

THE REPRODUCTIVE CYCLE OF NEW WORLD  
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TWO TEXT FIGURES AND FOUR PLATES (TWENTY-TWO FIGURES)

The present study deals with the changes in the reproductive tracts of spider monkeys (*Ateles geoffroyi*) and howler monkeys (*Alouatta palliata*). The material is presented for its interest to investigators of primate reproduction, for although the menstrual cycle is known in some detail in several catarrhine monkeys, for example, the rhesus monkey (*Macaca mulatta*) (Corner, '23; Allen, '27; Hartman, '32) and the baboon (*Papio porcarius*) (Zuckerman and Parkes, '32), comparatively little is known about the cyclic changes in the more primitive New World monkeys.

The mating behavior in both *Alouatta* and *Ateles* has been observed in the field by Carpenter ('34, '35), who believes that mating is fairly well restricted to an oestrous period lasting for 2 or 3 days. However, he points out that sporadic mating may occur at other times, and believes that oestrus in these forms is a period during which sexual motivation is greatly reinforced. Because of limitations imposed by the procedure involved in a field study, no data were obtained on the length of the reproductive cycle. Goodman and Wislocki ('35), however, studied a single adult *Ateles* female very carefully in captivity and found a definite vaginal cycle occurring every 24 to 27 days. This cycle consisted of slight bleeding, recognizable in vaginal lavages but never visible externally, lasting 3 or 4 days at each occurrence.

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The amount and character of the sediment obtained from vaginal lavage likewise underwent cyclical changes, being greatest in amount during the intervals between bleedings. These investigators were also able to show that ovulation, during at least two cycles, must have occurred during the interval.

#### MATERIAL AND METHODS

The material on which this study is based was obtained from animals killed in the field.<sup>2</sup> I am deeply indebted to Dr. G. B. Wislocki for permission to use the material and for his interest and advice throughout the preparation of the present article. Field notes were made concerning the behavior of some of the individuals prior to death by Dr. C. R. Carpenter. Notations were also made for the other animals concerning the presence or absence of vaginal plugs. These notes have all proved of great value in determining the stage of the cycle in certain individuals.

Immediately after death the reproductive tracts were dissected free and fixed in Bouin's fluid or 10% formalin. Later, dehydration and embedding in paraffin were effected. Serial sections of the ovaries, 16  $\mu$  in thickness, were prepared and stained in either Ehrlich's or Heidenhain's hematoxylin. Representative sections of vagina, uterus and mammary gland were also prepared and similarly stained.

Measurements of follicular size were made by reference to the Vernier scale of a mechanical stage. The two largest diameters were taken at right angles and the average computed. This procedure, although not rigorous, permits a numerical estimate of follicular size at various stages of the

<sup>2</sup>The material utilized in this study was collected by Drs. C. R. Carpenter, A. H. Schultz, F. F. Snyder, G. B. Wislocki and Mr. O. O. Heard on various trips to Central America. Acknowledgment is due the Linton Fund, established in memory of Dr. Edward S. Linton, a graduate of the Johns Hopkins Medical School, from which a grant was made for an expedition to Nicaragua in 1924. An additional grant was contributed by the Carnegie Institution of Washington. Subsequent trips in the Republic of Panama were made under the auspices of the Barro Colorado Island Laboratory for Tropical Research and the Gorgas Memorial Institute. The success of these trips was materially due to the aid and advice of Dr. James Zetek and Dr. Herbert Clark.

cycle. All follicles larger than 1 mm. diameter were measured in all ovaries and the largest normal follicle was used as an index of follicular size in correlations of the ovarian stage with the development of the uterus and vagina. The diameters of ova were measured directly with the aid of a micrometer eyepiece at a magnification of  $\times 325$ . Ten ova were measured in each of five follicular sizes and the average computed for purposes of comparison of ovum to follicular size.

In all, 51 specimens of howler monkeys and 45 specimens of spider monkeys were available for study.<sup>3</sup> Five howlers and three spiders were immature, 12 howlers and 17 spiders were lactating and three individuals of each species were pregnant. The remainder were adult animals in various stages of the reproductive cycle. For purposes of reference, these stages have been classified as early and late follicular and luteal phases.

