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ON A SERIES OF PLACENTAL STAGES OF A PLATYRRHINE
MONKEY (ATELES GEOFFROYD) WITH SOME REMARKS
UPON AGE, SEX AND BREEDING PERIOD
IN PLATYRRHINES

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With five plates

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INTRODUCTION

Our knowledge of more than isolated specimens illustrating the intrauterine development of Simiæ is scant. It is becoming recognized, however, that development and reproduction in man is difficult to trace without a phylogenetic understanding of the morphology and physiology of reproduction in mammalia in general and more specifically in the Simiæ. The present paper undertakes to describe a small, but rather well-spaced series of developmental stages of one of the lower monkeys. *Ateles geoffroyi*, a species of spider monkey, belongs to the group of platyrrhine or new-world monkeys indigenous to the American tropics. In addition to this, the paper contains some data gathered over a period of years upon the age, sex and breeding period of *Ateles* and other platyrrhines, as well as a few isolated observations upon the reproductive organs of both male and female *Ateles*.

MATERIAL

In the course of several summers spent in Central America the writer collected five pregnant uteri of *Ateles geoffroyi*, two from Nicaragua and three from the Province of Chiriqui, Republic of Panama. These uteri along with other reproductive material were carefully preserved in Bouin's fluid immediately after killing the animals.

The author is indebted to the Barro Colorado Island Laboratory for Tropical Research, Panama Canal Zone, for the opportunity to secure this valuable material. The specimens were obtained on an expedition to the Province of Chiriqui, Panama, in the company of Dr. H. C. Clark and Major L. H. Dunn of the Gorgas Institute and of Dr. A. H. Schultz of the Johns Hopkins University. The specimens from Nicaragua were obtained by Dr. Schultz and myself on an expedition aided by a grant from the Linton Fund of the Johns Hopkins Medical School.

The material consists of a quite young specimen in which there is an embryo of approximately 12 somites, of a uterus in which there is a fetus 48-mm. crown-rump length, and of three uteri containing fetuses near term measuring 187, 188 and 195 mm. crown-rump length respectively. The placenta of two of the larger fetuses (crown-rump lengths 187 and 195) were the subject of a previous communication (Wislocki, '26).

OBSERVATIONS ON AGE, SEX AND BREEDING PERIOD IN PLATYRRHINES

The following data, collected by Dr. A. H. Schultz and myself upon a number of genera of platyrrhine monkeys, including *Ateles*, are of considerable interest. They give information concerning the age, sex, fertility and breeding habits of several groups of wild monkeys. Previous observations of this kind on the Simiæ in their native habitat are non-existent, except the conclusion arrived at by Joa-

chimovitz ('28) from a study of an Asiatic monkey (*Pithecus fascicularis*) that conception reaches a peak in October and November, during the transition from the dry to the wet season, while the majority of the births occur in April at the beginning of the dry season. In this connection, too, the observations of Hartman ('29) should be quoted to the effect that "nineteen pregnancies in the Carnegie monkey colony (*Macacus rhesus*) have taught us that the months October to January constitute the optimum time for conception, fifteen cases falling within these months, with seven in November alone." The summer months constitute the non-breeding season in Hartman's colony of macaques. The collection of further similar data should lead ultimately to a better understanding of the physiology of reproduction in the Simiæ in general.

TABLE 1—Age and sex in platyrrhines collected in Nicaragua in 1923 and 1924 and in Panama in 1929

Species	Age	Sex undifferentiated	♂	♀	Species	Age	♂	♀	
<i>Ateles geoffroyi</i>	Embryos	1	0	0	<i>Saimiri oerstedii</i>	Fetuses	0	0	
	Fetuses	0	1	3		Juveniles	7	3	
	New-borns	0	1	2		Adults	17	19	
	Juveniles	0	8	9		Total	24	22	
	Adults	0	20	45					
Total	1	30	59						
<i>Cebus capucinus</i>	Embryos	2	0	0	<i>Oedipomidas geoffroyi</i>	Fetuses	0	0	
	Fetuses	0	0	0		Juveniles	3	0	
	Juveniles	0	4	5		Adults	7	4	
	Adults	0	23	20		Total	10	4	
	Total	2	27	25					
<i>Alouatta palliata</i>	Embryos	4	0	0	<i>Aotus zonalis</i>	Fetuses	0	0	
	Fetuses	0	7	5		Juveniles	0	2	
	New-borns	0	0	3		Adults	3	3	
	Juveniles	0	13	10		Total	3	5	
	Adults	0	58	83					
	Total	4	78	101					

Genus	No. adult females	No. pregnancies	Percentage of pregnancies	Sex ratios
<i>Ateles</i>	45	5	11.1	♂ ♀ 51 to 100
<i>Alouatta</i>	83	16	19.3	70 to 100
<i>Cebus</i>	20	2	10.0	108 to 100
<i>Saimiri</i>	19	0	0	90 to 100
<i>Oedipomidas</i>	4	0	0	
<i>Aotus</i>	3	0	0	

SEX-RATIOS

Ateles: 51 males to 100 females.
Alouatta: 70 males to 100 females.
Cebus: 108 males to 100 females.
Saimiri: 90 males to 100 females.

The animals from which our data are compiled were shot without reference to selection in their wild state, so that the figures can be relied upon as giving a true picture of the natural population. Our tables bring out a number of interesting points concerning the sex-ratios, fertility and the question of a breeding season.

SEX-RATIO

Females are found to preponderate in *Ateles* with 51 males to 100 females, with *Alouatta* (the howling monkey) next with 70 males to 100 females, followed by *Saimiri* (the titi monkey) with 90 males to 100 females.

The great preponderance of females in the spider and howling monkeys is an interesting observation which requires explanation. Either fewer males than females are produced in these species due to an uneven sex-ratio in the germinal cells or the males are subject to a higher intrauterine or post-natal mortality than the females. At present our series of intrauterine and early postnatal stages is too small to attempt to answer this question.

FERTILITY AND BREEDING SEASON

According to our data, there is a great difference in the percentage of pregnancies in the groups. *Alouatta* exhibits the highest percentage of pregnancies—almost twice as many as either *Ateles* or *Cebus*, which are about equal. In *Saimiri*, with approximately the same number of females as in the *Cebus* group, there are no pregnancies. The total number of observations for *Oedipomidas* (the marmoset) and for *Aotus* (the night-monkey) are too small to permit any deductions. In order to evaluate the figures for percentages of pregnancies in *Ateles*, *Alouatta*, *Cebus* and *Saimiri* we have to consider the question of their breeding season. It must be added at this point that our specimens were all caught during the months of July and August, although in separate years. Thus we are dealing with a survey of the population at a specific season of the year. Upon consulting the data of the table for *Ateles*, *Cebus* and *Alouatta*, it is seen that in these genera embryos, fetuses, new-borns and juveniles occur in about equal proportions. In other words, at any given moment one finds in the population representatives of all stages of development. It might be added, moreover, that the animals listed as juveniles range uninterruptedly in age from birth until maturity, as evidenced by the size of the specimens and the eruption of the teeth. The most likely inference from these data is that in *Ateles*, *Cebus* and *Alouatta* there is no fixed breeding season, but that the animals reproduce during all or at least a large fraction of the year.

The data for *Saimiri*, on the other hand, suggest the opposite, namely, that the breeding season is much more limited. Our series of adult females of *Saimiri* is too small, however, to advance this conclusion more than tentatively. Nevertheless, among the 10 juveniles collected there were only age-stages close to adult life in contrast to the wide variability of age-stages found in the juveniles of *Ateles* and *Alouatta*. The opinion of reliable native hunters is to the effect that the breeding season of *Saimiri*, *Oedipomidas* and *Aotus* is periodic. However the test of this opinion awaits actual proof. But it is interesting that the genera *Ateles*,

Alouatta and *Cebus*, in which a wide breeding season is suspected, are more highly differentiated than the other genera—*Saimiri*, *Oedipomidas* and *Aotus*—which are considered to be the most primitive representatives of the platyrrhines.

Assuming from our data that the genera *Ateles*, *Alouatta* and *Cebus* breed throughout all or most of the year, then the fertility-rate of *Ateles* and *Cebus*, compared with *Alouatta*, is low as judged by the percentage of pregnancy. The causation of the relatively low fertility rate of *Ateles* and *Cebus* is obscure. It might be ascribed to one of the diseases—filariasis, trypanosomiasis and malaria—to which these wild animals are subject to a large degree (Clark, '30). This seems not far-fetched as a causal explanation, as the two genera *Ateles* and *Cebus* which have an unprecedentedly low birth-rate are subject to severe abdominal filariasis. Every member of these two genera which has been autopsied by us—in all over 250 animals—shows a severe peritonitis associated with the presence of dozens of large filarial worms within the peritoneal cavity. There was without exception a sero-sanguinous exudate in the abdominal cavity accompanying a chronic inflammation of the serosa; this inflammatory process apparently led to widespread adhesions and the presence of shaggy granulation tissue over the surfaces of the viscera (including the ovaries). This pathological condition, although evidently not preventing ovulation, might well result in a great number of the ova becoming defective and failing to become fertilized.

PLACENTATION OF ATELES GEOFFROYI

The material of the present series may be conveniently grouped into three stages by reference to the condition of the uterus and of the development of the placenta. The early stage consists of the youngest specimen containing a 12-somite embryo. The intermediate stage consists of the uterus and placenta belonging to the 48-mm. fetus and the late stage is represented by the three specimens which are close to term. A description of these three stages will be given, followed by a discussion of the salient findings.

