SOME GENERAL OBSERVATIONS ON THE PLACENTA, WITH ESPECIAL REFERENCE TO THE THEORY OF EVOLUTION. By PROFESSOR TURNER.

(The following observations formed the conclusion of my 2nd series of Lectures "On the Comparative Anatomy of the Placenta," delivered in June, 1876, in the Theatre of the Royal College of Surgeons of England.)

FROM the description which I have now given of the diffused, the polycotyledonary, the zonary[1], the dome-shaped and the discoid forms of placenta, we are in a position to pass briefly in review the structure of the principal examples, with the view of ascertaining if the organ presents different types of structure in different mammals, or if the entire series of placentæ are constructed on such a uniform plan as would justify one in conceiving that the several structural modifications could have been evolved out of a simple fundamental form.

At the outset we may state that the presence of certain structures seems to be necessary for the performance of the functions of a placenta, and the most simple arrangement of these structures would constitute a placenta in its most generalized form. The fundamental condition of the fœtal part of the placenta would be a smooth plane-surfaced vascular membrane, covered by a layer of pavement epithelium. The fundamental condition of the maternal placenta would be a smooth plane-surfaced vascular membrane covered by a layer of columnar epithelium. The two membranes would be parallel to and in apposition with each other, the fœtal epithelium being in

[1] See this *Journal*, Oct. 1875, for an account of the diffused, polycotyledonary and zonary placentæ; also, and more in detail, my published *Lectures on the Comparative Anatomy of the Placenta*, 1st series, Edinburgh, 1876. I described the dome-shaped placenta of the Sloth in *Trans. Roy. Soc. Edinburgh*, 1873; but the detailed account of the discoid placenta has not yet been printed. I have not thought it necessary in this place to enter into the question of the relation of the utricular glands to the uterine crypts, and to the chorion, as I have, in my 1st series of Lectures, expressed my opinion on this matter.

contact with the maternal epithelium, so that the fœtal capillaries would be separated from the maternal capillaries by the two apposed layers of epithelium. This arrangement would occupy the whole of the surface of the chorion for the fœtal placenta, and the whole of the uterine mucous membrane for the maternal placenta (fig. 1).

The diffused placenta of the common Pig presents the least departure from this generalized form. The evidence of specialization consists in the formation of ridges and short simple villi on the surface of the fœtal chorion, and the coincident production of shallow simple depressions or crypts in the uterine mucous membrane. The two epithelia preserve their fundamental form and relative position, and the fœtal and maternal vessels continue of the size of ordinary capillaries. In this animal the villi and crypts are not diffused over the whole of the chorion and uterine mucous membrane; the polar portions of which are smooth, but preserve their vascularity (fig. 2).

In the diffused placenta of the Mare, the *Cetacea,* and the Lemurs, a somewhat more complicated, and more highly specialized arrangement exists. The short villi of the chorion give origin to simple microscopic offshoots, and the uterine crypts are divided into minute compartments for their reception, so that each villous tuft, with the corresponding depression in the mucosa, forms a microscopic cotyledon. The two sets of vessels preserve their capillary size, and the epithelia their relative positions; though the maternal epithelium may have undergone some modification in shape.

In the polycotyledonary placenta of the Ruminants, a still more specialized disposition exists. The villi are considerably elongated and give origin to numerous branches, and at the same time the uterine crypts are deepened into pits, from which shallow compartments proceed, for the reception of the long many-branched villi. From the aggregation of a number of these into definite masses the large cotyledons arise, which one is familiar with in the placenta of the Cow, Sheep, and other typical Ruminants. The fœtal and maternal vessels possess the size of ordinary capillaries, and the epithelia retain their fundamental relations to each other, though the maternal epithelium has not unfrequently lost its columnar form (fig. 3). The intercotyledonary parts of the chorion and uterine mucosa, as is the case in most Ruminants, are smooth, though retaining their vascularity and epithelial covered surfaces; but in the Giraffe, not only are smaller cotyledons, sometimes not more than two lines in diameter, developed in the interspaces between the normal cotyledons, but short villi spring from the external surface of the chorion either singly, or in rows and clusters.