The ovaries of both species are essentially similar in both gross and microscopic appearance. For this reason, no attempt has been made to describe each species separately, except for such minor differences as do occur.

#### OBSERVATIONS

*The ovary.* The ovaries of both forms are large, ovoid structures varying from 5 mm. in juveniles to 15 mm. or more in greater diameter in adults. This large size is accounted for in part by the size of the follicles, as it is not uncommon to find several follicles 2 to 4 mm. in diameter in a single ovary. Much more important, however, in the attainment of size is the large amount of interstitial tissue which is dispersed throughout the stroma.

In juvenile and certain adult animals the interstitial tissue is composed of a single cell type which appears indistinguish-

<sup>3</sup>It has also been possible to study a limited number of specimens of the capuchin monkey (*Cebus capucinus*). The reproductive tracts of this species, although not numerous enough for detailed comparisons, have many characteristics in common with *Ateles* and *Alouatta*, and occasional references to such similarities will be made in the text.

able from the granulosa cells. This interstitial tissue is frequently organized into more or less spherical bodies, with or without a central cavity, whose outlines suggest a follicular origin. Unbroken stages may be found from which the origin of these cells may be traced to atretic follicles.

These interstitial cells, however, are probably not of single origin, as their appearance in juvenile animals would suggest, but may be derived from both the granulosa and from the theca interna which hypertrophies markedly during atresia. At the time of ovulation lutein changes occur in some of these interstitial cells. Those cells occupying the center of the spherical masses, and therefore derived presumably from the granulosa elements, are transformed most rapidly and completely. Marked swelling of the peripherally located thecal derivatives occurs, but complete luteinization of these outer cells never takes place during the cycle. Figure 3 shows a follicle in an early stage of atresia in which hypertrophy of the theca interna is clearly shown. Beneath this follicle lies an ovoid mass whose center is composed of a core of large, typical lutein cells surrounding the remnant of a collapsed central cavity. The outer layer surrounding the lutein core is made up of smaller cells which are similar in appearance to the hypertrophied thecal cells of the atretic follicle.

Eight specimens are available in which it is known that copulation had occurred shortly before death. In seven of these ovulation had already taken place and recent corpora lutea whose diameters were 5 to 6 mm. were found in the ovaries (fig. 4). The ovaries of the eighth animal contained a large follicle, 6 mm. in diameter, and since this is the diameter of the largest normal follicles observed in any ovaries, it is thought that 6 mm. approximates the diameter of the follicle at maturity.

A progressive thinning of the ovarian wall occurs during the enlargement of the follicles, resulting in the formation of a well-defined stigma at maturity. The position of the cumulus and ovum bears no constant relation to the location

of the stigma, since the two have been observed to be opposite in two cases and less than  $90^\circ$  apart in at least three other instances.

The theca interna of the mature follicle is a well-defined structure, which, in the region adjacent to the cumulus, may reach a thickness of from five to ten cell layers (fig. 5). Its thickness diminishes with distance from the cumulus and may be only one cell layer in thickness or completely absent at its thinnest point opposite the ovum.

For a considerable period after ovulation, the corpus luteum is readily distinguishable from the dispersed interstitial tissue. Indeed, in very recently ruptured follicles, little luteal transformation is noted before ingrowth of capillaries into the granulosa layer occurs, although considerable amounts of interstitial lutein tissue may be found. Coincidentally with the ingrowth of the capillaries, swelling and fat deposition occur in both theca interna and granulosa cells, the former undergoing transformation more rapidly. Although luteinization of the granulosa elements occurs more slowly, these cells finally become larger and contain more fat than do the thecal derivatives. During the whole of the lifetime of the corpus luteum it is possible to distinguish between the thecal and granulosa elements on grounds of appearance and position.

Soon after ovulation the rupture point becomes covered by an epithelial outgrowth from the serosa and reunion of the tunica albuginea occurs (fig. 4). The rupture pathway through the theca interna and granulosa layers also becomes obliterated and the corpus luteum becomes a more or less spherical, thick-walled structure containing a central cavity, as is shown in figure 8. The period during which this central cavity is present has been designated as the early luteal phase. At this stage, and during pregnancy, no large follicles are found in the ovaries. The large follicles which do not rupture at ovulation rapidly become atretic and undergo luteinization. Many small follicles, ranging in size up to 1 mm. in diameter, may be found, but the larger of

these follicles invariably show signs of atresia while the continued presence of many small luteinized masses of about this size and shape scattered throughout the ovary attests to their ultimate fate.