EARLY STAGE

This specimen contains a well-preserved embryo of approximately 12 somites (figs. 3, 4 and 5). The enlarged body of the uterus is nearly globular (fig. 1). The ovaries are large, measuring 17 by 13 by 13 and 15 by 12 by 12 mm. respectively (fig. 1). The surfaces of the uterus and ovaries are slightly roughened, due to an exudative process resulting from abdominal filariasis. Cervix and vagina are relatively stout-walled and muscular. The cervix, which is oval and possesses a transverse orifice, protrudes markedly into the vagina. The surface of the cervix and of the vagina is rugous and to the touch gives the impression of being covered by horny scales or minute denticles (fig. 1).

The uterus was carefully dissected in order to reveal the blastocyst and placenta within the interior. On removing a cap from lower ven-

tral surface of the uterus, it was discovered that the blastocyst is attached to both dorsal and ventral endometrium, the intervening chorion being smooth and membranous. The uterus was next bisected coronally, following which the blastocyst was divided by cutting the membranous chorion equatorially. This allowed the uterus to separate into dorsal and ventral halves with one half of the bisected blastocyst attached to each segment of the uterus (fig. 2). At this stage of dissection, a minute embryo attached to the ventral endometrial surface was revealed under the dissecting microscope. Thus the blastocyst exhibits bi-discoidal attachment to the endometrium with the primary attachment on the ventral surface of the uterus. The regions of primary and secondary attachment of the chorion exhibit crater-like depressions in

the mucosa, as though at the points of contact of the blastocyst with the mucosa, the mucosal lining had been seared with a cautery (fig. 2). The region of contact of the blastocyst and of the mucosa appears in the gross extremely vascular, possibly hemorrhagic. The entire endometrial lining of the uterus looks tremendously hypertrophied, but in a curious way. Two cushions of mucosa have been formed, dividing the mucosal lining into elevations—one dorsal, the other ventral—the elevations being separated by a deep coronal cleft. The surfaces of the mucosal cushions are slightly puckered.

The embryo, together with its body stalk and a small amount of chorion, was removed for further study and the preparation of serial sections. Examination of the embryo under a Greenough dissecting microscope shows it to be excellently preserved. It is covered by a delicate transparent amnion and has an exceedingly large yolk-sac (fig. 3). The body of the embryo is markedly flexed at the point of attachment of the yolk-sac. Approximately 12 somites can be counted. Both anterior and posterior neuropores are wide open (fig. 5).

After removal of the embryo, portions of the sites of attachment of the blastocyst and of the uterus were taken for sections. The material was imbedded in celloidin and the sections stained in hematoxylin and eosin.

Sections taken equatorially through the entire uterus at the level of the placental sites reveal clearly under low magnification the relations of the layers of the uterus and of the placenta (figs. 11 and 12). The outline of the uterus is round. The muscle layers are approximately 4 mm. thick on the entire circumference of the section. The endometrium forms two cushions, one ventral and one dorsal each of which is approximately 10 mm. in thickness. On the surface of each endometrial cushion there is a crater-like depression, representing the areas of erosion of the mucosa by the blastocyst. The width of these depressions is approximately 4 mm. The wall of the blastocyst, fused with the superficial portion of the mucosa, constitutes the placenta. This attachment of the trophoblast forms a narrow zone, no more than 1 mm. in thickness, lining the crater (fig. 11). Thus the placenta at this stage is composed of a singularly thin and superficial layer in comparison to the total width of the endometrium.

Under higher magnification, the detailed structure of the placenta and uterus can be seen (figs. 11 and 12). The placenta at this stage

consists of a thin lamina of trophoblast which is invading the uterus. The trophoblast is composed of a layer of cytotrophoblast, in contact with the delicate fibro-reticulum of the chorionic mesoderm, and of plasmoditrophoblast or trophoblastic syncytium which consists of numerous anastomosing strands or sheets (fig. 17). The mesoderm sends numerous slender, tongue-like projections into the trophoblast. The cytotrophoblast is always contiguous to the mesoderm, whereas the plasmoditrophoblast, which forms the bulk of the trophoblast, is on the periphery, engaged actively in invading the endometrium. The interstices between the strands of trophoblastic syncytium are occupied by a pabulum or embryotrophe composed in part of disintegrating uterine mucosa and in part of extravasated maternal erythrocytes and of secretion from the endometrial glands.

The narrow zone of contact of the trophoblast with the disintegrating mucosa which is being invaded is complex (figs. 17 and 18). The mucosal surface has disappeared, so that the outermost portions of the uterine glands are destroyed. The lumina of the glands at the zone of contact contain secretion and extravasated maternal blood (fig. 18). The stroma between the glands in this narrow zone is extremely cellular and some of the cellular clumps are obviously undergoing disintegration. A number of extremely dilated venules are located in the zone. In these venous dilatations the blood has possibly stagnated and it appears as though these vessels would in all likelihood very soon be tapped by the advancing trophoblast, thus liberating their contents for the nourishment of the placenta and adding their lumina to the rapidly growing intertrabecular (intervillous) space.

As has been said, the bulk of the uterus is composed of uterine mucosa which has hypertrophied into two enormous endometrial cushions preparatory to the growth of the placenta (figs. 17 and 18). These cushions are composed of a multitude of glands extending for the width of a centimeter from the uterine surface to the musculature (figs. 19 and 20). The glands are not markedly dilated, but are long and tubular with numerous short lateral branches or recesses. The glands are separated from one another by slender connective tissue septa, the whole giving a delicate lace-like appearance to the endometrium (fig. 19). Except a narrow zone containing the deep or fundic portions of these glands, in contact with the musculature, the glandular layer is uniform in character. The fundic seg-

ments of the glands occur in a narrow zone less than 1 mm. in diameter in proximity to the muscle. The fundic enlargements are relatively widely spaced, are slightly dilated and do not appear to have proliferated, nor to have branched as have the glandular outer segments of the broad supervening layer (fig. 20). Moreover their epithelium is low columnar, in contrast to the cuboidal epithelium prevailing in the broad outer zone. In the inner zone, too, there is a pronounced cellular infiltration of the connective tissue, consisting mainly of leucocytes, some of which are eosinophiles. The cellular infiltration extends into the subjacent muscular layer.

Characteristic of many of the branched outer segments in the broad glandular layer of the endometrial cushions is that their endothelium is proliferating to produce minute solid sprouts or nests of epithelial cells which penetrate the interglandular stroma (fig. 19). Such proliferative changes are irregularly scattered but predominate at the zone of junction of the fundic enlargements with the outer segments. This zone is possibly one of maximum proliferation or growth of the endometrial glands.

The endometrium outside the placental areas is of interest. Here the surface epithelium is preserved and the endometrial glands open freely into the lumen of the uterus (figs. 23 and 24). At this stage the glands do not appear to be delivering extravasated maternal blood-cells into the uterine cavity. The surface mucosa is markedly oedematous, the stroma in places directly beneath the surface epithelium and between the outlets of the glands being swollen, quite acellular, and filled with a faintly pink staining colloid (fig. 24). The mucosa of the uterine wall in the cleft between the two endometrial cushions forms a narrow layer, less than a millimeter in thickness (figs. 23 and 24). Its stroma is also oedematous in places. The glands of this portion of the uterus are relatively simple, slightly dilated structures, identical in character with the fundic glandular segments in the deepest part of the endometrial cushions, contiguous to the musculature. Moreover, the homology of these glands with those of the fundic zone beneath the placenta can be established beyond a doubt by tracing this narrow glandular layer around the entire lumen of the uterus. Thus the endometrial cushions composed of large, branching gland outer-segments are superstructures, derived undoubtedly in the first instance from the simpler type of uterine

gland as it persists beneath the cushions and in the simply constructed uterine recesses.

INTERMEDIATE STAGE

The next stage consists of a larger uterus containing a fetus which measures 48-mm. crown-rump length (figs. 7, 8, and 9). The ovaries of this specimen measure 22 by 17 by 17 and 21 by 16 by 16 mm. respectively (fig. 7). The ovaries are therefore considerably larger in this specimen than in the preceding one. On opening the uterus, a well-developed female fetus is removed (figs. 8 and 9). As in the younger specimen the fetus is attached to a primary placenta on the ventral wall of the uterus (fig. 10). The umbilical cord attaches by a branching pedicle to the center of the primary placenta. From the pedicle, vessels radiate over the surface of the primary placenta, supplying it with blood, but continue toward the margin of the placenta which many of them leave to enter the membranous chorion. Traversing the membranous chorion, these vessels reach the secondary placenta which they supply with blood. Some 20 to 30 arteries and veins of various sizes cross to the secondary placenta, the majority running equatorially around the uterine cavity on the right or left, while a few follow the fundic curvature (fig. 10).

Both the primary and secondary placenta are roughly discoidal in shape and of about equal circumference. They are approximately 3 to 4 cm. in diameter and occupy respectively about one-third of the mid-ventral and dorsal walls of the uterine cavity (fig. 10). Each placental disk is composed of approximately a dozen loosely connected lobules which have nodular surfaces and irregular furrows between them. These circumstances, as well as the fact that the placental surfaces are elevated above the endometrium, give an embossed appearance to the placenta. The placental masses are a dark purple in contrast to the pallor of the remainder of the uterus. The chorion between the placental disks is thin and membranous and is merely loosely adherent to the surface of the uterine mucosa. The amnion is a transparent, avascular membrane which is only partially adherent to the meshes of mesenchyme on the inner surface of the chorion. Around the pedicle of the umbilical cord there is an extensive extracervical cavity filled with magna and traversed by the slender, mesenchyme-ensheathed placental vessels. The internal cervical outlet of the uterus presents a closed transverse slit.

