking place in the ovaries of young, sexually mature, non-pregnant sheep and shows a series of ovaries in which the differentiating processes in the organs can be observed in the progressive stages of their development.

For the sake of clarity the changes are shown both in the entire organs (Figs. a-k, inner circle), and in sections (Figs. a′-k′, outer circle). Only one of the two ovaries has been figured; the other organ had to be omitted so as not to complicate the diagram unnecessarily. The processes (formation of follicles and development of corpora lutea) do, of course, usually occur both in the right and in the left ovary, but nevertheless the diagram has been kept accurate: it is quite possible for these processes to be confined to one ovary for a time.

In the inner circle which illustrates the conditions in the entire organs, the series begins with an ovary (Fig. a) in which a mature Graafian vesicle (Fo.Gr.rpt. = Co.lut.I) has already ruptured and a fresh corpus luteum has been formed. The yellow body (Co.lut.I) appears as a small red papilla, in the centre of which the point of rupture can still be seen. If now we follow in a counter-clockwise direction the continuous line which connects the Figs. a, b, c, d, e, and f, we get an idea of the way in which a corpus luteum is formed from a ruptured follicle (Figs. a-f, Co.lut.I, or Fig. f, Co.lut.I, and Co.lut.I_2). We observe that the initially small papilla becomes larger and larger and finally, when it has reached its full development, takes on a plug-like shape in the ovary (Fig. f; since it is common in sheep for two follicles to rupture and for two corpora lutea to develop simultaneously, one such case with two corpora lutea has been included in the diagram).

If now we follow, in a counter-clockwise direction, the dot-dash-line from the stage of full development (Fig. f) of these two corpora lutea (Co.lut.I, and Co.lut.I_2) we meet in the following organs of the series (Figs. g, h, i, k) different stages of development of the corpus luteum, illustrating different phases of its reduction (Co.lut.Ir).

One sees, how the plug-like structure takes on the shape of a button, during which process the tissue undergoes characteristic changes of colour. The corpus luteum which at the stage of full development had a flesh-like appearance (Fig. f, Co.lut.I, and Co.lut.I_2), takes on a distinctly yellow colouration during the later stages of its regressive metamorphosis (Figs. i and k, Co.lut.Ir). If we wish to study the history of the corpus luteum beyond the stage in Fig. k (Co.lut.Ir), we have to follow the dot-dash-line, which connects all the subsequent stages in the reduction of the yellow body (Co.lut.II, Figs. a, b, c, d, e, f, g, h, i, and k). It will be noticed how the corpus luteum becomes less and less conspicuous on the surface of the ovary, until finally (Fig. k, Co.lut.IIr) it appears as a brownish pigmented speck. This speck is the only mark left by the yellow body, after its formation from a ruptured follicle and its period of evolution and involution. We can infer from this mark that the ovary has functioned and liberated an egg-cell some time ago.

In Fig. a we again find the corpus luteum (Co.lut.II) illustrated in Fig. k (Co.lut.Ir), as the reduced corpus luteum of a new interovulation period. We have to imagine that a new follicle has just ruptured [Fig. a, Fo.Gr.rpt. (or Co.lut.I)] and emptied its contents, whereby the corpus luteum, which in Fig. k belongs to the first interovulation period and is designated as corpus luteum I, now enters its second interovulation period and must be described as corpus luteum Secundum II.

To avoid a further complication of the diagram, we did not illustrate the new rupture of a follicle by means of another vesicle, but will refer to the same follicle which gave rise to the corpus luteum whose reduction we have been studying. When we find an ovary showing the morphological conditions illustrated in Fig. a, we may know that the two yellow bodies do not belong to the same period, but are derived separately each (Co.lut.I and Co.lut.II) from a mature Graafian follicle which ruptured.

Figures g, h, i, and k (Fo.Gr. or Fo.Gr.mt.) illustrate this process of gradual maturation of a Graafian follicle, which takes place in the ovary during the reduction of the corpus luteum in the latest interovulation period, and precedes the formation of a new corpus luteum. At the commencement of the reduction process of the corpus luteum (Fig. a, Co.lut.Ir) one or two follicles (Fo.Gr.) usually begin to enlarge and project beyond the surface of the ovary, whereby the wall of the vesicle is stretched by the increasing pressure and blood vessels appear during the last stages of maturation.

In Swiss and Central European breeds of sheep the corpus luteum (Fig a, Fo.Gr.rpt. or Co.lut.I) completes the various evolutionary stages (Co.lut.I in Figs. b, c, d, e) up to its full development (Fig. f, Co.lut.I_1 and Co.lut.I_2) in a period of 21÷2 days, i.e. 10 to 11 days. Then the reduction commences (Co.lut.Ir in Figs. g, h, i, k) and continues till the rupture of a new follicle (Fig. a) at which time the yellow body enters a new interovulation period (Co.lut.Ir in Fig. k becomes Co.lut.II in Fig. a). After 21 days the same process would be repeated with a new rupturing follicle.

The reduced corpus luteum (Fig. a, Co.lut.II) would then continue the second stage of its reduction [Co.lut.II in Figs. b, c, d, e, f, g, h, i, k (Co.lut.IIr)] and would ultimately be retained on the surface of the ovary as a brown speck, even if another cycle of 21 days should take place.

In Swiss and Central European sheep the cycle illustrated in our diagram is repeated every 21 days and normally goes on without interruption throughout the year if the animals do not become pregnant.

In South African persian woolled sheep and merinos this cycle would only take place at a certain time of the year (namely, according to our experience, in the months of April, May, first half of June, possibly also in January, February, and March) during the South African late summer and winter. During this season the cycle is repeated several times and requires a definite period for its completion. For the rest of the year only a portion of the cyclic changes illustrated in our diagram is observed, namely the metamorphosis of the ovary shown in Figs. g, h, i, and k; this whole period is occupied with the reduction of the corpus luteum (Figs. g, h, i, k, Co.lut.Ir) which developed during the last cycle of the active season (Figs. a, b, c, d, e, Co.lut.I and Fig. f, Co.lut.I_1, and Co.lut.I_2) and with the maturation of a Graafian follicle (Figs. g, h, i, Fo.Gr. and Fig. k, Fo.Gr.mt.).

Figs. a-k refer to the ovary as a whole.

Figs. a′-k′ refer to sections of ovaries.

PLATE III.

Explanation.

Diagram to illustrate the cyclical changes in the ovaries of young, sexually mature, non-pregnant goats, with special reference to the development of the corpus luteum and the maturation of the follicle.

Figures a-k (inner circle) illustrate the morphological changes in the ovaries due to the development of the corpus luteum and the maturation of the follicle.

Figs. a′-k′ (outer circle) show in sections the changes to which the yellow body is subject during its genesis in the ovaries of goats.