Another specialization is met with in the zonary placenta, in which the villi assume a sinuous form and give rise to broad lateral offshoots, or perhaps branch in an arborescent manner. In correlation with these modes of arrangement of the villi, the uterine mucosa assumes the form of complex sinuous folds, or it becomes divided into a microscopic trabecular frame-work, in the meshes of which the villi are lodged. The maternal epithelium may possess a well-marked columnar form as in the Seal and Fox; or it may be stunted and rectangular, as in the Cat; and the maternal vessels, instead of forming ordinary capillaries, may dilate into vessels two, three, or four times as large as the fœtal capillaries. In these placentæ the dilated maternal blood-vessels, invested by the maternal epithelium, lie amidst groups of villi (figs. 4, 5). Hence each maternal blood-vessel, with its epithelial investment, is in relation not to a single villus, as is the case in the diffused and polycotyledonary placentæ, but to the several villi which surround it. Although the subdivision of the maternal mucosa into trabeculæ causes it to lose the regular crypt-like arrangement of the diffused and polycotyledonary placentæ, yet the relative position of the several structures remains the same, and the fœtal and maternal blood-vessels are separated from each other by the layers of epithelium.

Another specialization is met with in the dome-shaped placenta of the Sloth, in which the maternal vessels are even more dilated than in the zonary placenta. They possess a serpentine course, and wind in and out between the villi. The maternal epithelium, which lies in close relation to the exterior of the maternal blood-vessel, is not columnar in form, but consists of polygonal flattened cells (fig. 6). The tortuous arrangement of the dilated vessels of the uterine mucosa obscures the crypt-like character of the depressions in which the villi are lodged, but

Fig. 1.

Fig. 2.

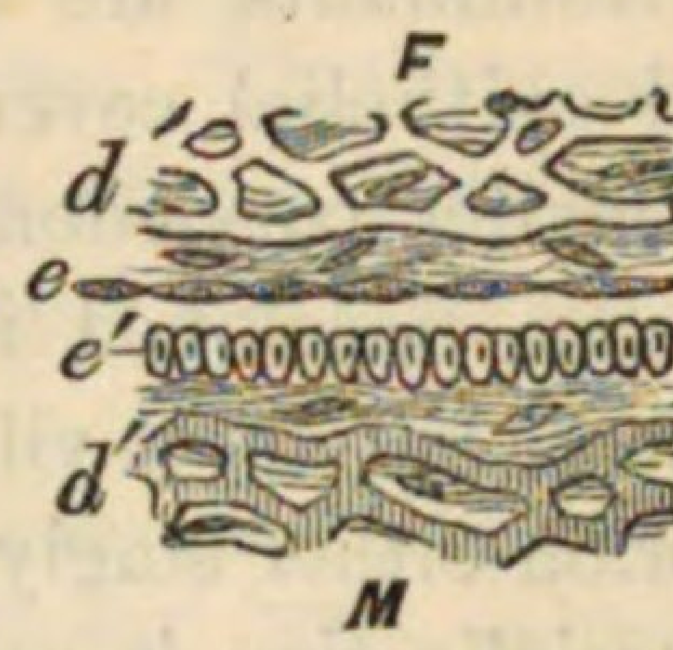


Fig. 3.

