The Placenta of a Lemur.

By

J. W. Jenkinson, M.A., D.Sc.,
University Lecturer in Embryology, Oxford; Late Fellow of Exeter College.

With Plates 15, 16, and 17, and 7 Text-figures.

Our knowledge of the placentation of the lemurs begins with the publication, in 1875, by A. Milne-Edwards and A. Grandidier, in their 'Historie naturelle des Mammifères de Madagascar,' of an account of the placenta in Propithecus and some other forms.

In this memoir the placenta is described as being diffuse and "en cloche" or bell-shaped, because villi are absent at one end of the chorion, namely, that towards which the head of the embryo is turned.

The uterus is bicornuate, the embryo lodged in one cornu, which is consequently much enlarged. The other, though invisible from the outside, is distinguishable internally, being marked off from the pregnant cornu by a fold (Text-fig. 6, *f*); it is occupied by an extension of the allantois and of the placenta.

The mucosa is folded, except near the cervix. The folds radiate from smooth areas in which open the mouths of glands, from 6 to 8 mm. in length. The chorion is correspondingly folded, except opposite these smooth areas and the cervix.

After pulling away the fœtal "villi," that is the folds, and injecting the maternal vessels, it is observed that none of

the injection fluid escapes. It is concluded that the placenta is indeciduate.

The allantois is very large, with two or three cornua, and sometimes some small stalked diverticula as well.

In Avahis and Indris the structure of the placenta and fœtal membranes is similar.

In the following year Sir William Turner presented to the Royal Society a description of the placenta in Propithecus diadema and Lemur rufipes.

In the first of these the fœtus was found to be lodged in the corpus uteri and left cornu.

The mucosa is folded, except in the numerous (twenty) smooth areas on which the glands open. On and between these folds are crypts, in which Turner states that he saw a persistent uterine epithelium. The chorion is covered with ridges, bearing villi which fit in between the folds and into the crypts respectively. Only at the cervical end is the chorion non-villous. In Lemur rufipes Turner observed a similar arrangement of folds, crypts, and villi, but there was a smooth non-villous area on the posterior side, and other such areas elsewhere in the cornu. The allantois was very large. Some years later the same author added a brief account of a full-time fœtus and placenta of Lemur xanthomystax. The fœtus was lodged in the left cornu, but the right cornu was also dilated, though less so.

In structure the placenta resembled that of Lemur rufipes, with smooth, non-placental regions in various parts.

The next author to deal with the subject was Hubrecht, who in his 'Spolia nemoris' (1894) showed that in the Mayalan species, Nycticebus tardigradus, the placenta was essentially similar in structure to that possessed by the Madagascan forms. In early stages the villi were seen to be short and cylindrical, later somewhat folded and wrinkled. They folded into crypts lined by a persistent uterine epithelium. "Chorionic vesicles" were also found—that is, recesses produced by an in-pushing of the chorion, with villi depend-

ing into them. In later stages the chorion was observed to be non-villous at the cervical end and also in a patch on the anterior side.

Next comes Strubl's memoir on the African species, Galago agisymbanus.

In the possession of short cylindrical villi this form resembles Nycticebus.

The villi are situated in crypts lined by a persistent uterine epithelium, and are covered by a columnar or cubical trophoblast. At the summit of each is a depression into which the uterine epithelium does not enter. In this depression a greenish substance is found.[1]

There are also "chorionic vesicles," again as in Nycticebus; with branched vascular villi hanging into them. The wall of vesicle is backed by a layer of smooth muscle fibres and some loose connective tissue.

Opposite each vesicle is a depressed "Turnerian" area, at the bottom of which open the uterine glands. Both this depression and the overlying vesicle are filled with a granular matter, in which leucocytes are intermingled, presumably the secretion of the glands.

The yolk-sac was found in early stages. The allantois is very large and covers the whole of the inner surface of the chorion. In later stages its cavity is subdivided by septa, in which travel the blood-vessels of the placenta.

Strubl has more recently (1905) investigated the placenta in Propithecus coronatus and Lemur albimanus and mongoz.

In the first of these genera the earlier description of the villi as folds is confirmed.

These folds are wavy, and later secondarily folded and lobed. The uterine epithelium persists. There are non-villous areas. In Lemur, on the other hand, the villi are not long ridges, but leaf-like, each with a narrow base. The uterine epithelium persists here also.