In Fig. a two mature follicles are shown (Fo.Gr.mt.) immediately before rupturing. The third mature follicle has already ruptured and hence the structure may be referred to as a corpus luteum (Fo.Gr.rpt.=Co.lut.I).

Proceeding in a counter-clockwise direction, the continuous line connects the successive stages in the development of the corpus luteum (Co.lut.I, Figs.

b, c, d, e, f). It will be seen how the distal portion of the growing corpus luteum projects more and more beyond the surface of the ovary, until it appears as a plug in the ovary (Fig. f, Co.lut.I). A distinct depression in the tissue at the distal end of the corpus luteum continues to indicate the spot where the Graafian follicle, out of which this yellow body arose, ruptured. The corpus luteum also continues to show, at least on the surface, a red colouration which, however, when compared with earlier stages (Figs. a, b, c, d, e, Co.lut.I), has become less pronounced and tends more and more to become brownish-yellow.

If now we follow the continuation of our line [interrupted line from the corpus luteum (Co.lut.I) in Fig. f, on], we meet the corpus luteum (Co.lut.Ir, respectively, Co.lut.Ir$_1$ and Co.lut.Ir$_2$) in Figs. g, h, i, and k, in progressive reduction. The distal part of the yellow body, on the surface of the ovary becomes less and less prominent and, in the end, is only a slight elevation (Fig. k, Co.lut.Ir$_1$ and Co.lut.Ir$_2$). The brown colour of the corpus luteum tissue which projects beyond the surface of the ovary, fades during the regressive changes of the yellow body to such an extent, that during the later stages the reduced corpus luteum has only a very inconspicuous pale yellow colour.

Although a number of small follicles appear on the surface of the ovary during the progressive development of the yellow body (follow the innermost dotted line in a counter-clockwise direction from Fig. b, Gr.fo. over c, d, e, and f), the actual enlargement and maturation of the follicles take place only during the period of regressive metamorphosis of the corpus luteum (innermost dotted line where it passes Gr.fo. in Fig. g, and Gr.fo.dlt. in Figs. i and k).

Shortly before rupturing the follicle (Fig. k, Gr.fo.dlt.) projects beyond the surface of the ovary, and its extraordinarily tender wall shows the capillaries clearly.

After the rupture of the follicle (Fig. a, Gr.fo.rpt.) the corpus luteum discussed by description (Fig. a, Co.lut.II) shows itself on the surface of the ovary as an inconspicuous yellow nodule, which, as can be seen in the accompanying section (Fig. a′, Co.lut.II′), consists of a considerably reduced mass of tissue. (In order to keep the diagram as simple as possible we have used, for the illustration of this process, the same Graafian follicle which served to show the development of the corpus luteum).

Through the rupture of a new Graafian follicle (Fig. a. Gr.fo.rpt.) the corpus luteum which until then belonged to the latest interovulation period (Fig. a, " Co.lut.I "), now becomes the corpus luteum of the last but one interovulation period (Fig. a, " Co.lut.II ").

If now we follow in counter-clockwise direction the dot-dash-line in the inner circle, starting from Fig. a and observing the reduced corpora lutea (Co.lut.II) of the last but one interovulation period; or if we follow the outer dotted line in the outer circle in the same direction, starting from Fig. a′ (Co.lut.II′), we see the changes which the reduced corpus luteum of the last but one interovulation period undergoes after the rupture of the follicle. We see (Figs. b, c, d, and e; or Figs. b′, c′, d′, and e′) that the corpus luteum appears as a pigmented, larger or smaller speck on the surface of the ovary, and remains visible even after the rupture of another follicle. Later on it can only be recognized in sections through the ovary as a remnant of tissue.

The outer circle, shows sections through the corresponding ovaries of the inner circle and illustrates the macroscopic changes in the corpus luteum of the first interovulation period (Co.lut.I′) throughout the whole cycle. Figures a′-f′ show the changes during the progressive metamorphosis (Co.lut.I′) g′-k′, during the first regressive (Co.lut.Ir′), and a′-f′ (outer dotted circle) during the second regressive metamorphosis (Co.lut.IIr′).

Figs. a-k refer to the ovary as a whole.

Figs. a′-k′ refer to sections of ovaries.

PLATE IV.

Explanation.

Diagram to illustrate the cyclical changes in the ovary of young, sexually mature, non-pregnant pigs (evolution and involution of a corpus luteum, maturation of Graafian follicles).

The diagram shows a few stages of a circular morphological-anatomical chain and elucidates the fate of the several stages in the differentiation of the ovary during its cyclical development.

Only one of the two ovaries has been figured in each case. However, normally, the other gland would show exactly the same conditions as illustrated by its partner.

We start from the ovary pictured in Fig. a, on the surface of which a number of mature follicles (Fo.Gr.mt.), ruptured Graafian vesicles (Fo.Gr.rpt.=Co.lut.I), and reduced corpora lutea (Co.lut.II) can be seen. The two ruptured follicles (Fig. a, Gr.Fo.rpt.) which can now be regarded as new corpora lutea (Fig. a, Co.lut.I) owing to the fact that ovulation has taken place, still show very clearly the opening, i.e. the point of rupture of the follicles.

The continuous line, running from the left newly formed corpus luteum (Fig. a, Co.lut.I) in a counter-clockwise direction, connects a number of ovaries, which illustrate the successive morphological changes in corpora lutea developing out of such newly ruptured follicles.

This line as it passes each ovary (Figs. b, c, d, e, f) touches the particular structure whose preceding stage is shown in the previous ovary. Since all these organs belong together genetically, they have been designated in the same way. (" Co.lut.I.")

In Fig. b the corpus luteum has assumed a berry-like shape. The tissue of the collapsed follicular wall starts growing rapidly, so that the structure protrudes more and more beyond the surface of the ovary and becomes very conspicuous on the surface, partly owing to its bright red colour.

In Figs. c, d, e, and f the yellow bodies (Co.lut.I) increase in size and gradually take on a spherical shape; the bright red colour slowly disappears.

The corpora lutea (Co.lut.I) which arose out of the mature follicles represented in Fig. a (Fo.Gr.rpt.), go through all the stages of their development, as shown in Figs. c (" Co.lut.I "), d, and e (" Co.lut.I "), and reach their full development in Fig. f (" Co.lut.I "). These corpora lutea, of which there are several in the ovary concerned, appear on the surface as conspicuous, flesh-like berries.

So far Figures a, b, c, d, e, and f have illustrated the stages of a progressive development of the corpora lutea, whereas, from now on, the dash-dot-line will join up (proceeding in a counter-clockwise direction), in the figures g, h, i, and k, the genetically corresponding corpora lutea (Co.lut.I in Fig. g, Co.lut.Ir in Figs. h-k), which pass through the phases of an involutionary metamorphosis.