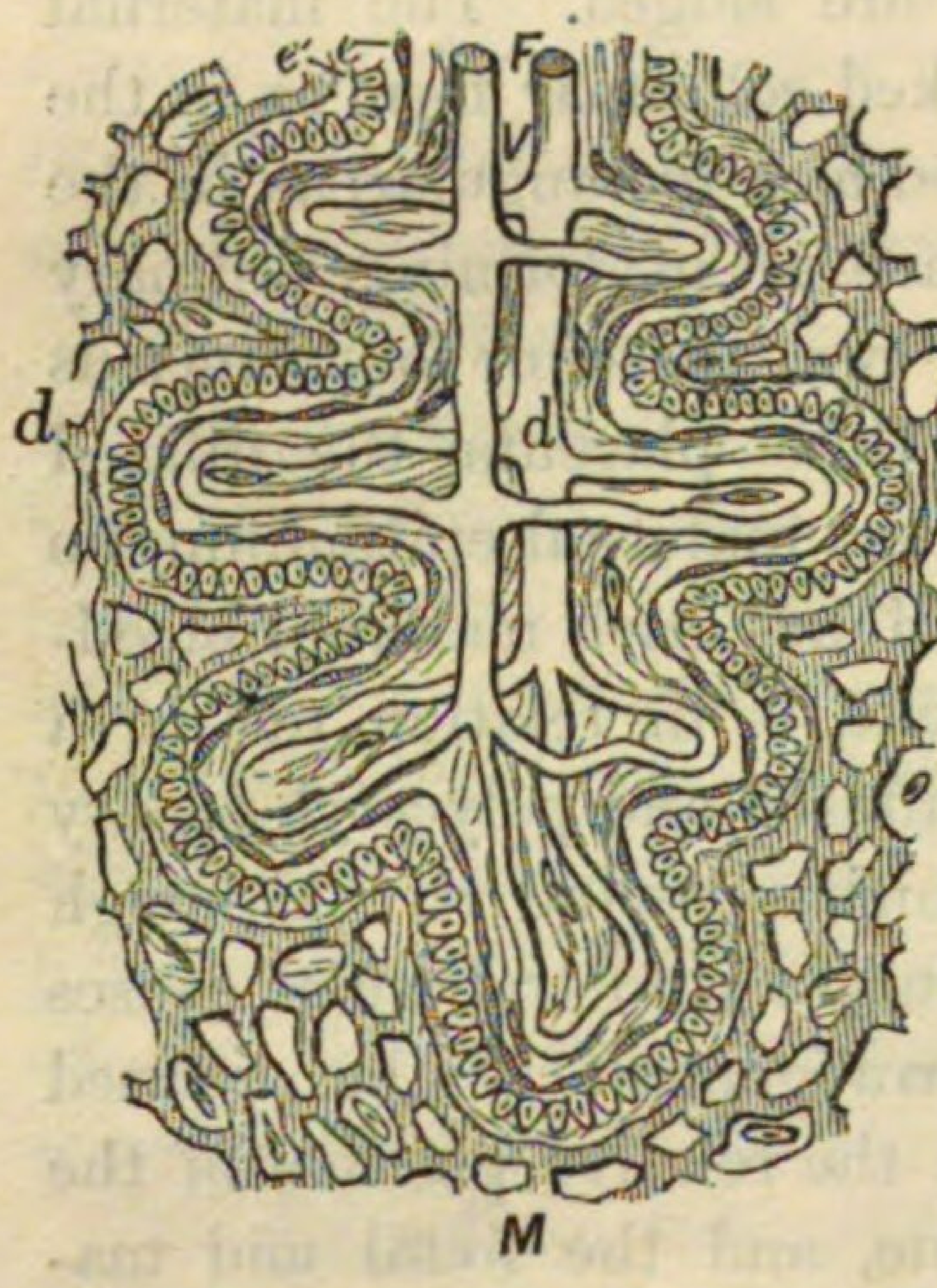