Later in the luteal phase the central cavity of the corpus luteum becomes infiltrated with connective tissue and disappears (fig. 9). The general outlines of the corpus luteum become less sharply defined until finally the luteal tissue becomes dispersed and indistinguishable from the interstitial lutein tissue (fig. 10). This phase, like the preceding one, is characterized by atresia of small follicles with the result that no large follicles are found.

The luteal phases described above are followed by a period of follicular development. At first, no change is evident in the amount of interstitial lutein tissue, but normal growing follicles whose diameters range up to 4 mm. may be found. These ovaries have been classified as early follicular phases, while ovaries which contain follicles 4 mm. or more in diameter have been arbitrarily classed as late follicular phases. Such ovaries continue to show interstitial lutein tissue, although there appears to be a progressive decrease in size and number of the lutein cells as the follicles become progressively larger. Nevertheless, considerable numbers of lutein cells may be found even in ovaries containing mature or very recently ruptured follicles, and it is therefore believed that at no time in the cycle is there a complete disappearance of these interstitial elements.

Measurements of ovum diameters were made in follicles of different sizes for purposes of comparison of the growth curves of the ova in relation to the enlargement of the follicles. These measurements were made in primordial follicles in which there is a single layer of follicular cells, in follicles containing two or three layers of follicular cells, in the smallest antrum-containing follicles, in follicles of 1 to 2 mm. diameter with well-formed antra and in mature follicles of approximately 6 mm. diameter. Ten ova were measured in each case, the average computed and the ovum diameter

plotted against follicular diameter (fig. 1). It will be seen that the ovum attains its maximum size soon after the antrum appears in the follicle, a situation similar to that found in other mammalian forms (Parkes, '31). The size of ova in relation to their follicles is approximately the same in both species during the early growth of the follicles, but in the older, larger follicles the ova in spider monkeys are larger than those found in howlers.

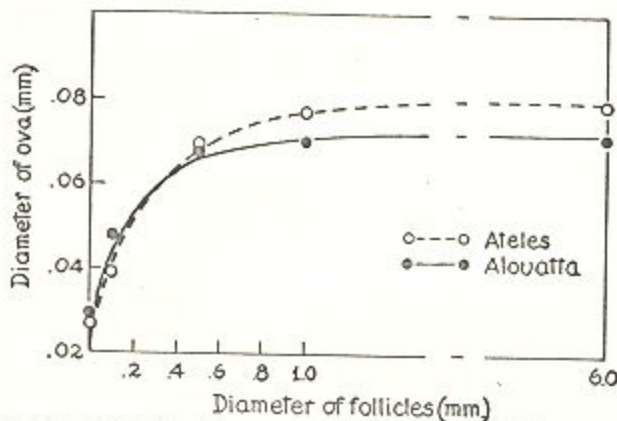


Fig. 1 The relationship between ovum diameter and follicular diameter in *Ateles* and *Alouatta*.

A further difference between the two species is the size of the follicle when the antrum forms. In howlers the largest solid follicles have only two or three layers of follicular cells and many antrum-containing follicles of only slightly greater diameter may be found. Spider monkey ovaries, on the other hand, contain solid follicles of 0.3 to 0.4 mm. diameter and no antrum-containing follicles smaller than this are ever found.

Two abnormal conditions which have been observed also deserve mention. The first of these is cystic degeneration of large follicles. These cysts apparently arise from failure of large follicles to rupture, since in the four cases observed the other follicles and interstitial tissue in the ovaries were in a condition comparable to that seen shortly after ovulation. These greatly enlarged follicles may have a diameter