[1] This may be a hæmoglobin derivative, from the digestion of extravasated maternal hæmatids.

The short communication of Anthony (1908) on the placenta of Propithecus varreauxii typicus adds little to what was already known. An interesting point is that the allantois does not extend over the whole of the inner surface of the chorion. The villi are long ridges. An internal fold marks the separation of the cornua.

It is sufficiently clear from these several accounts that the placenta in the Lemuroides is of the so-called indeciduate type, and it might well be supposed that there is very little for another author to add. The histological details given are, however, if not meagre (except in Strubl's memoir on Galago), at least not such as might be obtained by a more modern technique, and I therefore propose in the present paper to fill this lacuna as far as possible.

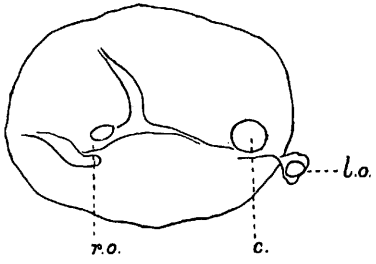
I have, unfortunately, only one stage at my disposal, the apparently full-time embryo and placenta of a Madagascan lemur, which I received a year or so ago through Sir Ray Lankester, from Mr. A. Dobrée. According to Mr. Dobrée's statement this uterus belongs to a grey lemur, known by the natives as "Bohengy," and was obtained on the west side of the island, about thirty miles from the coast in the Menabe district on the Tsuribilima river.

The fœtus evidently is a member of the sub-family Lemurinæ (the toes are not webbed and the cæcum not long), and possibly belongs to the genus Lepidolemur (Lepilemur), since I find that A. Milne-Edwards states that the native name for Lepilemur ruficaudatus is "Bouenghé." Beyond this I cannot identify it.

The gravid uterus (Text-fig. 1) is an oval sac measuring $2\frac{3}{4}$ in. by $2\frac{1}{8}$ in. Towards one end is the cut cervix, through which protrudes the chorion. At the same end, which I take to be the left, is one ovary and Fallopian tube: the other ovary and tube are about mid-way between the middle and the opposite end. Pieces of the broad ligament (mesometrium) remain, and its line of insertion on the uterus can be distinguished. This line runs on what is presumably the dorsal side of the cervix. The oval sac, as will be shown later,

is divisible, by an internal fold, into two cornua, of which one, the right, is much larger than the other, and contains the bulk of the embryo.

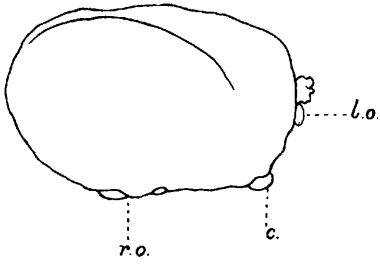
TEXT-FIG. 1.



Gravid uterus seen from the posterior (cervical) side: *c.* Cervix. *r.o.* Right ovary and tube. *l.o.* Left ovary and tube.

[Turner states that in Lemur xanthomystax, and also in Propithecus diadema, the fœtus is lodged mainly in the

TEXT-FIG. 2.



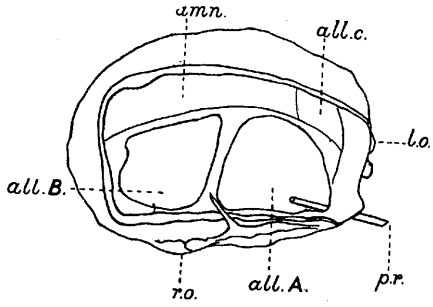
The same seen from the ventral aspect.

left cornu, which is more dilated than the right. That may be so in the present case. Orientation of the excised uterus is uncertain.]

On the ventral side a slight fold of peritoneum runs obliquely from the anterior right to the posterior left end (Text-fig. 2).

The uterus was opened from the ventral aspect by the removal of almost the whole of the wall on this side (Text-fig. 3). With the wall was removed the placenta, and the amnion and allantois were laid bare, the fœtus being indistinctly visible through them.

TEXT-FIG. 3.