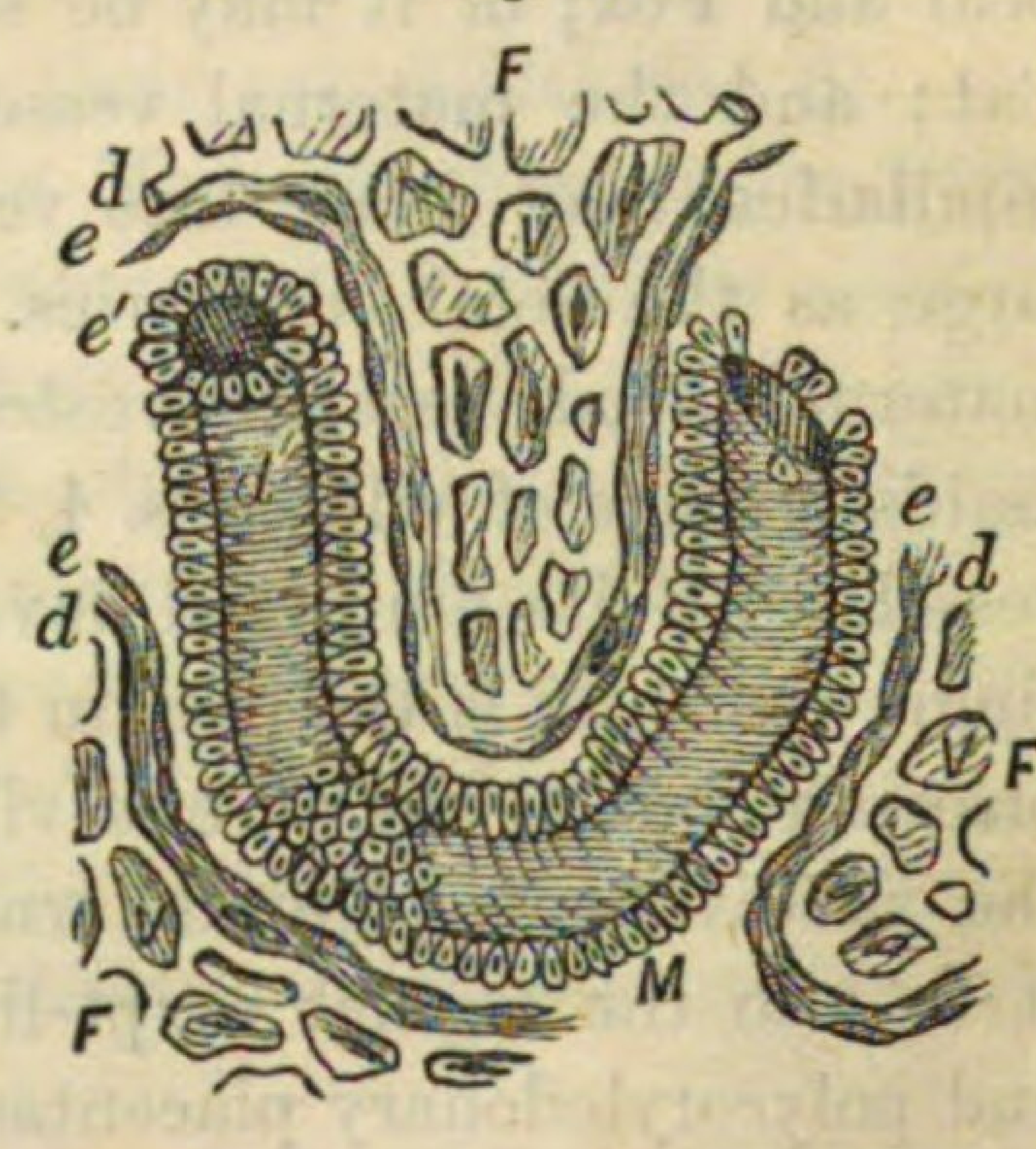