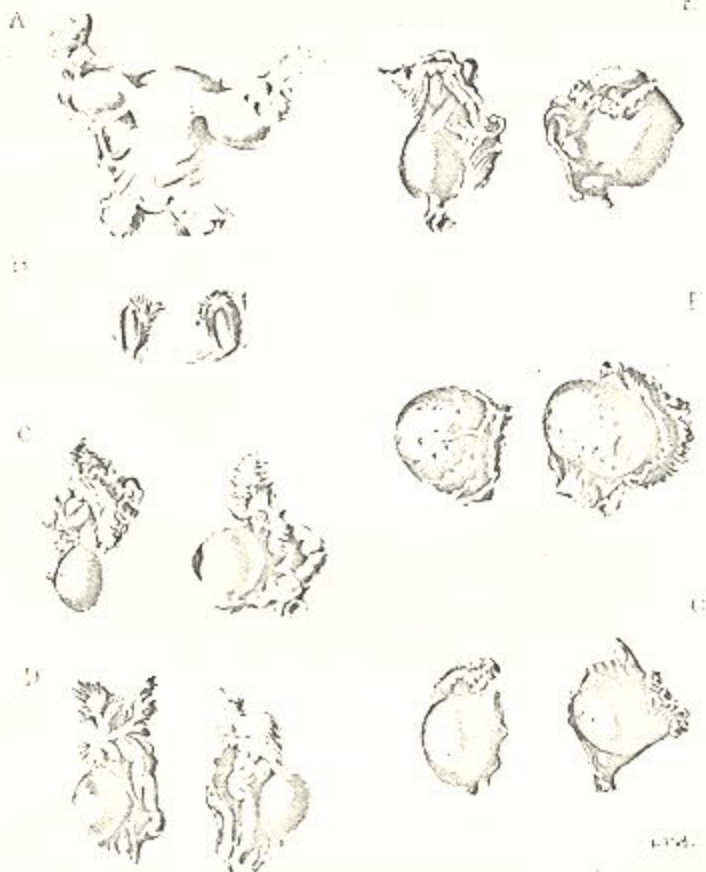


Fig. 2 (A) Ovaries and uterus of *A. lewisi* showing rupture point of recently ruptured follicle. (B) Ovaries from immature *Ateles*. (C) Ovaries from non-pregnant *Ateles*. A large cystic blood follicle may be seen in the right-hand figure. (D) Ovaries from non-pregnant *Ateles* during early luteal phase showing corpus luteum. (E) Ovaries of pregnant *Ateles* from which a 7-somite embryo was recovered. (F) Ovaries from pregnant *Ateles*, approximately middle of gestation. (G) Ovaries from pregnant *Ateles* near the end of gestation. All figures are  $\times 0.75$ .



of as much as 12 mm. and can readily be recognized as follicles by the presence of granulosa layers and ova. In some of these follicles the granulosa layer appears degenerate in certain places, but in others, the cumulus oöphorus particularly may appear quite normal. In all the observed cases the ovum was detached from its connections with the cumulus cells and in two instances degenerating maturation spindles were observed.

The second pathological condition, found in nine animals, is a cystic enlargement of the rudimentary rete ovarii tubules. These cysts are large, fluid-filled structures which in extreme cases may reach a diameter of 15 mm. The epithelium lining these cavities is of either a low cuboidal or stratified squamous nature, distinguishing these cysts from the follicular cysts mentioned above. Frequently, what appears from the surface to be a single large cyst will be found in sections to be composed of several freely communicating cysts, a fact which suggests their rete origin (fig. 5). They have been observed in *Alouatta*, *Ateles* and *Cebus*, and they are entirely comparable to similar cysts which have been observed in the ovaries of guinea pigs (Myers, Young and Dempsey, '36).

*The ovary during pregnancy.* The ovaries from the six pregnant specimens were all larger than those removed at other times. This relationship is shown quite clearly in figure 2. It will be seen that the ovaries corresponding to early, middle and late stages of pregnancy (E, F and G) are all considerably larger than the non-pregnant specimens of the same species (C and D). Moreover, the ovaries appear to attain their greatest size during the first half of pregnancy and to shrink somewhat in volume during the later stages. Histological examination shows that this enlargement during pregnancy is due to an increase in the amount of interstitial lutein tissue. Figures 11 and 12 are sections through the ovaries shown in figures 2E and 2G, and show the large quantities of interstitial lutein tissue which are present at these times.

The interstitial elements are composed of two cell types during the cycle, as has been described previously. During pregnancy, however, the large lutein cells become more and more numerous, until during the middle and latter stages the interstitial tissue is composed exclusively of this cell type and the ovaries present a solidly luteinized appearance. The formation of this interstitial luteal tissue has so obscured the true corpus luteum that its identity has been completely lost (fig. 12).