The vagina is similar in topography and appearance to that described for the preceding stage and requires no further description at this point.

Microscopically the architecture of the placenta has changed markedly from the previous stage (fig. 13). The musculature is somewhat thinner, measuring only 4 mm. The endometrium which was previously over 1 cm. thick has been reduced to a layer, less than 3 mm. in diameter, beneath the placental sites. Those portions of the uterine wall not preempted by placenta have an endometrial layer less than 1 mm. in thickness. The trophoblast meanwhile has given rise to placental disks composed of lobules 6 or 7 mm. in thickness (fig. 13). Thus the placenta has grown at the expense of the conspicuous endometrial cushions which have diminished very perceptibly. During the same period the uterine cavity has enlarged markedly, so that the originally narrow zone of shallow endometrium separating the two endometrial cushions now covers most of the interior of the uterus.

Under higher magnification there is also seen to be a marked change in the character of the placenta. The innermost layer of the musculature to a depth of 1.5 mm., as well as the inner glandular layer, is densely infiltrated with mononuclear cells and a few leucocytes (fig. 25). To what extent the mononuclear cells are identical with clasmatocytes and monocytes or, on the other hand, to the true decidual cells of the anthropoids and man can not be ascertained by the present technique. From examination of the sections, there is, however, little doubt but that the mononuclear cells in question are arising *in situ* in the connective tissue stroma of the uterus.

As has been stated, the endometrium has been markedly reduced (fig. 25); only the deepest portions of the glands are left. The fundic segments nearest the musculature are slightly more expanded and somewhat more flattened out than at the previous stage. The epithelium is slightly lower, being approximately cuboidal. The stroma between the glands is markedly infiltrated with polygonal mononuclear cells. Between the basal portion of the placenta and these glands there is a zone of marked complexity composed of a choriobasalis consisting of plasmoditrophoblast invading and intermingling with a field of practically acellular embryonic detritus, followed by a layer devoid of trophoblast in which the glands are in various stages of disintegration preparatory to their final usurpa-

tion by the trophoblast (fig. 25). In this layer, the cell-nests produced by proliferating glandular epithelium are still visible (fig. 25).

The placenta fetalis has become a thick, lobulated structure composed of trophoblast and fetal stroma. As is characteristic of all platyrrhines, so far known (Wislocki '29), the trophoblast produces a labyrinth which is trabeculated instead of villous (fig. 15). Villi as they are seen typically in the catarrhine placenta are not present, but the trophoblast forms an anastomosing network of trabeculae enclosing relatively narrow, maternal, intertrabecular blood-spaces. The major trabeculae contain stout cores of fetal mesoderm; the secondary trabeculae are slender and are composed solely of trophoblast (fig. 15). Another characteristic feature of the placenta, true of all platyrrhines thus far examined (Wislocki '29), is that the trophoblast, at a very early stage, becomes almost exclusively syncytial, mere rests of a cytrotrophoblast being found on a few of the major trabeculae. The secondary trabeculae, anastomosing everywhere with the major trabeculae, as well as those anchoring the placenta to the choriobasalis, in addition to the fetal elements of the choriobasalis itself, are composed solely of plasmoditrophoblast. The cytrotrophoblast disappears early, especially from the outlying invasive portions of the trophoblast, and hence a basal syncytium differing from the choriobasalis in the participation of plasmoditrophoblast in one, of cytrotrophoblast in the formation of the other, can not be distinguished. In describing platyrrhines, "basal syncytium" is superfluous as a term, unless it is deemed useful to retain it to designate merely the free surface of the choriobasalis. In keeping with the trabeculated, instead of villous, character of the platyrrhine placenta, the placenta fetalis attaches to the lamina basalis by numerous relatively slender trabeculae, instead of by a few anchoring villi as in catarrhines. The majority of these trabeculae are composed solely of trophoblast.

The mesodermal cores of the major trabeculae, in the placenta of *Ateles* at this stage, are worthy of special description (fig. 15). They are relatively large and composed of mesenchyme conveying the fetal blood-supply. In the stroma at this stage there are curious, large venules or sinusoids which immediately attract attention because they are filled with leucocytes almost to the exclusion of erythrocytes. On studying these vessels one gains the impression that the mesenchyme adjacent to some of them is the locus of origin of blood-cells. What

categories of cells are maturing in these areas it is difficult to elucidate, because the material was not fixed appropriately, nor sectioned sufficiently thin to undertake a study of blood-formation. With the possibility of blood formation in these areas in mind, the writer has examined material from another platyrrhine—*Alouatta*—and has found similar structures in them at the same stage of development. The material in hand certainly suggests that in the platyrrhine placenta at this stage, hematopoiesis is taking place in the walls of certain venules of the fetal circulation. This observation deserves more careful study with the techniques for blood-cells and the writer intends to pursue the matter further. If the observation proves to be correct, it will add the placenta to the extramedullary sources of fetal blood-cells.

Hubrecht ('06) has advanced the idea of hematopoiesis in the placenta of *Tarsius*, deriving blood elements, destined for the maternal circulation, from the trophoblast. *A priori* such an origin of blood-cells seems unlikely and his observations appear to have found no verification. The present observations, however, can be readily reconciled with the existing belief in the origin of blood-cells from the elements of the walls of certain vascular beds. It would appear to be not unlike the extramedullary formation of blood-cells in fetal life or under pathological conditions in the liver or kidney.

The placental border and the membranous chorion are worthy of description at this stage (fig. 13). As has been stated, the placental lobules appear elevated, so that the placenta is in no sense encapsulated by the endometrium; rather, the placental margins are slightly undercut, forming a shallow recess where the membranous chorion begins. The outlets of uterine glands course toward the paraplacental angle from underneath the placenta. The long, drawn-out, slender necks of these glands are separated by delicate septa. Scant secretion and no free blood appear to be reaching the lumen of the uterus via these glands at the present stage. The relationship of the membranous chorion to the thin layer of endometrium with which it comes in contact is simple. The endometrium consists of a thin lamina containing shallow glands with spacious, cleft-like lumina and bearing low epithelium. Slender, wavy septa separate adjacent glands. The glandular septa terminate—some free, some in contact with the membranous chorion—so that there exist empty, epithelium-lined spaces which could at any time re-establish a uterine lumen. The membranous

chorion overlying the tips of the glandular septa is extremely thin, and clinging to its outer surface are nearly amorphous remnants of former endometrium.

LATE STAGE

This stage is represented by three specimens with fetuses measuring 187, 188 and 195 mm. crown-rump lengths. That these fetuses must be at term is evident from the fact that several of our new-born specimens have a lesser crown-rump length than the uterine ones. Two of these specimens (187 and 195 mm.) were the subject of a previous communication (Wislocki '26) and will not be described in detail again. The additional specimen contains a fetus of 188-mm. crown-rump length. The ovaries are smaller than at either of the preceding stages. They measure 19 by 11 by 10 and 16 by 12 by 10 mm. respectively (fig. 6).

On opening the uterus, the placenta is found, as in the other stages, to be composed of two placental masses of about equal size occupying the dorsal and ventral walls of the uterus. In the present instance the primary placental disk, to which the umbilical cord attaches, lies dorsally. In the two previously described specimens of the same stage (187 and 195 mm.), the primary placenta was situated ventrally. The placental masses are roughly discoidal and of about equal size, with diameters of approximately 8 cm. The placenta is composed of a series of partially conglomerated lobules of which there are upward of 20. It is the uneven shape and size of the lobules which give the placenta an irregular contour. Almost isolated lobules may occur. The sulci separating the lobules are occupied by the major blood-vessels. An excellent figure of the gross topography of the placenta at this stage is given in the previous paper (Wislocki '26, fig. 1).

The umbilical cord attaches near the center of the primary placenta in contradistinction to the two other specimens of the same stage in which the cord was marginally attached. The umbilical vessels breaking up to supply the placenta produce a broad umbilical pedicle. In the present specimen the vessels after traversing the sulci, between the lobules of the primary placenta, enter the membranous chorion to pass to the secondary placenta.

Some 15 vessels, arteries and veins, cross between the two placentae, the vessels leaving and entering the placental masses at separate points on the circumference—on the sides and fundic margins, but none from the cervical borders.

The major vessels on the secondary placenta run also in the furrows between the lobules.

The amnion and the umbilical cord have smooth surfaces. The amnion, a thin, avascular sheet, can be readily stripped away from the membranous chorion and from the placental surfaces to which it adheres loosely. The membranous chorion, avascular, except for the interplacental vessels, separates easily from the uterine mucosa, its outer surface possessing minute wrinkles. On stripping off the amnion, the placental surface has the same lobulated, embossed appearance as at the previous stage. The lobules, however, have grown materially in diameter and somewhat in thickness, measuring 1 to 1.5 cm. in diameter as compared to about half this dimension at the 48-mm. stage.

On cross-section, the relations of the layers of the placenta and of the uterus can be observed (fig. 14). The placental lobules are now slightly thicker than at the preceding stage, approximately 8 mm. in width. The remains of the endometrium (the lamina basalis) is now hardly more than 1 mm. in diameter, while the musculature is as thick, if not slightly thicker than before, measuring 4 to 5 mm. in width. The placental labyrinth at term is consequently relatively shallow as contrasted to the much thicker placenta fetalis encountered in other platyrrhines (*Alouatta*, *Cebus*), as well as in the catarrhines.