The corpora lutea in Fig. g (Co.lut.I) have decreased considerably in volume when compared with the corresponding follicular glands in Fig f (Co.lut.I), owing to the degeneration of the corpus luteum tissue. Similar conditions are observed in the yellow bodies in Figs. h, i, and k (Co.lut.Ir) when compared with Figs. g (Co.lut.Ir) and i (Co.lut.Ir) respectively. At the same rate that the corpus luteum is reduced, the flesh-like colour which was still apparent at the stage of full development (Fig. f, Co.lut.I), disappears. The balls of tissue which project beyond the surface of the ovary, change first to a brownish-yellow, and then to a yellow colour (Fig. k, Co.lut.Ir, and Fig. a, Co.lut.II).

In Fig. a (Co.lut.II) the dash-dot line passes through that stage of reduction of a yellow body which corresponds chronologically exactly, with a certain stage in the maturation of the follicles to wit, the phase of rupture. We see (Fig. a, Co.lut.II) the reduced corpora lutea at the stage of regressive metamorphosis which is observed when follicles rupture in the ovary. [In our diagram the conditions have been so represented as if these reduced corpora lutea (Fig. a, Co.lut.II) arose genetically from the same follicles, which show just now ovulation, whereas, in reality they are formed from other follicles ruptured an interovulation period before.]

These reduced corpora lutea, as a matter of fact, originated from follicles which ruptured at an earlier period, during the preceding ovulation period, from follicles which are now in the ovary represented by visible vesicles (Fo.Gr.mt.) or, in so far as these vesicles have already ruptured, the new corpora lutea (Fig. a, Co.lut.I).

Since the reduced corpora lutea in Fig. a have already passed through a cycle, i.e. have developed from ruptured follicles to the stage of full development and then been reduced up to the period when new follicles ruptured, they enter on a new interovulation period from the moment the new follicles rupture, and have therefore been designated as corpora lutea secunda (Co.lut.II), in Fig. a, and following stages, whereas in Fig. k they still appear as corpora lutea prima (Co.lut.Ir.).

In order to study the fate of these corpora lutea (Fig a, Co.lut.II) during their further reduction, we have to follow the outer interrupted line from

Fig. a in a counter-clockwise direction. This line connects the regressive stages in the involution of the corpora lutea of the last but one interovulation period (Figs. b, c, d, e, and f, Co.lut.II).

Finally the inner dotted line on the right of the diagram passes through the different stages of maturation of Graafian follicles (Fo.Gr.) preparing themselves for rupture. We see, on the surface of the ovaries the numerous Graafian follicles, which in Fig. f are small, grow gradually bigger and bigger. Shortly before rupturing (Fig. k, Fo.Gr.) the tightly stressed wall of the enlarged vesicle shows a beautiful network of capillaries.

The cyclical changes represented in the diagram (ovulations, evolution, and involution of corpora lutea, maturation of new follicles up to the time of rupture) are repeated in Central European pigs certainly, and in South African pigs probably, regularly throughout the whole year.

PLATE V.

Explanation

Diagram to illustrate the changes in the ovaries of young, sexually immature, non-pregnant donkey mares with special reference to the differentiation of follicles.

The diagram shows a number of ovaries arranged in pairs in such a way that the organs on the left of the continuous line (both on the left and right of the plate) represent the right ovaries, those on the right of the line represent the left ovaries. These glands belong to young ,sexually immature, non-pregnant donkey mares and demonstrate the formation and gradual maturation of the follicles.

The series begins with a pair of organs (Fig. a) both of which (right and left ovary) appear as small glands of prune-like shape, which show, even at this early stage of development—the ovaries belong to a young, newly born foal—a few differentiating follicles. The follicles are seen spread over the whole surface of the ovaries.

Fig. b shows very similar conditions with this exception, that the middle part of the ovarian surface turned towards the observer, is somewhat depressed. This phenomenon stands in relation to internal tissue changes in the ovary.

The two ovaries in Fig. c are nearly full-grown and show Graafian follicles spread over the entire surface of the organs. Compared with Fig. b the follicles are larger; smaller and larger vesicles project beyond the surface of the ovaries.

In Fig. d the follicles have increased in number and size in both ovaries; it can be seen how some follicles begin to enlarge much more than other neighbouring vesicles. The ovary is still in the stage of active follicular differentiation.

Fig. e, which represents the two ovaries of a somewhat older animal, shows both glands considerably enlarged but the follicles (Fo.Gr.) on the surface not quite so conspicuous. In the organ on the left (right ovary) the distal apices of three follicles still protrude beyond the surface of the ovary, but most of the follicles are situated rather deeper and cause only a slight elevation on the surface. The arrangement of these superficial follicles in a row should be noted. In the organ on the right (left ovary) we see externally only two follicles whose distal parts project beyond the surface of the ovary.

The conditions in Fig. f are very similar to those in Fig. e, only in the ovary on the left the enlarged follicle, whose distal end protrudes beyond the surface of the ovary, has increased in size.

This enlargement of the follicle (Fo.Gr.dlt.) is very pronounced in the organ on the left in Fig. g. The enlarged follicle takes up two-thirds of the ovary. That part of its flattened wall which is in contact with the surface of the ovary, has a diameter of 2 cm. The strumatous tissue inside the ovary has been displaced, on account of the enlargement of the Graafian follicle, towards the periphery and especially towards the polar ends of the ovary. That part of the follicular wall which touches the surface of the ovary, is particularly thin and tender. The pole of the follicle, in the centre of the dome, is extraordinarily thin and can be recognized, even at this stage of the development, as the point where the rupture of the enlarged and mature follicle could easily take place. The ovary on the right also contains enlarged follicles, but none of them approaches in size the mature follicle in the ovary on the left.

Fig. h illustrates a further stage in the maturation process of the Graafian follicle (Fo.Gr.dlt.) in the ovary of the donkey. In the gland on the left we

see, as a result of the enlargement of the maturing follicle, compact strumatous tissue only in the region of the caudal ovarian pole. The entire remaining part of the ovary is taken up by the growing follicle (Fo.Gr.dlt.).

The ovary on the left (ov.d.) in Fig. i shows the follicle practically at the end of its maturation. This follicle now dominates the entire ovary. All the tissue has been used up in the formation of the follicle and has taken part in its construction. A particularly thin spot in the wall of the follicle, which has now reached its maximal enlargement, indicates the point of rupture, the centre of ovulation of the mature follicle. Blood vessels can be seen approaching the ovulation surface from the mesentery of the ovary. The ovary on the right (ov.l.) shows a number of smaller Graafian follicles (Fo.Gr.) some of which touch the surface of the ovary, but none of them has reached the dimensions of the mature follicle (Fo.Gr.dlt.) in the other ovary.