Throughout pregnancy no large follicles are formed. Many small antrum-containing follicles may be found, usually in clusters or islands at the poles of the ovaries. The largest of these follicles always show atretic transformation and lutein changes which are, on a lesser scale, entirely comparable to the changes described during the luteal phase of the cycle.

*The ovary during lactation.* Carpenter ('34) observed that sexual behavior does not occur in howler females which are carrying small infants, although mating behavior does occur long before weaning. From these facts he infers that there is a suppression of primary sex activity during the early part of lactation and that several oestrous periods may occur before a fertile mating takes place. If this were true, one would expect such a situation to be reflected in the condition of the ovaries during lactation. The ovaries from three of the twelve lactating howler females which were examined contained no large follicles and greater amounts of interstitial lutein tissue than was ever seen at any stage in the cycle. The ovaries from seven animals contained growing follicles of 2 to 4 mm. diameter, and in two animals indubitable corpora lutea were present. In all of these cases abundant interstitial lutein tissue was found. Unfortunately, no record exists concerning the size of the infants carried by these individuals, so a correlation of the ovarian condition with the early and late phases of the lactation period cannot be made. For the present, therefore, we can only arrive at the tentative conclusion that follicular

growth and ovulation appear to be suppressed in the ovaries of certain lactating howler females.

The evidence in favor of suppression of ovulation during lactation is considerably stronger for *Ateles*. None of the ovaries from seventeen lactating animals contained a corpus luteum. Interstitial lutein tissue was present in nine instances, in seven of which only small follicles were present, while in two instances growing follicles of 2 to 3 mm. diameter were found.

The ovaries from the remaining eight lactating spider monkeys contained no lutein tissue of any kind. The interstitial tissue contained only one cell type which resembled the granulosa cells of atretic follicles. Medium to large sized follicles, ranging from 2 to 4 mm. diameter were found in all of these cases (figs. 6 and 7). Three of the animals in this latter group were carrying large young when killed and therefore were approaching the end of the lactation period. Since no evidence of ovulation was found in the ovaries of these animals, it is believed that ovulation does not occur at any time during lactation in this species.

*The vagina.* The epithelial lining of the vaginal lumen in juvenile *Ateles* is a conventional, low stratified layer. Adult animals, however, show an extremely well-developed vaginal lining. The thick, stratified basal layer is surmounted by many cell layers of keratinized cells. During the follicular phase this outer, cornified layer is thrown into ridges, resulting in the formation of numerous denticles which project into the vaginal lumen (fig. 15). These denticles and the surface layers of cornified cells are sloughed off into the lumen during the late follicular phase and for a short time after ovulation. The desquamation of these surface layers is thought to be the origin of the sediment which Goodman and Wislocki ('35) observed in vaginal lavages from an adult spider monkey. Since these authors found the greatest amounts of sediment to occur at the mid-interval between bleedings, and since the greatest amount of desquamation occurs at near the time of ovulation, it is thought that this is further evidence

for the belief that ovulation occurs during the interval in this species.

Complete desquamation of the cornified layer, however, does not occur at the time of ovulation. Figure 16 shows a section taken through the vagina during the luteal phase. It will be noted that the cornified denticles are no longer present, although there is still a well-developed layer of cornified cells which lines the vaginal lumen.

The early stages of lactation are characterized by a low, stratified vaginal epithelium, comparable to that seen in juvenile animals. This low epithelium gradually grows higher as follicular growth occurs in the ovaries. Cornification of the outer layers of cells begins when follicles of 2.5 to 3 mm. diameter are present. The cornified layer grows thicker and the spinous denticles become more marked as the follicles grow larger until, during late lactation, the vaginal epithelium is indistinguishable from that seen during the late follicular phase.

The presence of a low, basal vaginal epithelium during the greater part of the lactation period presumably indicates the absence of large, maturing follicles in the ovaries. Likewise, the spinous denticles, which are always found together with large follicles, appear only during late lactation. For these reasons, it is thought that the appearance of the vaginal epithelium supports the belief that there is a suppression of follicular growth and ovulation during lactation.