Under higher magnification, the character of the individual layers of the placenta at term can be seen (fig. 26). The musculature has not undergone any pronounced change. The endometrial layer, however, intervening between the fetal placenta and the musculature, has become reduced to a thin ribbon. The part adjacent to the muscle is characterized by the remains of endometrial glands which present themselves as a series of extensive, flattened spaces or clefts separated by narrow septa (fig. 26). These remnants of the deepest endometrial glands are lined by low cuboidal epithelium and their cavities are usually empty, although occasionally containing a slight amount of acellular, eosin-staining secretion. The interglandular stroma, as well as the adjacent muscle tissue, is infiltrated with numerous polygonal and large round mononuclear cells, fewer in number than at the previous stage, but identical in morphology. Moreover, at this stage numerous mononuclear eosinophiles appear among the stroma of the muscle and glandular layers.

Intervening between the glands and the overlying placenta is an extremely narrow zone (pars

fibrosa) of partly necrotic, partly fibrinous, or fibrotic, endometrium which merges gradually with the cellular stroma of the glandular layer on one side and with the equally narrow choriobasalis on the other (fig. 26). This layer, the pars fibrosa or decidua compacta, stains with eosin and is acellular, except a few clumps of necrotic cells with disintegrating bodies which stain deeply with hematoxylin. Between the bases of adjacent placental lobules, the lamina basalis is much more extensive, producing a blunt wedge (septa placenta) in which several of the larger maternal vessels (afferent and efferent vessels of the placenta) may be seen, surrounded by a variable amount of glandular clefts and cellular or necrotic stroma.

The equally narrow choriobasalis is simple in architecture (fig. 26). It consists of a blending of wisps of the basal plasmoditrophoblast with the acellular, almost homogeneous, outer portion of the endometrium (pars fibrosa). Cytotrophoblast does not participate in the formation of the choriobasalis in platyrrhines, in contradistinction to the catarrhines. This is due to the different manner of growth and extension of the trophoblast in the new-world monkeys. Instead of the growth of villi, as in catarrhines, with the formation, subsequently, of anchoring villi, the cores of which are composed of cytotrophoblast which finally invades the endometrium at the points of attachment of the labyrinth to the basal plate, one witnesses in platyrrhines an early conversion of the cytotrophoblast into plasmoditrophoblast which invades the endometrium as a relatively close-meshed trabeculated syncytium leading to the formation of a choriobasalis composed of endometrium infiltrated by the plasmoditrophoblast of the numerous slender trabeculae which attach to the floor of the labyrinth. This circumstance makes it unnecessary to emphasize the distinction between the basal syncytium and the choriobasalis as in catarrhines, for, in the Western monkeys, the basal syncytium is merely the free surface of the plasmoditrophoblast present in, and an integral constituent of, the choriobasalis.

The placental labyrinth also differs at this stage from the preceding one and illustrates the growth to maturity of the placenta fetalis (fig. 16). The mesoderm has invaded the majority of the previously purely trophoblastic strands, producing a labyrinth of slender trabeculae of mesoderm clothed by a thin sheet of plasmoditrophoblast. These slender trabeculae, of nearly uniform size, focus around a number

of primary trabeculae attached to the closing plate. At the previous stage the mesoderm which was associated largely with primary trabeculae, not yet having invaded many of the intervening secondary trabeculae of trophoblast, gave the appearance of constituting a rather coarse system of relatively thick mesodermal stems (fig. 15). In the mesodermal system of the present stage no trace of the venules, interpreted as loci of blood-forming cells can be found. The plasmoditrophoblast on the trabeculae, as well as free, at this stage possesses less cytoplasm than previously; its nuclei are smaller, and they, as well as their accompanying cytoplasm, stain intensely with hematoxylin. Not a trace of cytrophoblast can be found anywhere. We see then at maturity, a somewhat radiating system of slender trabeculae enclosing a system of maternal lacunae or intertrabecular spaces (fig. 16). Thus the architecture of the labyrinth differs essentially from that encountered in catarrhines as has been discussed in detail in a previous paper (Wislocki '29).

The fetal blood-supply to the placenta is through grossly visible interlobular arteries which course on the surface of the placenta in the furrows between the lobules. The interlobular arteries give off a variable number of lobular arteries which proceed to the surface of a lobule, where they dip into the interior of the lobule, becoming the interlobular arteries. The latter run in the primary trabeculae of the labyrinth until these break up into a system of radiating secondary trabeculae when the interlobular vessels give rise to the capillary bed. The maternal arterial supply reaches the intertrabecular lacunae via the septa placenta between the lobules, while the efferent maternal vessels arise at the base of the lobule displacing the choriobasalis at their sites of origin and following a further course in the pars fibrosa.

The border of the placenta is extremely simple (fig. 14). The membranous chorion arises as a delicate sheet from the closing plate along the tapering margin of the lobules. The choriobasalis follows the curvature of the border upward to meet the closing plate at the line where the membranous chorion arises. In the angle formed between the choriobasalis in its upward course and the uterine musculature, the pars fibrosa and the pars glandularis increase in size for a brief space. The glands are slightly larger and deeper at the paraplacental border than beneath the placenta, and they possess more interglandular stroma, containing infiltrated polygonal cells, mononuclear eosinophiles

and occasional remnants of the glandular cell-nests of the previous stage. The mouths of the glands open in the paraplacental angle into the superimposed layer of fibrin and cellular detritus which encloses and partially fills the wide openings of the dilated, cleft-like glands.

A few millimeters from the border of the placenta, this wedge of detritus occupying the placental angle dwindles while the membranous chorion converges toward the uterine wall to spread out over the uterus as a loosely apposed membrane.

The chorion is covered by the amnion, which is a simple layer of low cuboidal cells without any special features. The chorionic mesoderm is scant and avascular, except in those places where it conducts the larger arteries and veins intervening between the primary and secondary placental disks. The chorionic epithelium supervening upon the mesoderm has a variable morphology, consisting of one or several layers of cells with indistinct outlines which are probably to a great extent syncytial. These cells are at times polygonal, at times more columnar, and again over large areas low or even flattened. In some regions, also, the chorionic mesoderm appears to be entirely denuded. Some of the columnar cells appear to be vacuolated. Intermingling and in contact with the epithelium is an exceedingly narrow layer of acellular, fibrinous material, similar in appearance to the substance of the choriobasalis. The chorionic membrane lies in loose apposition to the uterine wall. The latter presents innermost a much reduced endometrial layer, similar to the pars glandularis beneath the placenta at this stage. This narrow layer consists of sparse glands with shallow, cleft-like cavities which are separated by slender septa. Many of the shallow glands seem to have been so much drawn out laterally that they have been opened up to become virtually a part of the surface of the endometrium. The glandular and endometrial epithelium at this stage is variable in morphology. It may be quite flattened or, as is the rule, cuboidal; but in some areas it is columnar and the cells possess ciliated borders. A small amount of secretion may occupy the glandular clefts. Between the endometrial surface, or its cleft-like glands, and the chorion a space intervenes which is for all purposes an almost fully reestablished uterine cavity. Some of the glandular septa ending in this space are completely clothed with epithelium; others, however, are denuded and are still attached to the detritus on the surface of the chorion. The detritus

on the chorionic surface is doubtless in part of maternal origin, equivalent to the endometrial elements contributing to the formation of the choriobasalis. Destined to be shed at parturition along with the chorion, it is decidua in character.

The formation of cell-islands, by caking together or by fibrinous degeneration of villi, has not been observed in the placental material of *Ateles*, nor in fact in any of the platyrrhines (*Alouatta*, *Cebus*). Nor have areas of infarction been noted. The deposition of fibrin occurs, however. In *Ateles*, in the mature placenta, there is everywhere a subchorial stripe of fibrin beneath the closing plate. Moreover, fibrin stripes extend also in numerous places into the major placental trabeculae extending into the interior of the placental lobules. In spots this stripe may become denuded of syncytium, so that small fibrinous masses protrude, frequently, directly into the intertrabecular maternal lacunae. Fibrin is, as has been stated, also present in the choriobasalis.

It should be remarked that the histological character of the two placental disks is identical. This concludes the description of the last stage of placental development of *Ateles*. The placenta in hand tallies in its minute description very closely to that given for the two previous specimens of the same stage of development (Wislocki, '26). The present description of the three placental stages will be followed by some notes upon the ovaries of pregnancy in *Ateles* and by a few remarks upon the vagina and penis in the same animal. Finally the salient features of placentation in the platyrrhines, in comparison with the catarrhines, as brought out by this study, will be briefly discussed.

NOTES ON THE OVARIES OF PREGNANCY IN ATELES

A few notes have been made upon the ovaries of the present specimens. The ovaries are oval and without marked protuberances (figs. 1, 6 and 7). They present neither visible follicles, nor a corpus luteum. Their tremendous size is apparent. In three of the specimens the actual measurements of the ovaries are as follows: Early stage, 17 by 13 by 13 and 15 by 12 by 12 mm.; Intermediate stage, 22 by 17 by 17 and 21 by 16 by 16 mm.; Late stage, 19 by 11 by 10 and 16 by 12 by 10 mm. The ovaries of the second stage are materially larger than at either of the other stages (fig. 7). However, the latter exceed the largest ovaries of non-gravid females of the same species by a quarter to a third.

In gravid *Cebus* and *Alouatta* (howling) monkeys, too, the ovary of gestation exceeds in size the ovary of the non-gravid period.

Exceedingly large ovaries are characteristic of platyrrhine monkeys in both the gravid and non-gravid state, as judged by relative size to uterus, or by comparison with the ovaries of catarrhines of the same relative body size (macaque and gibbon). Amongst the platyrrhines the ovaries are relatively extremely large in *Ateles*, *Cebus*, *Alouatta* and *Saimiri* (titi monkey), but in *Oedipomidas* (marmoset) they are not remarkably large.