The ovary on the left in our diagram (Fig. k) shows the enlarged and fully matured Graafian follicle (Fo.Gr.mt.) immediately before rupture. The follicle has attained a diameter of several centimetres. Its wall is thin and tightly stretched. The ovarian blood vessels surround all parts of the apex with their network. The clear liquor folliculi shows through the stressed follicular wall. The fimbrae of the oviduct (Tb.ov.l.) at the cranial pole of the ovary also shows signs of congestion. The follicular differentiations (Fo.Gr.) on the ovary on the r'ght (ov.l.) in our diagram appear insignificant in comparison with the enormous structure (Fo.Gr.mt.) in the ovary on the left.

Thus our diagram illustrates two things: (1) that in the initial stages of organogenesis the formation of follicles in the ovary of the donkey is not localized, but may take place in all quarters of the ovary (like on ovaries of other domesticated animals); (2) that usually only one of the many follicles which appear macroscopically on the ovary, reaches full maturity and ruptures. The remainder of the follicles are reduced and appear as atretic follicles or stand over for a new interovulation period.

In our diagram we have connected, by means of a dotted line, the young follicles which seem to represent the successive stages of differentiation in the process of maturation of the follicles.

PLATE VI.

Explanation.

Diagram to illustrate the cyclical changes in the ovaries of young, sexually mature, non-pregnant donkey mares (formation, evolution and involution of corpora lutea, maturation of Graafian follicles).

This diagram, for the preparation of which a series of body-warm organs served gives an orientation about the morphological changes taking place in the course of a year in the ovaries of young, sexually mature, non-pregnant donkey mares.

The circle of figures connected by the continuous line and the dot-dash line illustrates the conditions shown by the entire organs; the interrupted line runs through figures illustrating the conditions as they appear in sections.

In every case the section is placed immediately beside the organ to which it belongs. Section a' belongs to ovary a, section b' to ovary b, section c' to ovary c, etc.

First of all we shall give a short description of the inner circle of figures representing entire ovaries. These figures follow each other in a counter-clockwise direction.

The series begins (Fig. a) with an ovary in which a mature Graafian follicle has ruptured (Fo.Gr.rpt.=Co.lut.I). The ruptured follicle has become an independent corpus luteum (Co.lut.I) at the moment of rupture.

In Fig. b the ruptured vesicle (Co.lut.I) has already been closed. The distal parts of the corpus luteum which appear as a bright red elevation on the surface of the ovary, indicate the situation of the follicular gland. The corpus luteum is situated in the region of the cranial ovarian pole.

Fig. c shows the corpus luteum (Co.lut.I) on the surface of the ovary in the shape of a red papilla; the same in Fig. d. The dark red colour of the tissue protruding beyond the surface of the ovary, decreases in intensity with the progressive development of the corpus luteum in the ovary (Fig. e, Co.lut.I).

In Fig. f a brownish-yellow nodule of tissue on the surface of the ovary (Co.lut.Ir) indicates the corpus luteum lying in the interior of the ovary and surrounded with struma.

The corpus luteum, which has started in involution at this stage of development (Fig. f, Co.lut.Ir), becomes less conspicuous (Fig. h, Co.lut.Ir)

or invisible (Figs. i, k, l), on the surface of the ovary. This phenomenon is explained by the fact that reductional changes are taking place everywhere in the mass of tissue of the corpus luteum, so that this structure is displaced more and more towards the centre (see sections Fig. i′ and Fig. l′) and either loses its connection with the surface altogether or retains it by means of a whitish band of connective tissue (Fig. k′, Co.lut.Ir′).

The figures a′ to l′ in the outer circle, joined together by means of the interrupted line and following on each other in a counter-clockwise direction, illustrate more particularly the condition of the corpus luteum (Co.lut.I′ or Co.lut.Ir′) throughout the whole period during which the described changes take place in the ovaries of the donkeys.

Fig. a′ shows in a longitudinal section the newly ruptured follicle (Fo.Gr.rpt.′), i.e. the freshly formed corpus luteum (Co.lut.I′). The follicular wall which now constitutes the corpus luteum, is still relatively thin. Masses of clotted blood adhere to the surface of the tissue facing the centre of the ruptured vesicle; as a matter of fact, the whole cavity of the former follicle is filled with coagulated and stagnant blood.

Fig. b′ (Co.lut.I′) shows more or less the same conditions as Fig. a′. The former follicular cavity has again been closed. The wall has increased in thickness through proliferating processes in the tissue of the wall.

One result of the progressive proliferation of the developing corpus luteum, can be seen in Fig c′ (Co.lut.I′). The former follicular wall has doubled its thickness, so that the original cavity of the Graafian vesicle has been reduced.

Figures d′ and e′ illustrate further results of the proliferation process in the tissue of the yellow body (Co.lut.I′). The developmental changes seem to be particularly active in the deeper parts of the wall tissue. Usually the decreasing cavity of the former Graafian follicle gets displaced at an advanced stage from the centre (Fig c′, Co.lut.I′) to the periphery (Fig. d′). When the ovary is cut along the longitudinal axis of the corpus luteum, we see that the main mass of corpus luteum tissue is formed in the interior of the ovary, whereas a relatively narrow strip of tissue runs over the former follicular cavity (now filled with blood coagula), between the surface of the ovary and the nucleus of the follicular gland (blood coagulum).

The corpus luteum (Co.lut.I′) reaches the highest stage of its differentiation soon after the phase represented by section Fig. d′. It then consists of a solid mass of tissue which has been formed by proliferation of the follicular wall of the former Graafian vesicle.

Figures f′, g′, h′, i′, k′ and e′ show the corpus luteum (Co.lut.Ir′) at different stages of its further reduction. The figures show how the cellular tissue of the follicular gland (Co.lut.Ir′) is reduced more and more, and how the corpus luteum occupies a smaller and smaller area of the section. Furthermore the tissue of the corpus luteum, while undergoing regressive metamorphosis shows a typical change of colour. At the time of full development the tissue has a fresh flesh-like colour, which gradually disappears during reduction. At first the tissue becomes yellowish (Figs. f′ and g′, Co.lut.Ir′ then brownish (Figs. i′ and k′, Co.lut.Ir′), and finally takes on very dark tone (Fig. l′, Co.lut.Ir′).

During the period of reduction of the corpus luteum (Fig. f to Fig. l) a new Graafian follicle matures (Fig. f, Fo.Gr.) and prepares itself for rupture (Figs. i, k, Fo.Gr.dlt.; Fig. l, Fo.Gr.dlt.). The interrupted line running from the Graafian follicle (Fo.Gr.) in Fig. f through the vesicle in Fig. g and continuing in a counter-clockwise direction, connects the different follicles in this maturation series.