The vaginal epithelium of *Alouatta* is much simpler in character and shows few changes which can be correlated with the ovarian cycle (figs. 13 and 14). Occasional females show an outer keratinized, non-nucleated layer of cells which, when it is found, occurs during the late follicular phase. This cornification, however, does not occur in all animals and it is never so marked as is the case of *Ateles*. Indeed, the vaginal epithelium in both juvenile and adult howler monkeys shows a marked resemblance to that observed in juvenile spider monkeys.

Field notes made at the time of autopsy mention that the vaginae of several specimens from both howler and spider monkeys contained a plug of soft, transparent gelatinous material which formed a cast of the vaginal lumen. The plugs were quite friable and easily broken up. This vaginal plug was similar in consistency to the agonal ejaculate which was observed occasionally at the external urethral orifice upon autopsying males. In two spider monkeys Doctor Wislocki reports having observed spermatozoa in the fresh plug, while in others no sperm could be found on microscopical examination. Sections of these plugs were not prepared because upon fixation they became entirely broken up into amorphous precipitate.

*The uterine endometrium.* The uteri of both species show marked changes during the reproductive cycle which are qualitatively similar to, but do not approximate in degree, those which have been described for the maeaque (Corner, '23) and human (Bartelmez, '33). During the follicular phase the cells lining the lumen are low columnar with basally located, densely staining nuclei. The uterine glands are straight and penetrate into the mucosa for only a short distance. The lumina of the glands are only slightly dilated and numerous mitotic figures can be observed (figs. 17 and 19).

During the luteal phase the surface epithelium increases in height while the nuclei enlarge and become vesicular. Marked spiral coils appear in the glands, and mitotic figures are still seen frequently in both the surface and glandular epithelium. Secretion products and cellular debris may be observed in the glandular lumina, resulting in marked distension, and the glands penetrate deeper into the basal layers than occurs during the follicular phase (figs. 18 and 20).

Later in the luteal phase, corresponding to stages in which the central cavity of the corpus luteum is becoming filled or in which growing follicles are first encountered, areas of degeneration and desquamation may be seen in the surface epithelium. The glandular lumina become filled with sloughed

off cells and leucocytes which may be seen migrating through the glandular epithelium. Red blood cells are found in the lumen of the glands, and occasional lacunae or pockets of extravasated erythrocytes may be found just under the surface epithelium. Erythrocytes may be seen entering the lumen of the uterus from the necks of the glands and from the lacunae when tissue breakdown occurs (figs. 21 and 22). Such bleeding has been observed in two specimens of *Ateles*, one specimen of *Alouatta* and in two specimens of *Cebus*. This is thought to be the source of the slight, cyclical bleeding which was observed in *Ateles* by Goodman and Wislocki ('35).

*Discussion.* The occurrence of large numbers of lutein cells in the interstitial tissue of the ovary throughout the entire reproductive cycle raises immediate questions concerning their origin. The presence of transition stages between atretic follicles and the spherical masses of interstitial tissue whose cores are composed of luteal cells indicates that this luteal tissue does not represent the remains of degenerating corpora lutea but that it is formed during the cycle in complete independence of the corpus luteum of ovulation.

Both theca interna and granulosa apparently contribute to the interstitial tissue. Marked thecal hypertrophy occurs in atretic follicles (fig. 3) and in early corpora lutea. During the cycle these peripherally located thecal elements retain their histological characteristics and are distinguishable from the central lutein tissue in both the corpus luteum and the smaller masses formed from atretic follicles. Luteinization of the outer, thecal derivatives apparently can occur if there is sufficient stimulus, since during the middle and latter stages of pregnancy only one cell type can be recognized, resulting in ovaries which are composed of solidly luteinized masses which are indistinguishable from the true corpus luteum.

Thecal enlargement and luteinization after experimental procedures and during pregnancy have been noted in other forms. Zuckerman ('31) has described lutein changes in small atretic follicles during early pregnancy in *Macaca irus*,

and Zuckerman and Parkes ('32) have reported similar structures in the ovary of the pregnant baboon. Occasional bodies are found in this latter species which contain a central core of large lutein cells. These authors believe these large, centrally placed cells are derived from the granulosa while the outer, smaller elements may be thecal in origin. These bodies are strikingly similar to the luteinized atretic follicles which are found in *Ateles* and *Alouatta*. In these New World monkeys, however, this type of luteinization occurs regularly during the cycle while during pregnancy still more marked lutein changes result in the complete transformation of all interstitial cells.