The microscopic structure of the ovaries in the present series of pregnant spider monkeys is interesting. It coincides with the findings of Snyder ('28), who has undertaken a study of ovaries in a large series of platyrrhine monkeys collected on the expeditions of which the present material is a part. He has found that by far the greater bulk of the ovaries in non-gravid *Ateles* and *Alouatta* is made up of large epithelial cells, closely packed together, and indistinguishable from granulosa cells of the follicle wall or from the theca interna cells.

In the present set of ovaries from three gravid specimens the organs are composed almost entirely of lutein cells. The extremely irregular fields of epithelial cells are partially and irregularly subdivided by trabeculae of connective tissue. On the periphery of the ovary there is a narrow shell or capsule of connective tissue, the innermost portion of which contains flattened islands of germinal epithelium and primary follicles. A few small graafian follicles are visible on the periphery, as well, but most of them are undergoing atresia. The atretic follicles show all stages of a transformation of the theca interna and granulosa into lutein cells with a gradual incorporation of the proliferating follicle, by the gradual loss of its boundaries, into the general mass of epithelial tissue in the interior of the ovary.

NOTES ON THE VAGINA AND PENIS IN ATELES

The vagina of *Ateles* is extremely capacious and thick-walled (figs. 1 and 27). It is flattened antero-posteriorly. The cervical musculature is also markedly developed and the cervix protrudes into the vagina, producing a vaginal recess about its oval circumvallation. The cervical orifice presents a transverse slit. In two non-gravid animals a gelatinous plug has been found occupying the upper part of the vagina in contact with the cervix and extending into

the fornices. The significance of the plug is uncertain, since on examining it after fixation, no spermatazoa were found. The cervix possesses low, radiating rugæ. The vaginal surface is covered by low bosses with a tendency to an arrangement into longitudinal rugæ. The surface of the bosses of the vagina and of the rugæ of the cervix are rough and to the touch give the impression of being covered with small cornified grains or scales.

On microscopic section the vagina is revealed as a stout, muscular-walled cavity, lined by an extremely thick layer of stratified epithelium, the outer half of which is cornified and raised in small elevations to produce microscopic denticles (fig. 27). In correlation with the morphology of the vagina some notes are of interest on the structure of the penis in *Ateles*.

The penis of the adult male *Ateles geoffroyi* is composed of a shaft which terminates in a blunt squared-off end, the margin of which is slightly expanded to form a corona. The urethra opens near the ventral margin of the somewhat concave, blunt end. The penis is pigmented, excepting a few small patches of unpigmented epidermis on the corona and on the blunt end. The observation of interest, however, is that the entire penis—shaft, glans and blunt end—is covered by small, shiny, black cornified denticles which are visible to the naked eye. These

cuticular appendages are about 0.25 to 0.5 mm. long and are constructed like pointed barbs. The large ones on the shaft are set 1 to 2 mm. apart; the small ones covering the head of the penis are approximately 1 mm. apart. The barbs are stout and resistant to the touch and are oriented backward from head to base of the penis. On microscopic section these denticles are found to be differentiated epidermal structures produced by a cornification of the outer layers of the epidermis (figs. 2 and 22). Pocock ('20, '25) does not refer to these structures in his description of the external genitalia of *Ateles*. Cornified epidermis occurs on the penis of many rodents, insectivores and carnivores, less frequently in marsupials. Friedenthal ('10) mentions the occurrence of denticles upon the corona of the glans in certain lemurs and Simians (*Lemur macaco*, *Lagothrix*). In the orang he speaks of small serrated, cornified ridges which give the glans a corrugated appearance; and in man, as well, during fetal stages (84 to 144 days), he, besides others, has described minute cornified appendages which he believes are homologous to the cornified structures of other mammals. To the present writer's knowledge, however, these epidermal derivatives in the *Simia*, in both male and female, are nowhere so highly developed as in *Ateles*.

DISCUSSION AND SUMMARY

This study presents a picture of placental development in *Ateles*, one of the platyrrhine monkeys. Our knowledge of placentation in this species, together with the previous studies of two other species of platyrrhines, *Cebus* (Strahl and Happe ('04), Strahl ('05, '13), Wislocki ('29)) and *Alouatta* or *Mycetes* (Strahl and Happe ('04), Strahl ('05, '13), Wislocki ('26, '29)) give us some understanding of placental development in new-world monkeys, and a basis for comparison, with the development of the old-world forms.

In the following pages the essential knowledge of placentation in the platyrrhines will be summarized and discussed, as well as a comparison made with placentation in the catarrhines.

I. THE ENDOMETRIUM AND IMPLANTATION

In *Cebus* and *Ateles* the blastocyst makes early contact with both dorsal and ventral endometrial walls, thus forming two placental disks. In *Alouatta*, on the other hand, contact is as a rule established with only one wall, either ventral or dorsal, so that a single placenta results. One double discoidal placenta has been described in this species by Strahl and Happe. Double or single implantation is no more characteristic of platyrrhines as a group than it is of catarrhines. Thus the phylogenetic scheme of Selenka ('00), based on the assumption that there

is a distinctive difference between catarrhines and platyrrhines, on the ground of whether one or two placental contacts are formed, is no longer tenable.

Characteristic, however, of the platyrrhines is the topography of the endometrium at the time of implantation. As Strahl and Happe have shown in *Alouatta* and *Cebus*, and Wislocki has found in *Ateles* and *Cebus*, the endometrium in the early stages hypertrophies to produce two endometrial cushions within the uterus, one occupying the dorsal wall, the other the ventral wall of the uterus. It is to one or both of these endometrial swellings that the blastocyst may attach itself. Other than frank dorsal or ventral implantations have never been described in platyrrhines. These cushions are well illustrated in the specimen of *Cebus* in a previous paper (Wislocki ('29), Plate 4, figs. 16 and 17) and in the early stage of *Ateles* in the present study (figs. 11 and 12). In the catarrhines, on the other hand, evidence indicates that the endometrium hypertrophies everywhere, so that the implantation site within the uterus is variable. In the macaque for example the broad glandular layer may be seen in the interval between the two placental disks (Wislocki and Hartman ('29), Plate 1, and Plate 3, fig. 9).

In the platyrrhines such as *Alouatta*, in which only one endometrial cushion is preempted by the blastocyst, the opposite endometrial cushion very soon atrophies, according to Strahl and Happe, leaving in the later stages no traces of its existence. This unoccupied, transitory cushion has been called "the placentoid" by Strahl and Happe. In one species of howling monkey (*Alouatta palliata*), however, the existence of the placentoid, if it occur at all, must be extremely brief, for in three young specimens of this species the writer was unable to find a trace of endometrial swelling on the wall opposite the placenta.

2. THE TROPHOBLAST

The character and mode of growth of the trophoblast is perhaps the most striking feature which differentiates the placenta of the old-world monkeys from that of the new-world forms. The trophoblast and its associated mesoderm do not produce a villous placental labyrinth, but a trabeculated labyrinth. Strahl and Happe were cognizant of this fact, but nevertheless they did not abandon the terms "villus" and "intervillous space" in their descriptions. The writer, after the study of a comprehensive series of platyrrhines, catarrhines and anthropoids, showed that the placental labyrinth of platyrrhines is so characteristically different from the traditional villous labyrinth that it is advisable to use the terms "trabeculae" and "intertrabecular spaces" instead of "villi" and "intervillous spaces" for this type of labyrinth (Wislocki, '29). Moreover, the writer showed that phylogenetically the trabeculated labyrinth is probably related by transitions to the labyrinthine placenta of other orders, as well as to certain placenta in lower catarrhines, intermediating to the typically villous placenta as it is seen in anthropoids and man.

The difference in mode of growth of the trophoblast in platyrrhines arises early and is stamped by a relatively profuse growth of a plasmoditrophoblast in the form of a trabeculated network associated with an early conversion of the

cytotrophoblast into a syncytium with relatively early disappearance of the trophoblast. This can be seen in the author's figures ('29, Plate 4, fig. 18, Plate 6, figs. 29, 30 and 31) as well as in figures 15, 16 and 17 of the present material.

The present series gives interesting pictures of the progressive growth of the labyrinth, particularly of the initial growth of the trophoblast in a trabeculated manner (early stage) with the slow ingrowth of the mesoderm (intermediate stage) to form relatively few stout trabeculae containing mesoderm, connected by a profusion of finer trabeculae composed solely of plasmoditrophoblast. And, finally, the occupation of the majority of the trophoblastic strands by mesoderm to form a system of relatively slender trabeculae composed of a thin covering of plasmoditrophoblast upon a core of mesoderm (late stage) can be seen. The present observer ('29) has found no evidence for deriving the covering of the trabeculae from anything but trophoblast of fetal origin, and dismisses the argument of Strahl and Happe ('04) that the covering of the trabeculae is in part of maternal origin.

In keeping with the character of the platyrrhine placenta, there are no anchoring villi, but, instead, a profusion of small trabecular attachments to the lamina basalis. The attaching trabeculae may consist of syncytial trophoblast alone, or possess a slender core of mesoderm. The trophoblast at these points, however, is entirely syncytial and never composed of cytotrophoblast.