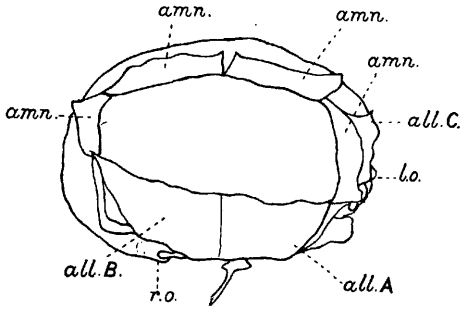
A rectangular piece of the ventral wall has been removed displaying the amnion, *amn.*, and the allantois, *all. A*, *B*, and *C*. *pr.* Probe passed from the allantoic cavity *A* into the cervical extension of this cavity. The outer wall has been removed from cavities *A* and *B*.

The allantois comes up on this, the ventral side only halfway towards the anterior end; at which end only the amnion intervenes between the embryo and the chorion.

Removal of the outer wall of that part of the allantois exposed showed it to be here divided by an antero-posterior septum into two compartments: *A* on the left and *B* on the right. A probe was passed from cavity *A* into the cervical extension. A third division of the allantois (*C*) was laid open in a later stage of the dissection. This lies on the left, and towards the anterior end.

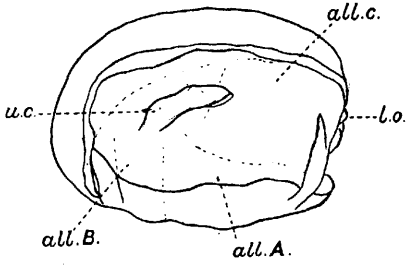
An incision was now made along the extreme margin of the allantois and the latter turned back posteriorly (Text-fig. 4).

TEXT-FIG. 4.



The amnion and allantois have been folded back, exposing the fœtus. The outer wall of allantoic cavity *C* has been folded back.

TEXT-FIG. 5.



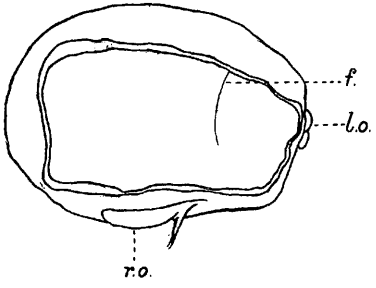
The fœtus has been removed, exposing the interior of the amniotic cavity. The dotted lines mark the limits of the allantois and its compartments *A*, *B*, and *c*. which are seen, of course, through the amnion. *u. c.* Umbilical cord.

The third division (*C*) of the allantois was turned back to the left, the flaps of the amnion to the front and to the right.

The body of the fœtus, its head to the left, was now exposed to view and could be easily extracted, and the umbilical cord severed (Text-fig. 5). The extent of the space occupied by the allantois could now be seen. On the dorsal side it reaches almost to the anterior end on the left, but in the other direction reaches neither to the anterior end nor to the right-hand side.

Divisions *A* and *C* of its cavity are separated by a septum which runs obliquely from the left towards the umbilical

TEXT-FIG. 6.



The rest of the amnion, together with the inner wall of the allantois, have been removed. The inner surface of the wall of the uterus is now seen (through the outer wall of the allantois and through the chorion). *f.* Fold marking the division of the cornua from one another.

cord, *C* and *B* by one coming from the anterior margin on the dorsal side to the same point, *A* and *B* by one coming from the anterior margin on the ventral side, and passing posteriorly towards the insertion of the cord.

The relation of these cavities can be seen better when the inner wall of the allantois has been removed by a marginal incision (Pl. 15, figs. 1, 2).

The inner side of the dorsal wall of the uterus is now displayed to view, with only the thin amnion, or outer wall of the allantois, as the case may be, intervening, and the slight

internal fold which separates the more distended from the less distended cornu can be seen (Text-fig. 6, *f*). Examination of this wall by reflected light shows that there are thin patches, especially on either side of the inter-cornual fold. In these thin patches the placenta is ill-developed, as is made

TEXT-FIG. 7.