Fig. 4.



EXPLANATION OF FIGURES.

Throughout the series of diagrammatic representations of the minute structure of the Placenta the same letters have been used to indicate similar parts. *F* the fœtal, *M* the maternal placenta. *e* epithelium of chorion. *e'* epithelium of maternal placenta. *d* fœtal blood-vessels. *d'* maternal blood-vessels. *v* villus.

Fig. 1. Structure of placenta of a Pig.
Fig. 2. Placenta in its most generalized form.
Fig. 3. Structure of placenta of a Cow.
Fig. 4. Structure of placenta of a Fox.

Figs. 5, 6.

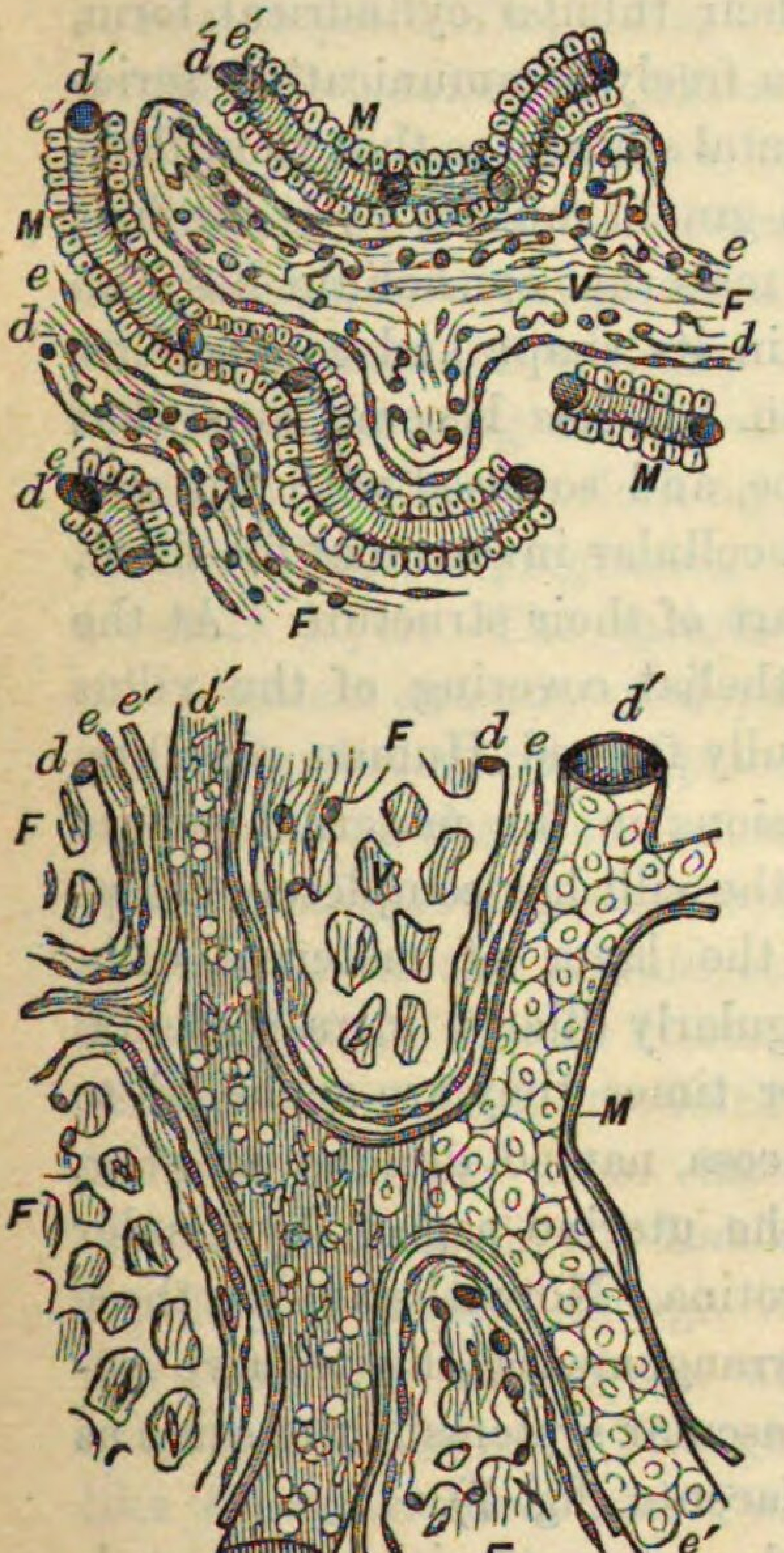


Fig. 7.