3. THE LAMINA BASALIS

The lamina basalis is quite distinctive in platyrrhines. The most obvious characteristic of this portion of the placenta is the tremendous development of the glandular portion—the pars glandularis or spongiosa—as compared to comparable examples from the catarrhines. This is the direct result of the tremendous initial proliferation of the endometrium in platyrrhines. The tremendous development of the pars glandularis is well shown in the early stage of the present series (figs. 11, 12, 18, 19 and 20), as well as in *Cebus* and *Alouatta* in the previous papers by Strahl and Happe ('04) and Wislocki ('29). Although a tremendous development of the endometrial glands is a constant feature in the platyrrhines, the morphology of the glands varies from species to species. For example, one observes inevitably in *Cebus* tremendously dilated glands ('29, Plate 4, figs. 16 and 17), whereas in *Ateles* the glands are not dilated, but appear like closely packed sheaves. Moreover, the writer has pointed out slight differences in the glands between *Ateles* and *Alouatta* ('26).

It is interesting to follow in the present series the almost complete destruction of the tremendous glandular layer and its absorption by the growing fetal placenta. One other feature worth emphasizing in platyrrhines is the widespread proliferation of the epithelium of the uterine glands to produce cell-nests, both beneath the placenta and in the paraplacental mucosa. This process can be seen in all stages of the present material, but more particularly in the first stages during the phase of maximum growth of the glands. During the ensuing period of destruction of the endometrium by the growth of the labyrinth, these cell-nests, too,

invariably undergo degeneration. This manner of proliferation is not exclusively a character of platyrrhines, for Selenka ('00) has described a similar proliferation in various catarrhines. On the whole, though, it appears to be a much more pronounced and widespread feature in platyrrhines, judging from the present material. In several macaque (catarrhine) placentæ of relatively young stages (Duckworth ('07), Wislocki and Hartman ('29)) no signs of epithelial proliferation could be found.

The other layers of the lamina basalis—the pars fibrosa and the choriobasalis, adopting Strahl's nomenclature—have a typical topography in platyrrhines. Strahl defines the choriobasalis as a layer composed of Langhans cells and uterine connective tissue.

I would like to enlarge Strahl's definition of the term to mean a layer composed of trophoblast—either syncytial, cellular or a mixture of both—intermingled with uterine elements. Naturally, following his definition, Strahl finds the choriobasalis lacking in platyrrhines because the cytotrophoblast disappears early and never plays a rôle at the trophoblastic endometrial junction. Nevertheless, there is a narrow but very definite line of fusion of the trophoblast with the endometrium in platyrrhines, as well as catarrhines, with the one specific difference that plasmoditrophoblast, instead of cytotrophoblast, cooperates in the fusion. I see no reason for denying the presence of a choriobasalis or stressing its absence as a distinguishing feature of the two. The choriobasalis is necessary as a term in our classification of the placental layers in platyrrhines with the sole need that its definition be enlarged to include an essentially similar layer in the two groups. Because of the multiple, delicate, trabecular attachments, the choriobasalis is narrower than in catarrhines where we have a few relatively stout, widely-spaced, anchoring villi which produce much deeper and wider bases of attachment to the endometrium.

The amount of penetration of the endometrium by plasmoditrophoblast to form a choriobasalis is somewhat more pronounced in one species of platyrrhine than in another. Thus in *Ateles*, the trophoblast intermingles with the uterine tissue to a greater extent than in *Alouatta*. The pars fibrosa is generally rather shallow in platyrrhines—more so in *Ateles* than in *Alouatta*—but aside from this the structure and character of the degenerating layer is very much the same in the old- and new-world species.

The basal syncytium is a variable structure in the *Simiæ*. In the old-world forms in which the cytotrophoblast persists for a relatively long period, particularly in the anchoring villi and in the choriobasalis, basal syncytium is a useful term with which to designate the outermost syncytial trophoblastic layer where it completely or partially lines the floor of the intervillous spaces. In platyrrhines, in which there is no cytotrophoblast in the choriobasalis from which to distinguish the syncytium there is practically no need to retain the term. What might be called basal syncytium—namely the complete (*Ateles*), or in later stages partly degenerate (*Alouatta*), trophoblastic covering of the floor of the intertrabecular spaces—is an integral part of the basal plasmoditrophoblast of the chorio-

basalis and there would appear to be no reason for arbitrarily dividing the floor into two separate laminae, since there are not two kinds of trophoblast present.

4. PLACENTAL BORDER AND THE PARAPLACENTAL ENDOMETRIUM

The placental and paraplacental borders of platyrrhines are relatively simple. Here the membranous chorion attaches to the border of the placenta and encloses between it and the uterus and the curved margin of the placenta a space, the boundaries of which it is of interest to examine. The character of this region is well displayed in the present series. The placental border tapers off to a wedge which does not undermine the endometrium. The choriobasalis and pars fibrosa of the lamina basalis clothe this wedge on its under side to the point where the membranous chorion attaches. Adjacent to the wedge, in the angle beneath it, large endometrial glands open into the uterine cavity. It is characteristic in platyrrhines for these glands of the paraplacental border to persist until term, although they eventually become extremely drawn out and flattened by the gradual lateral spread of the expanding placenta. During the final stage they exist as deep clefts separated by narrow septa extending up from underneath the placenta. This can be seen in the present figures of *Ateles* (figs. 13 and 14), as well as in the previous ones of *Cebus* and *Alouatta* (Wislocki ('29), Plate 4, fig. 17, Plate 5, figs. 22 and 27). *Alouatta*, in its initial stages, forms an exception, in that during the early period its trophoblast tends to undercut the mucosa which it is invading. Traces of this process may be left in later stages in that the more compact placenta of *Alouatta* is relatively deeply set in the uterine wall, so that the choriobasalis and compacta extend relatively farther up its curving border. These circumstances may be associated with the fact that its implantation is on one wall of the uterus only. To speak of a capsularis incompleta in *Alouatta* or in *Cebus*, as Strahl and Happe do, is unconvincing. In the present specimens of *Ateles* and *Cebus* there is no evidence of such a structure, nor in *Alouatta* is there at any time sufficient undermining of the mucosa to awaken the belief that encapsulation is occurring in the sense that one finds it in the higher apes and man.

The paraplacental glands in the platyrrhines open freely at first into a uterine cavity. After the membranous chorion grows to fill the entire uterine cavity, the most superficial portion of the endometrium degenerates, leaving denuded interglandular septa many of which regenerate their epithelium immediately, resulting in septa projecting freely into a potential uterine space. Some, however, remain loosely attached to endometrial detritus clinging to the surface of the membranous chorion. In lower catarrhines certainly, during the earlier part of gestation, an open uterine cavity exists, as for example in the macaque (Wislocki and Hartman ('29), Plate 3, fig. 9). Later, however, judging from the observations of Strahl and Happe on *Semnopithecus* and *Macacus cynomolgus*, the uterine cavity becomes almost entirely obliterated and the uterine glands become rather completely sealed off by a fusion of the membranous chorion with the extensively degenerating endometrium. There appear to be some grounds for this difference

in behavior. First of all the endometrium outside the placental sites in the catarrhines is thicker than in the platyrrhines, hence there is more opportunity for degeneration. Secondly Selenka, Strahl and Happe, as well as others, have observed a marked œdema of the superficial portions of the endometrium in catarrhines—a finding that suggests that much of the mucosa is destined to undergo necrosis with ample possibility for a scaling off of the endometrial glands and occlusion of the uterine cavity. On the other hand the writer has never observed œdema of the endometrium in platyrrhines, with the exception of the uterus in the first stage of the present series. Correlated with this observation may be that in *Ateles* the membranous chorion seems to be in the latter stages somewhat more attached to the uterine wall than in either *Alouatta* or *Cebus*. On the whole there appears to be ample ground to agree with Strahl and Happe, that it is characteristic of platyrrhines for the uterine glands to open more freely into the uterine cavity than in the catarrhines.

5. EMBRYOTROPHE AND ENDOMETRIAL BLEEDING

Besides the nourishment of the fetus through the establishment of a labyrinthine circulation, there is considerable reason to postulate that in the platyrrhines there is a relatively large fraction of embryotrophe available for the nutrition of the embryo. Two things suggest this: the tremendous hypertrophy of the endometrium, with its subsequent rapid invasion and destruction by the trophoblast; and the large size and quantity of the endometrial glands. In the various stages of the development of *Cebus*, *Ateles* and *Alouatta* the rapid disappearance of the endometrium can be followed and it is difficult to believe that it would be resorbed by any other structure than the trophoblast itself. Moreover, in the first stage of the placental development of *Ateles*, at the zone of junction of fetal and maternal tissue, lakes of œdematous fluid as well as slight extravasations of maternal blood can be seen. Finally secretion can be observed in the endometrial glands which have their outlets into the same zone of invading trophoblast. In the early stages the large paraplacental glands undoubtedly secrete material into the uterine cavity which may be used for the nourishment of the growing membranous chorion. During the latter half of gestation, however, the remnants of glands found in the narrow lamina basalis appear to have become completely inactive, judging from the character of their epithelium and the absence of secretion. Furthermore, at this period, although the paraplacental glands persist as relatively spacious clefts, their secretory function, as judged by histological signs, seems to be almost completely in abeyance. Similarly, the endometrial glands distributed over the uterine surface, appear to be completely inactive, having undergone changes adapted rather to restoring the continuity of the uterine surface than for active secretion.