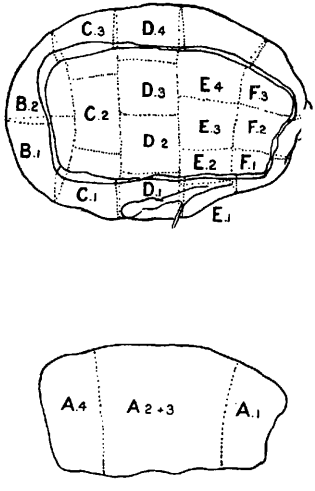


Diagram of the pieces into which the wall of the uterus was cut up.

clear by microscopical examination. For this purpose the whole uterine wall, including the piece excised from the ventral side, was cut up into small pieces, lettered and numbered as in the diagram (Text-fig. 7), and consigned to the microtome.

The sections show a well-developed indeciduate placenta—composed of branching villi dipping into crypts of a corresponding form, and lined by a persistent uterine epithelium—in the thick parts, while in the thinner parts the placenta is

much reduced, or absent, the trophoblast in the latter case not being produced into villi.

The fully-developed placenta is found in all regions except A 1, F 1, and parts of A 2 + 3, A 4, B 1, D 1, E 1, E 2, E 3, E 4, F 1, F 2, and F 3. In A 1, A 2 + 3, D 1, E 1, E 2, E 4, F 1 the villi are small, while in A 4, A 2 + 3, B 1, D 1, E 3, and F 1, F 2, F 3 there are places where the trophoblast is not folded at all.

We may begin with the simpler conditions in the non-placental regions.

The trophoblast is a columnar epithelium of coarsely vacuolated cells (Pl. 15, fig. 3), with frequently a denser region—with thicker walls to the vacuoles—round the nucleus or near the basal end. At this end is a basement membrane, and behind this branched connective-tissue cells. The free ends of the trophoblast cells appear to be amœboid, and protruded into a striated or granular (Pl. 15, figs. 4, 5) coagulum, apparently a secretion of the uterine epithelium. Some of these cells appear to be glandular, at least they contain an internal mass of fine granules, which appears to be poured out into the space between them and the uterus (Pl. 15, fig. 5). The uterine epithelium is composed of shorter columnar cells, with scattered vacuoles in the densely staining cytoplasm, and amongst these elements are goblet gland cells (Pl. 15, fig. 3). Underneath it is a layer of dense fibrous tissue.

In many cases the uterine epithelium may be folded while the trophoblast remains simple (Pl. 17, fig. 15). The folding may be trifling or considerable, and the folded part may be itself folded over an adjacent portion of the wall (Pl. 16, fig. 7).

Between the epithelium and the muscularis are the glands. These are lined by columnar cells, with broad stout necks, through which the granular secretion is ejected (Pl. 16, fig. 8, seen in section in fig. 8, *a*). Round the basal nuclei are some deeply staining granules.

The glands were found to open at the base of depressions.

The trophoblast is here non-villous. In the placental regions the trophoblast is thrown into folds or villi, which are lodged in uterine crypts. In the thinner parts the folds are exceedingly slight and the crypts correspondingly shallow: in the fully developed placenta, villi and crypts branch in the most complicated way, and the placenta becomes very thick (up to 3·5 mm.) (Pl. 17, figs. 18–19).

Every transition is found between the two extremes, and every transition from the columnar trophoblast and columnar uterine epithelium of the non-placental to the flat layers which cover the villi and line the crypts of the placental regions (Pl. 16, figs. 9, *A–C*, 10). The cytoplasm of the trophoblast still remains vacuolated, and the uterine epithelium dense. Everywhere in the crypts both are found, and closely adherent to one another.

The villi are leaf-like, with irregular branches perpendicular to their surface. In vertical sections a main villus is frequently cut throughout its length (Pl. 17, fig. 19), the flattened leaf form is best seen in tangential section (Pl. 17, fig. 20).

The maternal connective tissue is dense and fibrous, the fœtal composed of loose stellate cells often very abundantly branched and of large size (Pl. 16, fig. 10). In addition there are numerous aggregations of smaller vacuolated elements (Pl. 16, fig. 10a).

The fœtal blood-vessels are lined by a simple endothelium. In the connective tissue between the amnion and allantois are found large cells, stuffed with globules, and some of them containing pigment; the pigment may be a hæmaglobin derivative. In any case the cells are probably phagocytic (Pl. 16, fig. 12).

The allantoic epithelium is very flat and covered by a cuticular layer (Pl. 16, fig. 13).

The amniotic epithelium is exceeding flat (Pl. 16, fig. 14).

In the umbilical cord are two arteries and two veins, and the stalk of the allantois.