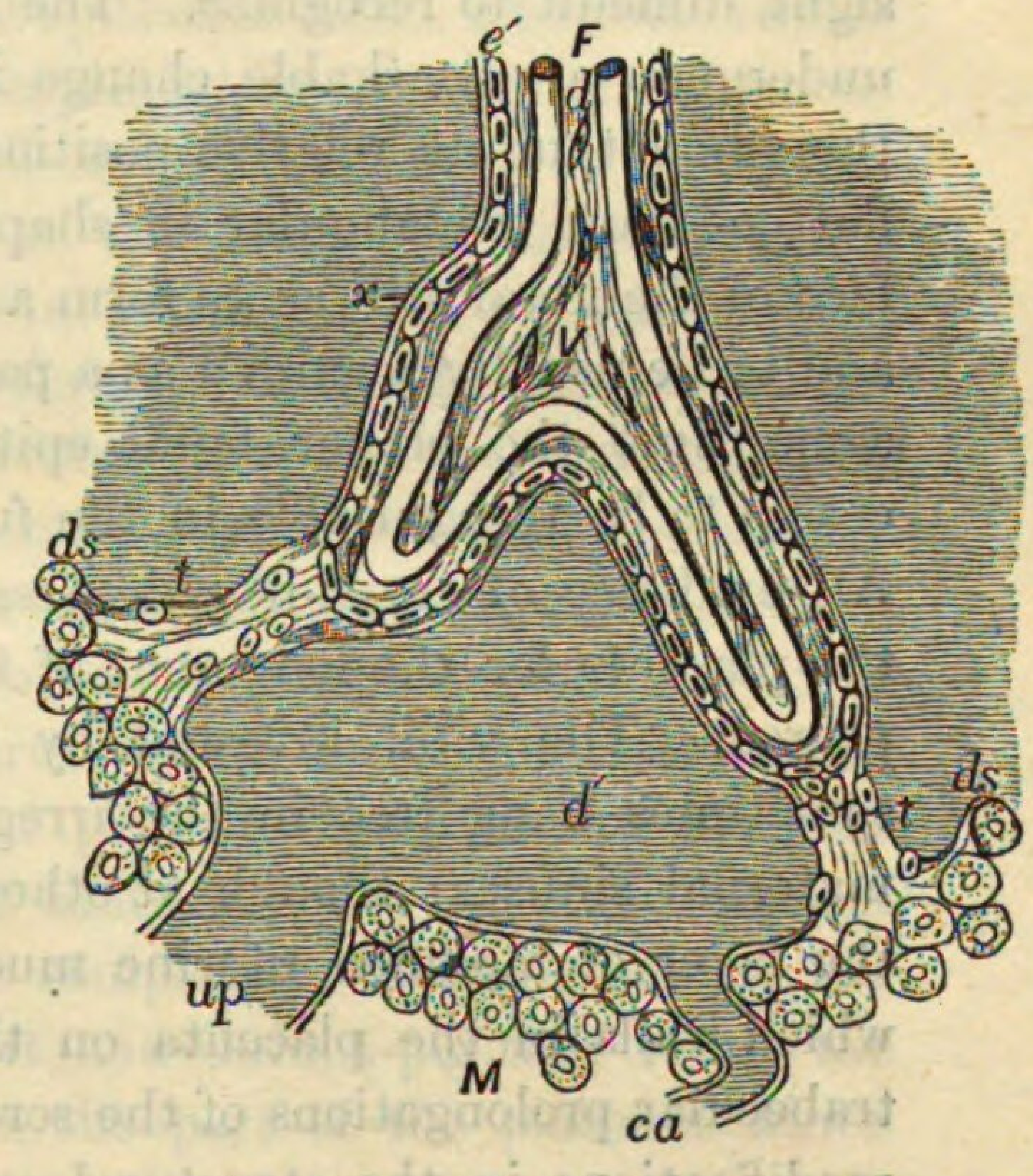


Fig. 5. Structure of placenta of a Cat.