The processes illustrated in Figs. a, b, c, d, e, f, and g take place *in South African donkey mares* during the active season, i.e. during the months of October (latter half), November, December, January, February, March, April (first half). They find expression in the act of ovulation, in the formation, development, and the first stages of reduction of corpora lutea and in some cases, in the beginning of another follicular development. On the other hand the processes illustrated in Figs. h, i, k, and l take place during the inactive season. These latter processes occur in the ovaries of South African donkeys in the months of May, June, July, August, and September. The processes consist essentially of a reduction of the yellow body or bodies which may have begun in the active season, and of the continuation of the formation or maturation of Graafian follicles. However, no ovulation takes place.

In our diagram we had to take into account the fact that during the active season (oestral and ovulation season) the processes described above and figured (ovulation, formation development, and first stages of reduction, of the corpus

luteum) may be repeated once or more than once. This possibility is indicated by the continuous line running from Fig. g to Fig. a in a counter-clockwise direction, thus enclosing a smaller cycle within the larger.

The larger cycle (Figs. a, b, c, d, e, f, g, h, i, k, and l) represents in this case the annual cycle, whereas the smaller cycle (Figs. a, b, c, d, e, f, g, and again a) indicates the seasonal cycle during the active period.

The seasonal cycle may be repeated once, twice or several times. After the reduction of the yellow body which arose out of a ruptured follicle (Fig. a, Fo.Gr.rpt.), new follicles (Fig. f, Fo.Gr.) may develop and rupture (Fig. g, Fo.Gr.rpt.=Co.lut.I), whereupon all the processes illustrated in Figs. a. b, c, d, and e, recur.

Through the rupture of a new Graafian follicle and the formation of a new corpus luteum (Fig. g, Co.lut.I) the corpus luteum which up till then belonged to the latest interovulation period (Fig. g, not visible Fig. g′ Co.lut.I′) now belongs to the last but one interovulation period; or, in case ovulation occurs for the third time, to the third last interovulation period.

This latter possibility is indicated in the diagram in the series of sections by the outmost dotted line Fig. g′, Co.lut.I′ till Fig. c′, Co.lut.IIr′.

If, however in the course of the active season, a single ovulation takes place, as is usually the case in very young animals just reaching sexual maturity, then the processes following this ovulation (Fig a′, Fo.Gr.rpt.′) can be studied by following the dotted line through the Figs. b′, c′, d′, e′, f′, g′, h′, i′, and l′ (dotted line from Fig. a′ till g′ neighboured to the outmost dotted line, from Fig. g′ till Fig. l′ outmost dotted line).

PLATE VII.

Explanation.

Diagram to illustrate the morphological changes in the ovaries of young, sexually mature, pregnant donkey mares during the period of gestation.

The inner circle of organs (Figs. a to i) illustrates the progressive morphological changes in the entire ovaries of animals during pregnancy. The series starts at Fig. a which represents an ovary at the beginning of gestation, and ends with Fig i which illustrates an ovary taken from an animal at the end of the gestation period. The organs between Figs. a and i, which are connected by a continuous line running in a counter-clockwise direction, show the changes in the ovary during gestation.

The outer circle (Figs. a′ to i′) refer to sections through ovaries in different stages of development during pregnancy. Fig. a′ represents a longitudinal section through the ovary illustrated in Fig. a, Fig. b′ is a section through the ovary in Fig. b, Fig c′ the longitudinal section through Fig. c, and so on.

Of the two ovaries only one (with its section) has been illustrated in the diagram. In every case that particular ovary was chosen in which the corpus luteum of the gestation period had been formed. The external morphological conditions were similar in the other ovary which was not figured, and have therefore been omitted from the diagram for the sake of clarity. If now we observe the individual members of the series (continuous line from Fig. a through b, c, d, e, f, g, h, and i in a counter-clockwise direction) we notice, first of all, a marked reduction in the size of the organ with the progress of pregnancy. If, at the beginning of the gestation period we have a massive, tuberous ovary, we see at the end a narrow, elongated gland much reduced in volume. We observe further that conspicuous follicles are only present at the beginning of the period, not towards the end of it. There is, therefore, no evident formation of new Graafian follicles at the same time that the ovary reduces its size or corresponding with the reduction of the corpus luteum. During the gestation period the maturation process ceases in the stock of ovarian follicles.

Whereas at the beginning (Fig a′) or even later (Fig e′) during the gestation period, we may find in sections (Figs. a′ and c′, Fo.Gr.) a series of follicles. these become rarer towards the end of the period and are less conspicuous in comparison with the ovarian struma. The diagram shows clearly, how the Graafian follicles present at the beginning of the gestation period, are reduced numerically and morphologically (follicular atresia). During pregnancy the follicular structures become atrophied.

Furthermore we may observe in ovaries taken from animals in an advanced state of pregnancy a falling-in of the lateral surface (ovulation surface) which is turned towards the observer. Thereby the ovary is transformed morphologically and takes on the shape of a boat (Figs. f. g, and h). The reduction

in volume is partly caused by the progressive reduction of the corpus luteum, which is illustrated by the sections Figs. a′ to i′ (outer circle dotted line Co.lut.grav.′ and Co.lut.I′) as well as by other circumstances.

At the beginning of the gestation period (Fig a′) the corpus luteum graviditatis (Co.lut.grav.′=Co.lut.I′) occupies a considerable portion of the tissue of the ovary. Nevertheless reduction soon begins and often, during the early stages of pregnancy, the corpus luteum does not appear to project beyond the surface of the ovary. Soon connective tissue and strumatous tissue grow over the corpus luteum so that its distal portions no longer touch the surface of the ovary.

At the beginning of pregnancy the corpus luteum tissue is characterized by a dark red colour (Fig a′ Co.lut.grav.′), and in the centre of the original follicle, which is not yet filled by corpus luteum tissue, we find a static mass of red blood.

During later stages (Fig. f′-i′) when the process of reduction has commenced in the corpus luteum tissue, this mass of blood is replaced by a nucleus of connective tissue. As pregnancy proceeds the corpus luteum (Co.lut.grav′) decreases in volume, as can be judged by the smaller area it occupies in sections. Shortly before parturition the corpus luteum graviditatis (" gravidity body ") is seen in a section as a narrow strip of tissue, with a centre of connective tissue, whose axis is perpendicular to a tangent on the surface of the ovary. Only in exceptional cases does the, usually very small, remnant of tissue reach the surface of the ovary, so that the corpus luteum graviditatis can be observed and recognized by external observation of the ovary.