No trace of the yolk-sac was found.

It is evident the placenta and fœtal membranes of this species of Lemur conform in structure to those of other members of the Lemuroidea, with the exception of Tarsius. In the Lemuroid placenta the relation between fœtal and maternal circulations is brought about by the production of vascular trophoblastic villi, which fit into crypts lined by a persistent uterine epithelium. So the placenta therefore resembles that of an Ungulate: it is of the so-called "Indeciduate" type. The allantois is large and occupies a great deal, if not the whole, of the space between the amnion and the chorion.

In Tarsius, on the other hand, the uterine epithelium disappears at the point of formation and attachment of the placenta, and the latter consists of a thickened trophoblast excavated by the lacunæ in which the maternal blood circulates, and penetrated on the fœtal side by the capillaries of the allantois. Of this type are the placentas of the Anthropoid Primates, of Rodentia, Insectivora, and Cheiroptera. In Tarsius, further, the allantois is rudimentary, while at an early stage there are a diminutive yolk-sac and a precociously developed extra-embryonic cœlom. In these respects also Tarsius resembles the Anthropoids. But while these resemblances very strongly support the view that Tarsius, an aberrant Lemur at best, should be ranked with monkeys and man, it is not, of course, to be concluded that the other Lemurs should be separated from the Primates and grouped with other "Indeciduata."

The Lemuroid placenta seems indeed to have developed features of its own with variations characteristic of each subfamily. Thus, while in the Galaginæ and Lorisinæ the villi are roughly cylindrical, in the Lemurinæ and Indrisinæ they are ridges, ridges which in the former are broken up into short leaves, as in the genus, Lepidolemur, described above.

But such general characters as the Lemuroid placenta does possess in common with that of Ungulates, Cetacea, Sirenia, and perhaps some Edentata, may be the inheritance from a common ancestral "indeciduate" type. And in that case we

should probably have to believe that the "deciduate" type observed in monkeys and man has been developed—independently of that of rodents and other orders—from the simpler Lemuroid form.

EXPLANATION OF PLATES 15, 16, AND 17,
Illustrating Mr. J. W. Jenkinson's paper, "The Placenta of a Lemur."

PLATE 15.

Fig. 1.—The inner wall of the allantois removed, viewed from the amniotic side, except for the reflected portion at the posterior end. *A*, *B*, and *C* the three cavities. *ce.* Cervical extension of cavity *A*.

Fig. 2.—The same seen from the allantoic side.

Fig. 3.—Simple columnar trophoblast, *tr*, and simple columnar uterine epithelium, *ut. ep.*, from a non-placental region. Between the two a striated coagulum, the secretion of the uterus.

Fig. 4.—Examples of highly columnar trophoblast cells with amœboid free ends, from non-placental regions.

Fig. 5.—Columnar trophoblast, *tr.*, and slightly folded uterine epithelium, *ut. ep.*, from a non-placental region. Between the two a granular coagulum. Gland-cells may be seen in the trophoblast.

Fig. 6.—Slightly folded uterine epithelium, from a non-placental region, with its striated coagulated secretion.

PLATE 16.

Fig. 7.—Simple trophoblast, and complexly folded uterine epithelium, from a non-placental region.

Fig. 8.—Gland cells of a uterine gland. *a.* Transverse section of mouth of a gland cell.

Fig. 9.—Transition from the columnar trophoblast and uterine epithelium of the non-placental regions. *A.* To the flattened layers of the placental region. *B*, *C.* Intermediate condition.

Fig. 10.—Trophoblast and uterine epithelium in the completely placental region. *f. c. t.* Branched fœtal connective-tissue cells. *f. b. v.* Fœtal capillaries. *m. b. v.* Maternal capillaries. *tr.* Trophoblast. *ut. ep.* Uterine epithelium.

Fig. 10a.—Small vacuolated fœtal connective-tissue cells.

Fig. 11.—Small fœtal blood-vessel, with granular and fibrous connective-tissue cells.

Fig. 12.—Large fœtal connective-tissue cells, filled with globules, and in two cases pigment granules.

Fig. 13.—Allantoic epithelium, with its cuticle. Below, connective-tissue cells.

Fig. 14.—Amniotic epithelium, with underlying fibrous tissue.

PLATE 17.