Fig. 6. Structure of placenta of a Sloth. On the right side of the figure the flat maternal epithelial scales are shown *in situ*. On the left side they are removed, and the dilated maternal vessel with its blood-corpuscles is exposed.

Fig. 7. Structure of Human placenta. In addition to the letters already referred to, *ds*, *ds*, represent the decidua serotina of the placenta; *t*, *t* trabeculæ of serotina passing to the fœtal villi; *ca* curling artery; *up* utero-placental vein; *x* a prolongation of maternal tissue on the exterior of the villus outside the cellular layer *e′*, which may represent either the endothelium of the maternal blood-vessel, or delicate connective tissue belonging to the serotina, or both. The layer *e′* represents maternal cells derived from the serotina. The layer of fœtal epithelium cannot be seen on the villi of the fully formed human placenta.

The diagrams were drawn on wood by my assistant, Dr J. H. Scott.

the relative position of the constituent structures is the same as in other forms of placenta[1].

In the discoid Human placenta a more highly specialized arrangement exists. The maternal vessels in the substance of the placenta have not only lost their tubular cylindrical form, but have become expanded into a freely communicating series of irregular, cavernous, intra-placental sinuses, so that their derivation from the vessels of the non-gravid mucosa is, at the first sight, difficult to recognize. The maternal epithelium has also undergone a remarkable change in its shape and connections, though not in its relative position. It has become somewhat flattened and rectangular in shape, and so fused with the surface of the fœtal villi as to form a cellular investment for them, and to be usually regarded as a part of their structure. At the same time the proper fœtal epithelial covering of the villus ceases to be recognisable in the fully formed Human placenta. All evidence of crypt-like depressions in the maternal part of the placenta for the lodgment of the villi has completely disappeared. The villi, invested by the layer of maternal cells, sometimes hang free in the irregularly dilated intra-placental maternal sinuses; though at other times they are anchored to the layer of modified uterine mucosa, named *decidua serotina*, which walls in the placenta on the uterine aspect, by slender trabecular prolongations of the serotina. Notwithstanding these modifications in the structural arrangements, the relative position of the fœtal and maternal vascular systems is the same as in the least specialized forms of placenta (fig. 7).

The different varieties of the placenta met with in mammals

[1] When I wrote in 1873 (*Trans. Roy. Soc. Edinburgh*, 1873) my memoir on the Placentation of the Sloths, I had not then recognised the presence of a layer of cells situated between the dilated maternal blood-vessels and the villi of the chorion, and belonging to the uterine or maternal part of the placenta. The observations which I have since that time made on the placenta in various animals, more especially in the *Carnivora* and *Pinnipedia*, and the recognition in the mammalia generally of a layer of maternal epithelium interposed between the maternal blood-vessels and the chorion, have led me to re-investigate the Sloth's placenta with especial reference to this question. As the result of my enquiries I have found a layer of flattened, polygonal cells, in close apposition to each other by their margins, lying on the dilated maternal blood-vessels, and interposed between them and the villous chorion. These cells occupy therefore the same relative position as the columnar epithelium in the placenta of the Pig, Fox or Seal, but from the thinness of the layer do not so easily attract attention.

all possess the structural characters of the common or fundamental type-form, and may be conceived as having been evolved out of this simple type by slight modifications in arrangement. The process of evolution would be effected by the assumption of a greater extent of complexity in the foldings, on the one hand of the villous chorion, on the other hand of the uterine mucous membrane, with, in addition, in some placentæ, modifications in the relative size of the maternal blood-vessels and in the form of the maternal epithelial cells. The fœtal vessels always remain of ordinary capillary size, and the squamous epithelial covering of the villi may either persist, or become so obscured as the interlocking of the fœtal and maternal parts of the placenta progresses, that it cannot be recognised as a separate layer. The various forms of diffused placenta present the smallest amount of departure from the fundamental type, whilst the discoid human placenta is the most highly specialized.