These luteinized interstitial cells were observed in the ovaries of *Ateles* and *Alouatta* by Snyder ('28), who discussed their significance in relation to ovulation. In the present study such cells have been found in *Ateles*, *Alouatta* and *Cebus*. Moreover, Wislocki ('38) has described a similar condition in the ovaries of the marmoset, *Oedipomidas geoffroyi*. Apparently, therefore, interstitial lutein tissue occurs quite generally in platyrrhine monkeys.

The functional significance of this extreme luteinization is unknown. Lutein tissue is the generally accepted anatomical indicator of the action of luteinizing hormone, and is the site of production of progesterone. Cyclic changes in the uterus, however, indicate that variation in the progesterone output occurs despite the continued presence of large quantities of morphologically unchanged lutein tissue. Similarly, large amounts of lutein tissue are present at the time of ovulation although ovulation is inhibited by progesterone in rodents (Makepeace, Weinstein and Friedman, '37; Dempsey, '37). It seems clear, therefore, that the physiological activity of the luteal tissue cannot be correlated too closely with its anatomical presence. Whether or not the large amount of luteal tissue is, in fact, an indicator of equally large amount of luteinizing hormone and progesterone must remain a question for experimental procedures to answer.

The observation of cystic degeneration of large follicles in four cases of the present series indicates the possibility that anovulatory cycles may occur in these species as well as in the macaque (Hartman, '32) and human (Bartelmez, '33). The continued formation of interstitial lutein tissue from atretic follicles makes it impossible to estimate whether or not ovulation had occurred during the preceding cycle. However, the conversion of atretic follicles into interstitial tissue occurs so generally during the luteal phase of the cycle that it offers support to the belief that cyclic changes were occurring in these ovaries, regardless of the failure of ovulation.

It has already been mentioned that the ovarian condition supports Carpenter's belief that there is a temporary sterile period during lactation in *Alouatta*. In *Ateles*, moreover, this period of sterility apparently lasts throughout the entire period of lactation and must therefore operate to limit the number of young produced by a given female during her lifetime. This lactation sterility may well account, at least in part, for the low birth rate which has been observed in this species (Wislocki, '30).

#### CONCLUSIONS

1. During the reproductive cycle and pregnancy large quantities of interstitial tissue are formed in the ovaries as a result of luteal transformation of atretic follicles. This interstitial tissue is of two cell types, a large cell, apparently derived from the granulosa and indistinguishable from the cells of the corpus luteum, and a smaller cell whose appearance and position suggest its derivation from the theca interna. During pregnancy, complete luteinization of all interstitial elements occurs, resulting in complete loss of identity of the true corpus luteum.

2. Follicular growth does not occur during the luteal phase of the cycle. Some time after degenerative changes appear in the corpus luteum, however, enlargement of the follicles begins. Likewise, during pregnancy there is a suppression



of follicular growth. During lactation, ovulation appears to be completely suppressed in *Ateles*, while in *Alouatta* reestablishment of the cycle and of ovulation occurs before the end of lactation.

3. Cyclic desquamation of the extremely thick, cornified vaginal epithelium occurs in *Ateles*. *Alouatta*, on the other hand, has a less well-developed vaginal lining in which cyclic changes are quite inconspicuous.

4. Cyclic changes occur in the uterine endometrium which are comparable to those described for other primates. Degeneration and desquamation of the uterine epithelium occur at the time of the breakdown of the corpus luteum, and loss of blood into the uterine lumen has been observed.

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## PLATE I

## EXPLANATION OF FIGURES

- 3 Atretic follicle from *Ateles* showing beginning of thecal hypertrophy, and adjacent interstitial body with core of large lutein cells surrounded by smaller, presumably thecal, cells.  $\times 55$ .
- 4 Section of recently ruptured follicle from *Alouatta*, showing rupture point and beginning of luteinization of granulosa.  $\times 55$ .
- 5 Section of 6-mm. mature follicle of *Ateles* showing granulosa and theca interna.  $\times 55$ .
- 6 Ovary from lactating *Ateles*, showing enlarged rete ovarii cyst and medium-sized follicles.  $\times 3\frac{1}{2}$ .
- 7 Ovary from lactating *Ateles*, showing many medium to large sized follicles and very little interstitial tissue.  $\times 3\frac{1}{2}$ .