Fig. 15.—Thin portion of the uterine wall, where there is no placenta, the trophoblast being simple, the uterine epithelium only slightly folded. *a.* Allantoic epithelium. *tr.* Trophoblast. *ut. ep.* Uterine epithelium. *gl.* glands. In this and the following figures the trophoblast is stippled, the uterine epithelium black.

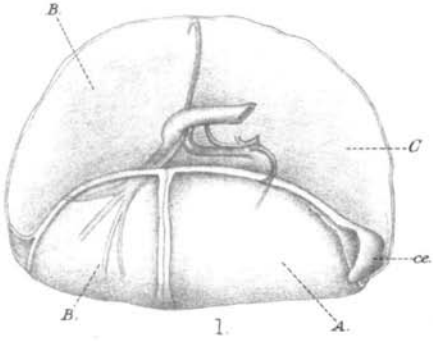
Fig. 16.—Thin part of the uterine wall where the trophoblast is slightly folded. Both it and the uterine epithelium are very thin.

Fig. 17.—The uterine wall is slightly thicker, the folds of trophoblast and uterus better developed.

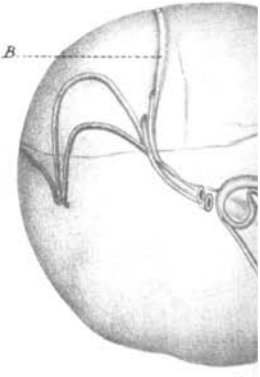
Fig. 18.—The edge of a placental region; the folds of the trophoblast and of the uterus are much better developed. Letters as in fig. 15.

Fig. 19.—Section through the thickest part of the placenta. *a.* Allantoic epithelium. *f. c. t.* Fœtal connective-tissue in the villi. *m. c. t.* Maternal connective-tissue in the walls of the crypts. *gl.* Glands. *m.* Muscularis.

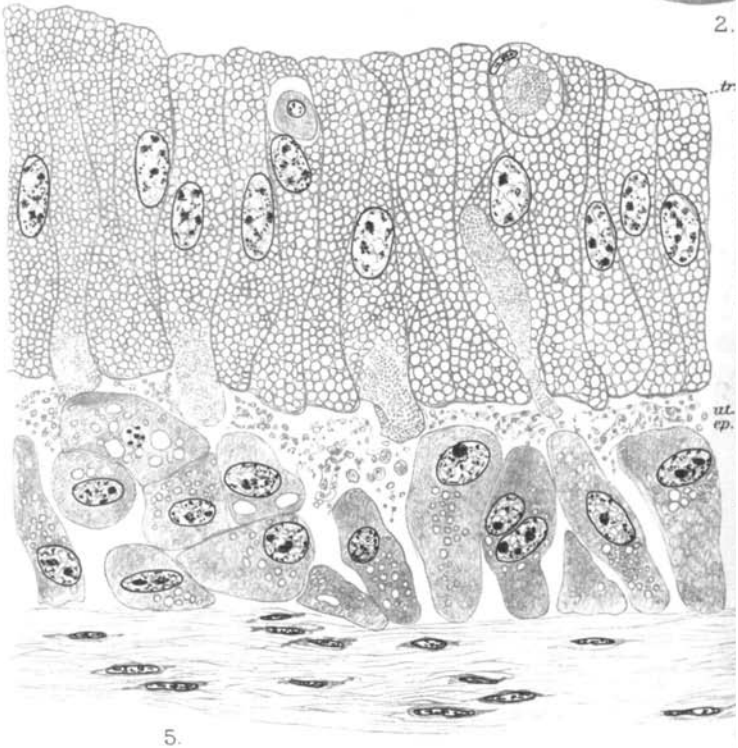
Fig. 20.—Tangential section across one of the leaf-like villi, showing the lateral leaf-like branches.



1.

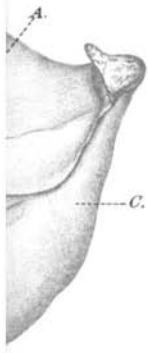


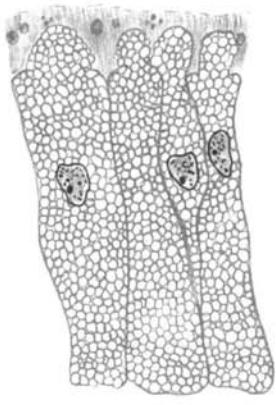
2.