The change of colour of the corpus luteum during pregnancy is characteristic. At the beginning of the period the corpus luteum tissue has a dark red colour (Fig. a′ Co.lut.grav.′ and Fig. b′ Co.lut.I′), which changes to a lighter red (Figs. d′ and e′, Co.lut.grav.′) or brownish-red (Fig. f′, Co.lut.grav.′) or a reddish-brown tone (Figs. h′ and i′, Co.lut.grav.′).

In our diagram a second corpus luteum (Fig. b′, d′, f′, Co.lut.II′) has been figured in addition to the corpus luteum graviditatis (Co.lut.I′ or Co.lut.grav.′). The former does not belong to the period of pregnancy (latest interovulation period), but to the previous, last but one interovulation period. This observation, that in sections through ovaries of young, pregnant donkey mares two corpora lutea are occasionally found, one belonging to the period of pregnancy, the other to a period prior to pregnancy, definitely supports the view that two (in other cases three) follicles may rupture during the same oestral or ovulation season. There can be no doubt that these two corpora lutea belong to the same ovulation season. This can be deduced from the comparatively unadvanced stage of reduction of the corpus luteum not belonging to the period of pregnancy. If this corpus luteum belonged to the previous active season (oestral or ovulation season), it would have been reduced much further during the period (inactive season) between the old and new active seasons—as we know from experience. In our case, however, the structure is comparatively fresh. On the other hand, it is certain that the two (in other cases three) ovulations which led to the formation of the two corpora lutea (Fig b′ Co.lut.II′ and Co.lut.I) belonged to two different periods and did not occur at the same moment. The different morphological condition of the two bodies at the beginning and during the course of pregnancy, justify this conclusion.

PLATE VIII.

Explanation.

A.—Donkey foal, ♀ , " *Do fo.* 137," *24th August*, 1925.

Right and left ovary *in toto* and sections through these organs.

Fig. a.—Right ovary with its ovulation surface (Lateral surface) turned towards the observer. Numerous follicles (Fo.Gr.) distributed over the surface of the organ.

Fig a′.—Longitudinal section through the right ovary, " brown ovarian tissue " (xx) taking part in the structure of the gland. Developing Graafian follicles (Fo.Gr.′) under the convex surface of the ovary.

Fig b.—Ventral aspect of the right ovary. Ventral surface also showing Graafian follicles (Fo.Gr.).

Fig c.—Left ovary wtih its ovulation surface turned towards the observer. Numerous follicles (Fo.Gr.) visible on the ovulation surface.

Fig. c′.—Longitudinal section through the left ovary, which is largely formed of " brown ovarian tissue " (xx). Several Graafian follicles (Fo.Gr.′) under the convex border (ovulation surface).

Fig. d.—Left ovary with its dorsal surface turned towards the observer. Follicles (Fo.Gr.) have developed on the dorsal surface of the ovary.

Fig. e.—Left ovary with its ventral surface turned towards the observer. Numerous follicles (Fo.Gr. spread over the whole surface of the gland.

B.—Donkey ♀, "*Do* 149," *5th August*, 1925.

Right and left ovary *in toto*, and median longitudinal section of left ovary.

Fig. a.—Right ovary *in toto*. Ovulation surface (lateral surface) arched convexly, turned towards the observer. Numerous follicles (Fo.Gr.) spread over the surface of the ovary.

Fig. b.—Left ovary. Convex ovulation surface turned towards the right side. The bloodvessels (Art.ut.) leading to the ovary, as well as the fimbriae of the oviduct (Inf.tb.) and the end portion of the uterus have also been illustrated.

Fig. b'.—Median longitudinal section through the left ovary. The edge of the free ovulation surface is turned downwards (lat.), and the edge where the ovary is fixed by means of the suspensory ligament to the ligamentum latum uteri, is turned upwards. The interior of the ovary consists of "brown ovarian tissue" (xx) as can be seen in the section. Graafian follicles in various stages of development (Fo.Gr.') are situated towards the free edge of the organ. A Graafian follicle in an early stage of maturation lies just beneath the ovarian (lat.) surface.

C.—Donkey, ♀, "*Do.* 123," 10*th October*, 1925.

Right and left ovary in toto, and median longitudinal sections through both organs.

Fig a.—Right ovary in toto. Ovulation surface turned towards the observer. A number of Graafian follicles (Fo.Gr.) on the surface. Fimbriae of the oviduct (Inf.tb.) at the cranial end of the ovary and the suspensory ligament (Lig.susp.ov.) at the caudal pole.

Fig. a'.—Median longitudinal section through the right ovary. Remnants of "brown ovarian tissue" (xx) to be seen in the struma near to the border of the organ. Opposite the edge of the ovulation surface (med.).

Fig. b.—Left ovary in toto. Protrusion of the distal end of the corpus luteum of the latest interovulation period (Co.lut.I) in the neighbourhood of the point of attachment of the fimbriae (Inf.tb.). The retracted part of the reddish papilla indicates the point where the follicle of the latest ovulation period ruptured.

Fig b'.—Median longitudinal section through the left ovary. The section passes through the corpus luteum of the latest interovulation period (Co.lut.I') in the centre of which a red mass of tissue indicates the situation of the original follicular cavity, the reduced corpus luteum of the latest interovulation period but one (Co.lut.II'), and the reduced corpus luteum of the interovulation period previous to that (Co.lut.III', third latest interovulation period).

D.—Donkey, ♀, "*Do.* 0.18," 16*th November*, 1925.

Right and left ovary in toto; longitudinal sections and part of sections through the organs.

Fig. a.—Right ovary in toto with its ovulation surface (lateral surface of the organ) turned towards the observer. The distal portion of the corpus luteum (Co.lut.I) of the latest ovulation period protrudes beyond the free surface of the ovary and appears as a bright red papilla on the ovulation surface, close to the oviduct (Inf.tb.) at the cranial pole of the ovary.

Fig. a'.—Median longitudinal section through right ovary with corpus luteum of the latest interovulation period (Co.lut.I') cut longitudinally and enlarged Graafian follicle (Fo.Gr.') embedded in the ovarian tissue.

Fig. a''.—Part of a section through the right ovary with reduced corpus luteum of the third latest interovulation period (Co.lut.III').

Fig. a''' .—Part of a section through the right ovary with remnants of "brown ovarian tissue."

Fig b.—Left ovary in toto, with its ovulation surface turned slightly towards the left, and with an enlarged Graafian follicle (Fo.Gr.) which touches the surface of the ovary.

Fig. b'.—Median longitudinal section through the left ovary with a reduced corpus luteum (Co.lut.II') belonging to the latest interovulation period but one.

PLATE IX.

Explanation.

E.—Donkey, ♀, "*Do.* 16.757," 18*th August*, 1926.

Right and left ovary in toto; median longitudinal sections and parts of sections.

Fig. a.—Right ovary with its ovulation surface turned to the left and partly towards the observer. The corpus luteum of the latest ovulation period (Co.lut.I) is reduced and stands in relation to the surface of the ovary.