The question should also be raised as to whether in platyrrhines there is a placental sign consisting of uterine bleeding during any part of the early stage of pregnancy, as it has been described in the macaque by Hartman ('28) and Wislocki and Hartman ('29). In the macaque, at a stage when the embryo is 7 mm. long,

the uterine glands are large and many of them are filled with extravasated maternal blood which can be traced to the uterine cavity into which it escapes. From the uterus this blood flows in the living macaque into the vagina where it can be recovered from the vaginal fluid. In the present series of early stages of *Ateles*, *Cebus* and *Alouatta*, nothing comparable to the uterine glands distended with blood as in the macaque has been seen. Nor do Strahl and Happe remark upon the presence of extravasated blood in their specimens. Anatomically the escape of blood in the platyrrhines into the uterine cavity and thence into the vagina would be possible. The nearest approach to the occurrence of bleeding of this character in platyrrhines is seen in the youngest specimen of *Ateles*, in which extravasated maternal blood is observed in the lamina basalis, free, and within the orifices of glands which open directly beneath the trophoblast. However, in glands to one side which open freely to the surface of the endometrium, no free blood is visible. So, for the time being, we have to answer the question in the negative, unless examination of further placental stages brings affirmative evidence.

REFERENCES CITED

- CLARK, H. C. 1930. A preliminary report on some parasites in the blood of wild monkeys in Panama. *Amer. Jour. Trop. Med.*, vol. 10, p. 25.
- DUCKWORTH, W. L. 1907. The histology of the early placenta of *M. nemestrinus*. *Proc. Camb. Phil. Soc.*, vol. 14, p. 299.
- FRIEDENTHAL, H. 1910. Sonderformen der menschlichen Leibesbildung. G. Fischer, Jena.
- HARTMAN, CARL G. 1929. A breeding and non-breeding season in the monkey, *Macacus rhesus*. *Anat. Rec.*, vol. 44, p. 226.
- HUBBRECHT, A. A. W. 1898. Ueber die Entwicklung der Placenta von Tarsius und Tupaja, nebst Bemerkungen über deren Bedeutung als hämatopoietische Organe. Fourth Internat. Congress Zoology, Cambridge, 1898, Appendix B, p. 343.
- JOACHIMOVITZ, R. 1928. Studien zur Menstruation, Ovulation, Aufbau und Pathologie des weiblichen Genitales bei Mensch und Affe (*Pithecus fascicularis mordax*). *Biol. gen.*, vol. 4, p. 447.
- POCOCK, R. I. 1920. On the external characters of South American monkeys. *Proc. Zool. Soc., London*, p. 91.
- . 1925. Additional notes on the external characters of some platyrrhine monkeys. *Proc. Zool. Soc., London*, p. 27.
- SELENKA, E. 1900. Entwicklung des Gibbon (*Hylobates* und *Siamanga*) Menschenaffen. 3 Lief. Chap. 3, p. 173.
- SNYDER, F. F. 1928. Unpublished communication. Also: Ovulation in the American monkey. *Proc. Amer. Assoc. Anatomists, Anat. Rec.*, vol. 38, p. 62.
- STRAHL, H. 1905. Doppelt-diskoidale Placenten bei amerikanischen Affen. *Anat. Anz.*, vol. 26, p. 429.
- , und H. HAPPE. 1905. Ueber die Placenta der Schwanzaffen, Menschenaffen, Herausgegeben von E. Selenka. 8 Lief., p. 493.
- . 1913. Zur Entwicklung von *Myceles* und *Cebus*. *Anat. Anz.*, vol. 43, p. 501.
- WISLOCKI, G. B. 1926. Remarks on the placentation of a platyrrhine monkey (*Ateles geoffroyi*). *Amer. Jour. Anat.*, vol. 36, p. 467.
- . 1929. On the placentation of primates, with a consideration of the phylogeny of the placenta. *Contributions to Embryology*, vol. XX, Carnegie Inst. Wash. Pub. No. 111, p. 51.
- , and C. G. HARTMAN. 1929. On the placentation of a macaque (*Macacus rhesus*) with observations on the origin of the blood constituting the placental sign. *J. H. H. Bull.*, vol. 44, p. 165.

DESCRIPTION OF PLATE

PLATE I

- FIG. 1—Uterus of the youngest specimen (embryo of 12 somites). Large ovaries can be seen, as well as cervix and vagina. Rugous surface of cervix and vagina is shown. Dorsal view. $\times 1$.
- FIG. 2—Uterus opened to show sites of implantation. Above, dorsal half of uterus, showing crater-like depression at site of attachment of trophoblast to endometrium (secondary placenta). Below, primary attachment of blastocyst (on ventral wall), causing a similar excavation of mucosa. In center of crater, within interior of blastocyst, two small vesicles, yolk-sac and amnion, can be seen. Endometrial cushions can be observed to which placental poles are attached. $\times 1$.
- FIG. 3—Embryo, surrounded by amnion and with yolk-sac attached, has been dissected out. It is attached by its body-stalk to a small block of placenta on uterine wall. Dissections and photographs of embryo, as illustrated in figures 3, 4 and 5, were made by Dr. C. H. Reuser. $\times 10$.
- FIG. 4—Embryo with amnion removed, seen from side. $\times 12$.
- FIG. 5—Embryo with amnion removed, seen from dorsal surface. $\times 12$.
- FIG. 6—Ovary of mature stage. $\times 1$.

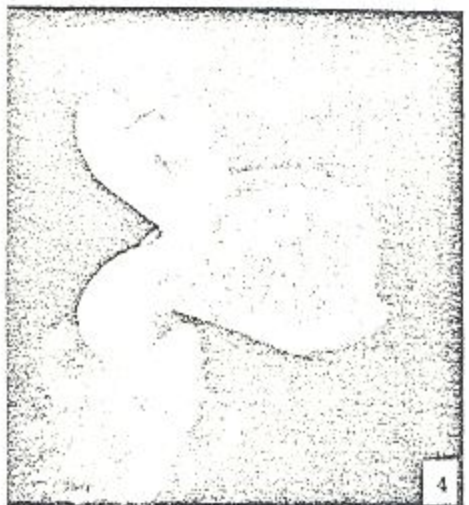
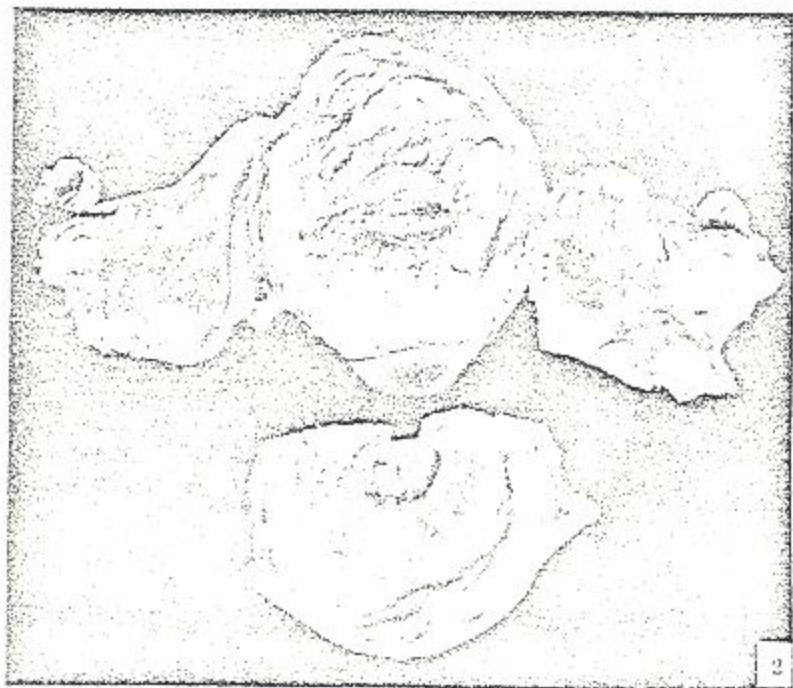
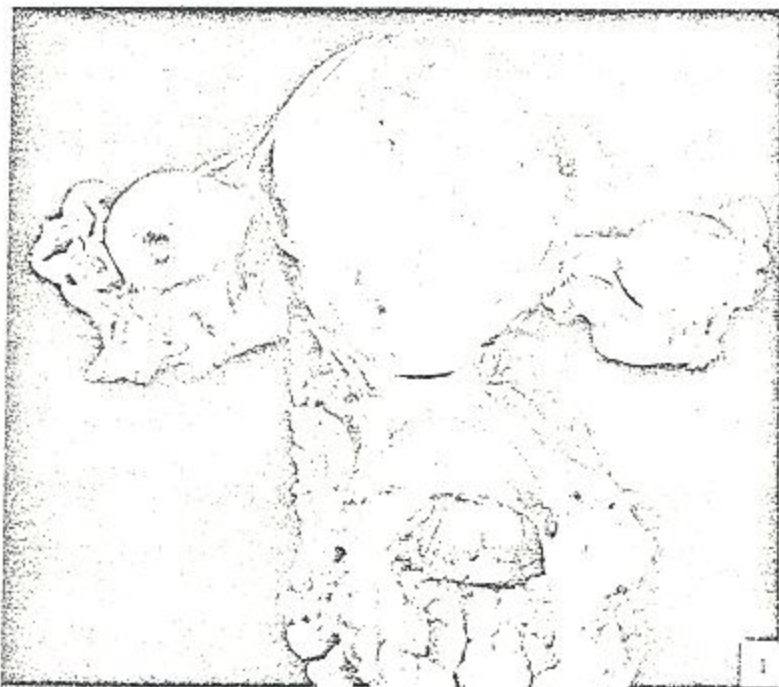


PLATE 2

FIG. 7—Uterus of intermediate stage (fetal crown-rump length 48 mm.). Tremendous size of ovaries can be seen. $\times 1$.

FIG. 8—Lateral view of fetus from this uterus. $\times 1$.

FIG. 9—Opposite lateral view of same fetus. Typical four-fingered condition of hands in *Ateles* can be seen in this and preceding figure. $\times 1$.