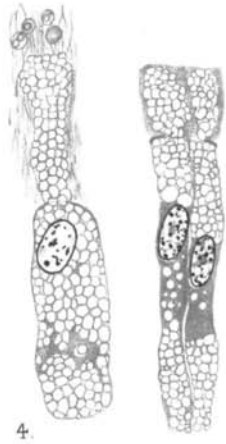


5.

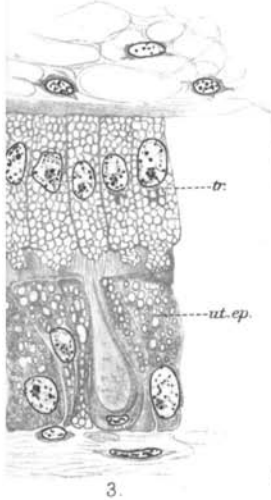
JENKINSON—



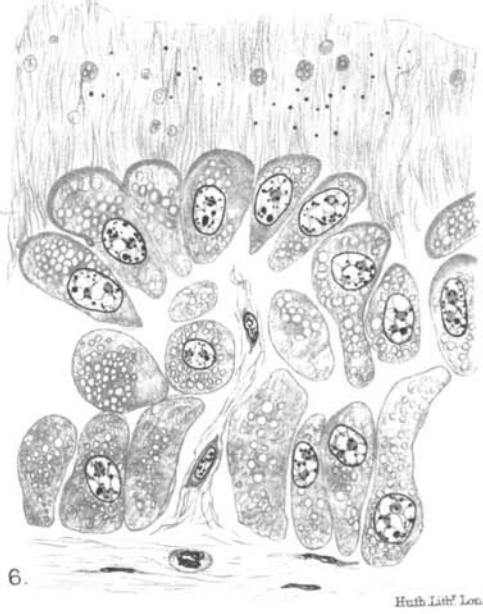




4.



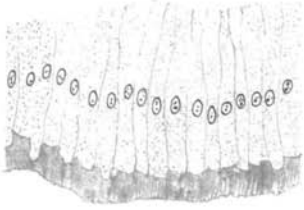
3.

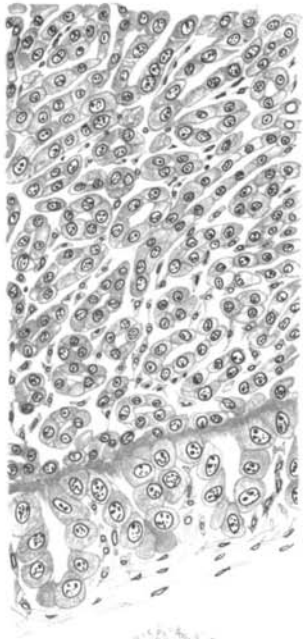


6.

Huth Lith^r London.

:NTA OF LEMUR.

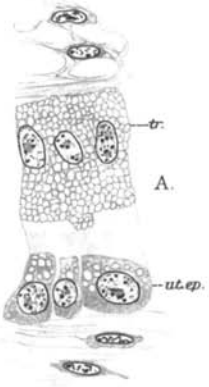




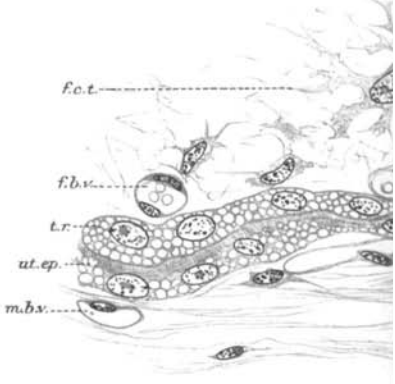
7.

a.

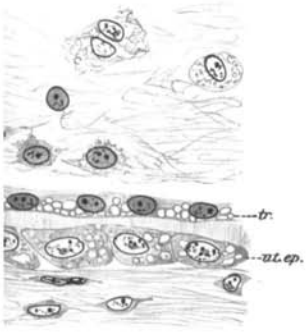
8.