Fig. a'.—Median longitudinal section through the right ovary, passing through one of the four corpora lutea of the latest interovulation period (Co.lut.I_1').

Fig. a''.—Part of a section through the right ovary, passing through one (the other) of the two corpora lutea of the latest interovulation period (Co.lut.$1'_2$).

Fig. a''' .—Part of a section through the right ovary, with the reduced corpus luteum of the last interovulation period but one (Co.lut.II').

Fig b.—Left ovary with its ovulation surface turned slightly towards the left and showing a Graafian follicle (Fo.Gr.) which touches the surface.

Fig b'.—Median longitudinal section through the left ovary with the infundibulum of the oviduct (Inf.tb.).

Fig. b''.—Part of a sagittal section through the left ovary with reduced corpus luteum of the third latest interovulation period (Co.lut.III').

F.—Horse foal, ♀, "*Ho.fo.* 527," 14*th October*, 1925.

Right and left ovary in toto and longitudinal sections through these organs.

Fig. a.—Right ovary in toto with its ovulation surface turned towards the left; fimbriae of the oviduct (Inf.tb.) and suspensory ligament (Lig.susp.ov.pr.).

Fig a'.—Median longitudinal section through the right ovary. Under the ovulation surface, "white strumatous tissue" (x), in a deeper situation "brown tissue" (xx) with numerous stages of follicular development. The larger developing Graafian follicles are pushing their way into the white tissue.

Fig. b.—Left ovary in toto with its ovulation surface turned slightly towards the right side; cranially the infundibulum of the oviduct (Inf.tb.) and caudally the suspensory ligament (Lig.susp.ov.pr.).

Fig. b'.—Median longitudinal section through the left ovary. Beneath the concave retracted surface white strumatous tissue (x); deeper down "brown tissue" (xx) with follicles in various stages of development, two of which are growing into the white tissue (Fo.Gr.').

G.—Horse foal, ♀, "*Ho.fo.* 12.332," 9*th September*, 1925.

Right and left ovary in toto; median longitudinal section through the right ovary, and transverse section through the left ovary.

Fig. a.—Right ovary with fimbriae of the oviduct (Inf.tb.) and suspensory ligament (Lig.susp.ov.pr.). Ovulation surface turned towards the observer. Ovary with typical boat-shape (ovulation surface retracted towards the ventral border of the gland).

Fig. a'.—Sagittal longitudinal section through the right ovary. Beneath the ovulation surface we see white ovarian strumatous tissue (x) and, beneath that, brown ovarian tissue (xx) in which different stages of follicular development are embedded (Fo.Gr.').

Fig. b.—Left ovary with its ovulation surface turned slightly towards the left, showing a Graafian follicle (Fo.Gr.) on the surface of the gland.

Fig. b'.—Transverse section through the left ovary. Under the ovulation surface, white strumatous ovarian tissue (x). Underneath the opposite surface, layers of brown ovarian tissue (xx) with embedded Graafian follicles.

H.—Horse, ♀, "*Ho.* 521," 5*th December*, 1925.

Fig. a.—Right ovary with its ovluation surface turned slightly towards the left. A Graafian follicle (Fo.rpt.) whose distal apical portion protrudes beyond the surface of the ovary, has just ruptured. Point of rupture (↓), capillaries (Va.cap.) in the follicle, and superficial blood-vessels of the ovary (Va.va.ov.) are clearly visible.

PLATE X.

Explanation.

G.—Horse, ♀, "*Ho.* 512," 19*th November*, 1925.

Right and left ovary in toto. Median longitudinal section and part of a section through right ovary; median longitudinal section through left ovary.

Fig. a.—Right ovary with its ovulation surface turned outward (lateral surface).

Fig a'.—Median longitudinal section through right ovary.

Fig. a''.—Part of a section through right ovary with the corpus luteum of the latest interovulation period but one (Co.lut.II') cut longitudinally.

Fig. b.—Left ovary with its ovulation surface (lateral surface) turned towards the observer. Former follicle (fresh yellow body, Co.lut.I) closed on the outside, with its apex protruding slightly beyond the surface of the ovary.

Fig. b'.—Median longitudinal section through left ovary with halved corpus luteum of the latest interovulation period (Co.lut.I'). The thickened wall of the new corpus luteum can be seen to be in proliferation. In the vicinity of the point of rupture of the former follicle, the dark red colour indicates the continued bleeding of the follicular wall tissue.

PLATE XI.

Explanation.

K.—Mule, ♀, "*Mlt. x* 8," 27*th October*, 1925.

Right and left ovary in toto and median longitudinal sections through the organs.

Fig. a.—Right ovary in toto. Ovulation surface (lateral surface) turned towards the observer. Mature follicle (Fo.Gr.dil.) near the cranial pole of the ovary.

Fig. a'.—Median longitudinal section through the right ovary and the enlarged mature follicle (Fo.Gr.dil'.).

Fig. b.—Left ovary in toto with its ovulation surface turned towards the observer. The pole of an enlarged Graafian follicle shows through the covering membrane in the middle of the ovulation surface (Fo.Gr.dil.).

Fig. b'.—Median longitudinal section through the left ovary with its Graafian follicle (Fo.Gr.dil.').

PLATE XII.

Explanation

L.—Mule, ♀, "*Mlt. x* 12," 21*st December*, 1925.

Right and left ovary in toto and sections through these organs.

Fig. a.—Right ovary in toto. Ovulation surface turned towards the observer. Ovary cup-shaped. Ovarian surface drawn in, approaching the opposite surface. Fimbriae of the oviduct (Inf.tb.) at the cranial pole, suspensory ligament of the ovary (Lig.susp.ov.pr.) at the caudal pole. The distal portion of the red tissue of the corpus luteum of the latest interovulation period (Co.lut.I) touches the surface of the ovary on the retracted ovulation surface, close to the caudal pole.

Fig. a'.—Longitudinal section through the right ovary. The corpus luteum of the latest interovulation period (Co.lut. I') is cut longitudinally, exposing the thickened wall of the original follicle (now yellow body), as well as the lumen and canal of the former Graafian follicle. The proximal portion of the corpus luteum is enclosed in "brown ovarian tissue" (xx), the distal portion in "white strumatous ovarian tissue" (x).

Fig. b.—Left ovary in toto. Ovulation surface turned slightly towards the right. At the cranial pole the fimbriae (infundibulum) of the oviduct (Inf.tb.) are visible, at the caudal pole the insertion of the suspensory ligament (Lig.susp.ov.pr.).

Fig. b'.—Median longitudinal section through the left ovary. The section shows white strumatous tissue (x) towards the ovulation surface and "brown ovarian tissue" (xx) towards the convex border of the gland.