FIG. 10—Uterus (intermediate stage) opened to show secondary (ventral) and primary (dorsal) placenta. Umbilical cord is attached to primary placenta. Vessels can be seen in membranous chorion extending from primary to secondary placenta. Lobulated, embossed appearance of placental disks is shown. Membranous chorion detaches easily from uterine wall. $\times 1$.

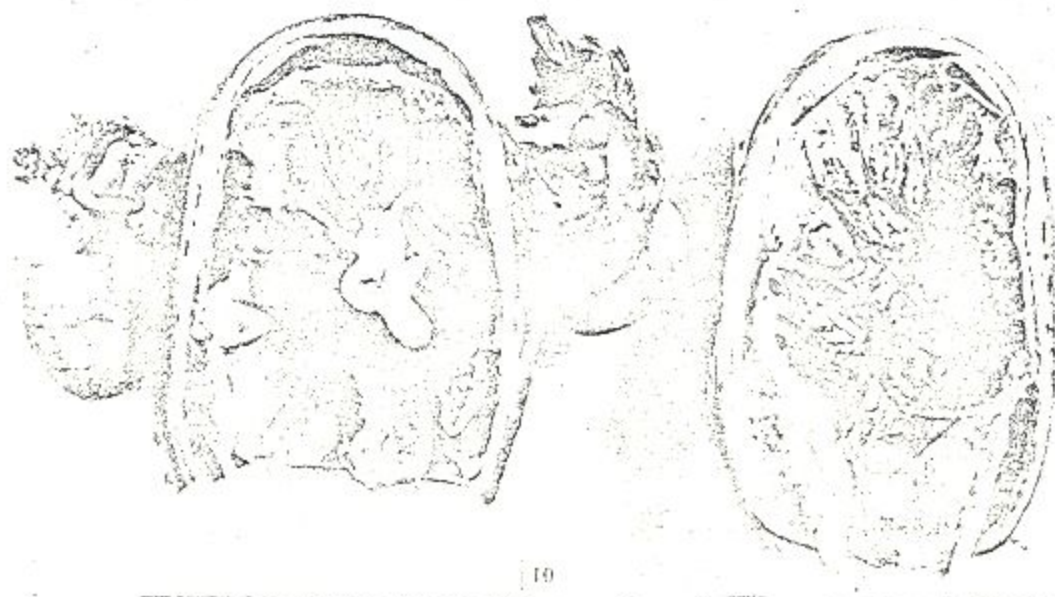
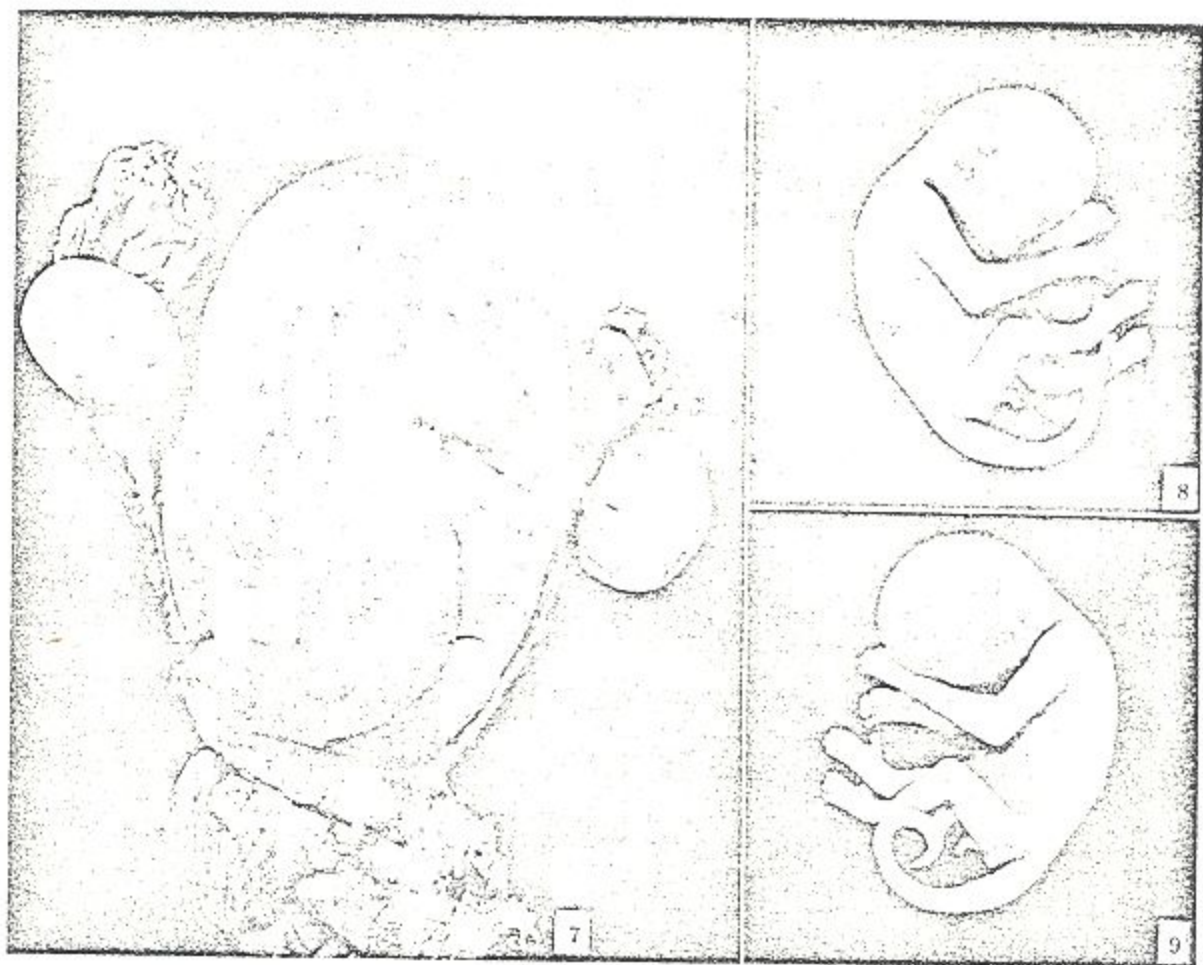


PLATE 3

- FIG. 11—Section through placental site at early stage, showing tremendously developed endometrium. Below, endometrium rests on uterine muscle; above, surface of endometrium is excavated. In wall of excavation a narrow zone of trophoblast can be seen establishing a placenta. At junction of placenta and endometrium are many conspicuously distended glands. $\times 8.5$.
- FIG. 12—Section through another placental site, showing excavation lined by trophoblast and resting on a markedly hypertrophied endometrium. $\times 8.5$.
- FIG. 13—Section showing lobule of placenta (intermediate stage). Endometrium has undergone a pronounced reduction compared to preceding stage. $\times 8.5$
- FIG. 14—Section showing lobule of mature placenta. Same magnification as preceding figure. Endometrium has almost entirely disappeared at this stage, except narrow wedge of almost completely disintegrated endometrial tissue at placental border which can be seen in present figure. To right, membranous chorion, with shreds of endometrium clinging to it, for most part separated from uterine wall. $\times 8.5$.
- FIG. 15—Typical appearance of placental labyrinth in intermediate stage, showing fetal trabeculae—partly invaded by mesenchyme, partly composed of delicate syncytial strands—enclosing intertrabecular blood-spaces. $\times 44$.
- FIG. 16—Typical appearance of placental labyrinth in mature specimen at same magnification as preceding section. Notice by comparison how slender trabeculae have become and how much more numerous those are which contain mesoderm. $\times 44$. Similar difference in character of trabeculae at two stages may be noted also in figures 14 and 15, both of same magnification ($\times 8.5$).



PLATE 4

FIG. 17—Section showing trophoblast invading endometrium (early stage). $\times 44$.

FIG. 18—Portion of endometrium just beneath proliferating trophoblast in early stage, showing dilated glands containing secretion, as well as edematous interglandular stroma. $\times 44$.

FIG. 19—Portion of endometrial cushion (early stage) showing its composition. It is made up of glands separated by narrow septa. In several places in field, cell-nests, produced by proliferation of glandular epithelium can be seen. $\times 44$.

FIG. 20—Deepest portions of glands (early stage) adjacent to uterine musculature. Note that in this region glands have not proliferated so extensively and that there is marked interglandular cellular infiltration. $\times 44$.

FIG. 21—Low power magnification of surface of penis of *Ateles*, showing minute horny denticles of epidermis. $\times 8$.

FIG. 22—High-power view of a denticle of penis. $\times 52$.



PLATE 5

- FIG. 23—Section at extreme border of endometrial cushion (early stage) showing endometrial proliferation in upper part of figure and ordinary uterine endometrium in lower part of figure; the two separated by lumen of uterine cavity. X44.
- FIG. 24—Similar section showing an endometrial cushion above, and ordinary endometrium below. Note that superficial portion of endometrial cushion is becoming edematous. X44.
- FIG. 25—Section through lamina basalis (intermediate stage) showing choriobasalis, pars fibrosa and pars glandularis, the latter exhibiting numerous cell nests. X44.
- FIG. 26—Section through lamina basalis (mature stage), showing by comparison with previous figure further reduction and disintegration of pars glandularis. At bottom of figure are cleft-like remains of deepest portions of uterine glands. On wall of one of these, nearest bottom of figure, columnar, ciliated epithelium is forming over a short distance. X44.
- FIG. 27—Section through vaginal wall of *Ateles*, showing outer cornified layer of epidermis which in numerous places forms minute denticles. X8.