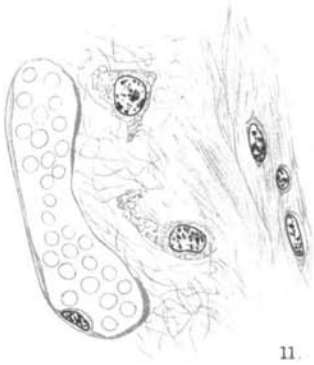
9.



JENKINSON.



C.

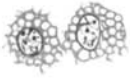


11.

B.

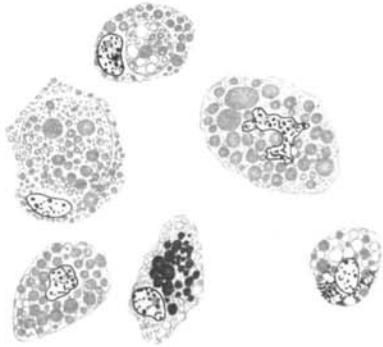
tr.

ut. ep.



10a.

10.



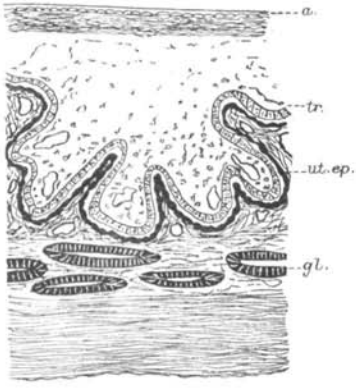
12.

13.

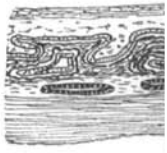
14.

ITA OF LEMUR.

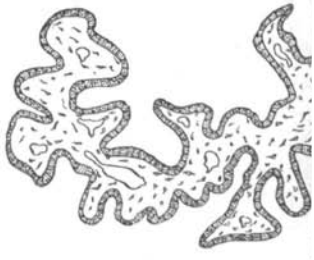
Huth, Lith. London.

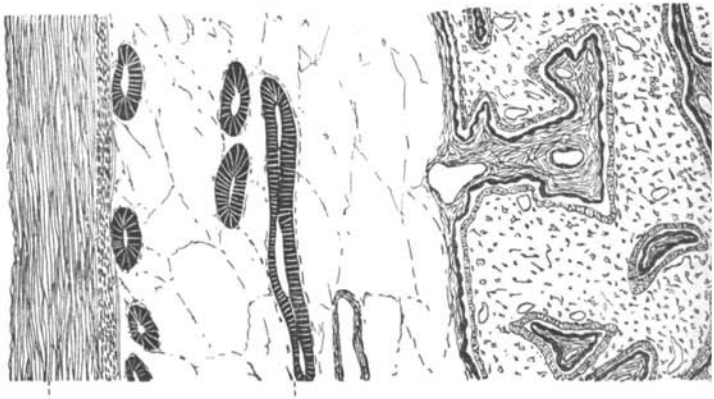


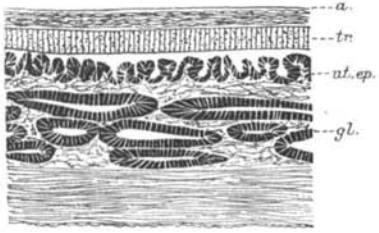
18.



17.

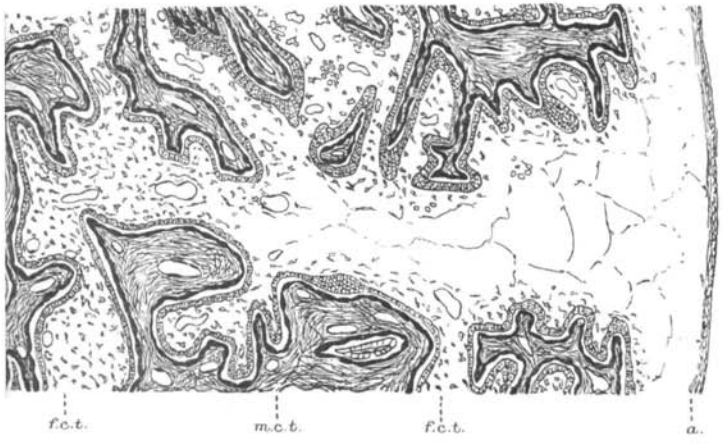






15.

16.



NTA OF LEMUR.