PLATE XIII.

Explanation.

M.—Mule, ♀, "*Mlt. x* 13," 13*th November*, 1925.

Right and left ovary in toto and median sections through the organs.

Fig. a.—Right ovary, ovulation surface (lateral surface) turned towards the observer. Near the point of attachment of the infundibulum of the oviduct (Inf.tb.) the protruding distal portion of the corpus luteum of the latest interovulation period (Co.lut.I) can be seen.

Fig. a'.—Median longitudinal section through right ovary, with corpus luteum of the latest interovulation period (Co.lut.I'), reduced corpus luteum of the last but one (Co.lut.II') and the previous third latest (Co.lut.III') interovulation period.

Fig. b.—Left ovary. Ovulation surface (lateral surface) turned towards the observer. Fimbriae of the oviduct (Inf.tb.) very much reddened.

Fig. b'.—Median longitudinal section through left ovary, with considerably enlarged almost mature Graafian follicle (Fo.Gr.dil.').

N.—Jennet, ♀, "*Jen. xx* 2, 18*th November*, 1925.

Right and left ovary in toto and longitudinal sections through the organs.

Fig. a.—Right ovary with its ovulation surface turned towards the left. Enlarged Graafian follicle (Gr.Fo.) showing through on the ventral surface of the ovary.

Fig. a'.—Sagittal longitudinal section through right ovary. The remaining tissue of the reduced corpus luteum of the latest interovulation period but one (Co.lut.II'), which belong to ovulation and oestral season of the previous year, can be seen in the ovarian tissue.

Fig. b.—Left ovary with corpus luteum of the latest ovulation period (Co.lut.I) and developing Graafian follicle (Fo.Gr.dil.).

Fig. b'.—Median longitudinal section through left ovary with halved corpus luteum of the latest interovulation period (Co.lut.I') and maturing Graafian follicle (Fo.Gr.dil.').

LIST OF ABBREVIATIONS.

Art.ut. = arteria uterina—uterine artery.
Caud. = caudal.
Co.lut.I = corpus luteum primum—corpus luteum of the latest interovulation period.
Co.lut.I_1 = one of the two corpora lutea of the latest interovulation period (corpus luteum primum).
Co.lut.I_2 = one of the two corpora lutea of the latest interovulation period (corpus luteum primum).
Co.lut.I' = section through corpus luteum of the latest interovulation period (corpus luteum primum).
Co.lut.I_1' = section through one of the two corpora lutea of the latest interovulation period (corpus luteum primum).
Co.lut.I_2' = section through one of the two corpora lutea of the latest interovulation period (corpus luteum primum).
Co.lut.Ir. = corpus luteum primum reductum—reduced corpus luteum of the latest interovulation period.
Co.lut.Ir_1 = one of the two reduced corpora lutea of the latest interovulation period (corpus luteum primum reductum).
Co.lut.Ir_2 = one of the two reduced corpora lutea of the latest interovulation period (corpus luteum primum reductum).
Co.lut.Ir_2'=section through one of the two reduced corpora lutea of the latest interovulation period (corpus luteum primum reductum).
Co.lut.Ir_1'=section through one of the two reduced corpora lutea of the latest interovulation period.
Co.lut.Ir_2' = section through one of the two reduced corpora lutea of the latest interovulation period.
Co.lut.II = corpus luteum secundum or corpus luteum of the latest interovulation period but one.
Co.lut.II' = section through corpus luteum of the latest but one interovulation period (corpus luteum secundum).

Co.lut.IIr = corpus luteum secundum reductum or reduced yellow body of the last but one interovulation period.
Co.lut.IIr′ = section through reduced corpus luteum of the last but one interovulation period (corpus luteum secundum reductum).
Co.lut.III′ = section through corpus luteum of a previous interovulation period (corpus luteum tertium).
Co.lut.grav. = corpus luteum graviditatis—corpus luteum of pregnancy period.
Co.lut.grav.′ = section through corpus luteum of pregnancy period (corpus luteum graviditatis).
Co.lut.r′ = reduced yellow body—corpus luteum reductum.
Co.ut.d. = cornu uteri dextrum—right horn of the uterus.
Co.ut.l = cornu uteri laevum—left horn of the uterus.
Cran. = cranial.
Dors. = dorsal.
Fo.Gr. = folliculus Graafii—Graafian follicle.
Fo.Gr.′ = section of Graafian follicle (folliculus Graafii).
Fo.Gr.dlt. = folliculus Graafii dilatus—enlarged Graafian follicle.
Fo.Gr.dil. = folliculus Graafii dilatus—enlarged Graafian follicle.
Fo.Gr.dil.′ = section through enlarged Graafian follicle (folliculus Graafii dilatus).
Fo.Gr.mt. = folliculus Graafii maturus—mature Graafian follicle.
Fo.Gr.mt.′ = section through mature Graafian follicle (folliculus Graafii maturus.
Fo.Gr.rpt. = folliculus Graafii ruptus—ruptured Graafian follicle [corpus luteum of the latest interovulation period (Co.lut.I)].
Fo.Gr.rpt.′ = section through ruptured Graafian follicle (folliculus Graafii ruptus).
Fo.rpt. = folliculus ruptus—ruptured Graafian follicle.
Inf.tb. = infundibulum tubae, fimbriae oviductus—infundibulum (fimbriae) of the oviduct (tube).
Inf.tb.′ = section through the infundibulum of the oviduct (tube) (infundibulum tubae).
Lat. = lateral.
Lig.susp.ov. = ligamentum suspensorium ovarii—suspensory ligament.
Lig.susp.ov.′ = section through suspensory ligament (ligamentum suspensorium ovarii).
Lig.susp.ov.pr. = ligamentum suspensorium ovarii proprium—ovarian suspensory ligament.
Lig.susp.ov.pr.′ = section through ovarian suspensory ligament (ligamentum suspensorium ovarii proprium).
Med. = medial.
Msp. = mesosalpinx—part of broad ligament which slings the uterine tube.
Ov.d. = ovarian dextrum—right ovary.
Ov.d.′=section through right ovary (ovarium dextrum).
Ov.l. = ovarian laevum—left ovary.
Ov.l.′ = section through left ovary (ovarium laevum).
Tb.ov.d. = infundibulum tubae ovarii dextrum—infundibulum of the right ovarian tube.
Tb.ov.l. = infundibulum tubae ovarii laevum—infundibulum of the left ovarian tube.
Va.cap. = capillaries.
Va.va ov. = vasa vasarum ovarii or ovarian blood vessels.
Ventr. = ventral.
↓ = point of rupture of the follicle.
x = white strumatous ovarian tissue.
xx = brown strumatous ovarian tissue.
xxx = brown ovarian tissue.