## PLATE 2

### EXPLANATION OF FIGURES

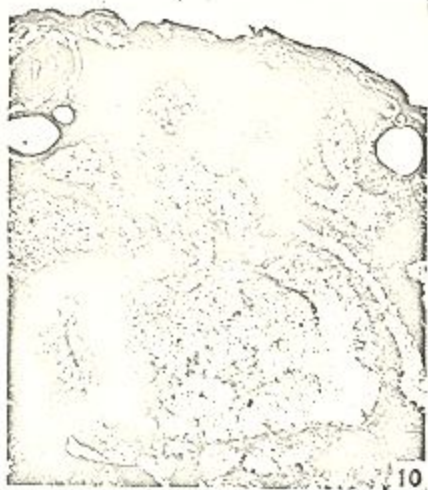
8 Early corpus luteum of *Alouatta*, showing central cavity.  $\times 17$ .

9 Corpus luteum of *Alouatta*, showing filled-in central cavity and repaired rupture pathway.  $\times 17$ .

10 Degenerating corpus luteum of *Alouatta*. The irregular outlines and the general similarity to the interstitial tissue are characteristic. Compare with the lower part of figure 3.  $\times 17$ .

11 Section through *Ateles* ovary of early pregnancy shown in figure 2E. The corpus luteum, shown at the top, can still be identified although extremely large amounts of interstitial lutein tissue are present.  $\times 3\frac{1}{2}$ .

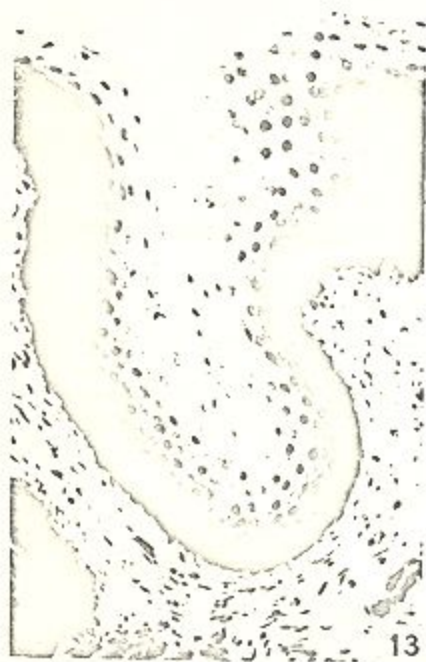
12 Section through *Ateles* ovary of late pregnancy shown in figure 2G. The ovary is composed almost entirely of luteinized tissue and the true corpus luteum can no longer be identified.  $\times 3\frac{1}{2}$ .



### PLATE 3

#### EXPLANATION OF FIGURES

- 13 Vaginal epithelium of *Alouatta* during late follicular phase.  $\times 165$ .
- 14 Vaginal epithelium of *Alouatta* during mid-luteal phase.  $\times 165$ .
- 15 Vaginal lining of *Ateles* during late follicular phase, showing denticles in outer layer and de-quamation into the vaginal lumen.  $\times 65$ .
- 16 Vaginal lining of *Ateles* during the mid-luteal phase.  $\times 65$ .



## PLATE 4

### EXPLANATION OF FIGURES

- 17 Uterus of *Alouatta* during late follicular phase.  $\times 140$ .
- 18 Uterus of *Alouatta* during mid-luteal phase.  $\times 140$ .
- 19 Uterus of *Ateles* during late follicular phase.  $\times 140$ .
- 20 Uterus of *Ateles* during mid luteal phase.  $\times 140$ .
- 21 Uterus of *Ateles* during late luteal phase. Sloughed off epithelium may be seen in the lumen. Erythrocytes and leucocytes are present in the lumina of the degenerating glands.  $\times 140$ .
- 22 Uterus of *Ateles* during late luteal phase. A degenerating gland opens into a denuded surface area. Leucocytes may be seen migrating through the glandular epithelium.  $\times 140$ .