It is to be observed that a correspondence in external form between different placentæ by no means indicates an exact accordance in the minute structure of their constituent parts. For whilst the discoid Human placenta has its intra-placental maternal vessels so modified that all trace of their original tubular, capillary form has completely disappeared, in the discoid placenta of the Rabbit and Guinea-pig they retain the capillary character, though in the part of the placenta which lies next the wall of the uterus they present a considerable extent of dilatation. Though the placenta in *Orycteropus* has, like the *Carnivora* and *Pinnipedia*, a zonary form, its fœtal and maternal portions may be so easily separated from each other, that it would seem to be referrible to the non-deciduate group of placentæ, and not, as is the case with the Seals and Carnivores, to the deciduata.

Throughout the whole series of placentæ there is interposed between the vascular chorion of the fœtus and the maternal blood-vessels—whether those blood-vessels be simple capillaries, dilated capillaries, or irregular cavernous spaces—a layer of cells, which is in close relation to the maternal blood-vessels. They constitute, or are derived from, the epithelium of the uterine mucous membrane, and belong to the maternal part of the placenta. They sometimes retain the fundamental columnar form, but not unfrequently are modified in shape. This cell-layer is, I believe, a layer of secreting epithelium destined to elaborate material from the maternal blood for the nutrition of the fœtus.

But whilst the structure of the placenta in different mammals is so uniform in its main features, that the possibility of an evolution of the more complex from the more simple forms is quite conceivable, the anatomical structure does not favour the supposition that the evolution has gone on as a continuous process from the diffused, through the polycotyledonary, zonary and dome-shaped group-forms, until at length the highly specialized discoid placenta of Monkeys and of Man has been produced. There is indeed no difficulty in conceiving the evolution of a polycotyledonary placenta out of a diffused, through the atrophy of villi and crypts on some portions of the chorionic and uterine surfaces and their increased development on others, but the evidence is against the view, that the zonary has been evolved out of the polycotyledonary and the discoid out of the zonary. In the zonary placenta the villi and crypts, notwithstanding their specialized form, are yet diffused over the area of the placental girdle, whilst the poles are smooth. As smoothness of the poles of the chorion exists also to a greater or less degree in most examples of the diffused placenta, it would seem as if the evolution of the zonary had been directly from the diffused, through the occurrence of a more extensive atrophy, in the polar regions, in conjunction with certain specializations in the equatorial zone; and the placenta of *Orycteropus*[1] would appear to present a transition between the more characteristic examples of the diffused and zonary forms. That the discoid placenta has been evolved out of the zonary or the dome-shaped is also very improbable, for the latter group-forms exhibit in some features of structure a greater extent of specialization than the discoid placenta does in certain animals. Thus dilated maternal capillaries occur throughout the placenta in the Seals, Carnivores and Sloths, and form a more highly specialized condition of the vessels of the maternal placenta than exists in the discoid placenta of the Rabbit and Guinea-pig, in which the dilatation of the maternal vessels appears to be limited to the part of the

[1] This *Journal*, July, 1876, p. 693.

placenta which lies next the wall of the uterus, and not to be general throughout the entire organ. In some other features of structure, however, the placenta of the Rabbit or Guinea-pig is more highly specialized than is the zonary placenta. It seems to me therefore much more probable, if the several forms of placenta have been produced by a process of evolution, that they have arisen from some common fundamental form, the closest existing representative of which is the diffused placenta, rather than that the evolution has been in a continuous series through the various group-forms. This conclusion is supported by the well-known fact that in the highly specialized Human placenta the villi of the chorion in an early stage of development are diffused over the whole of its surface, and between this stage and the final discoid condition they never assume either the polycotyledonary or zonary mode of arrangement. Hence every Human placenta, during its own development, illustrates the direct evolution of the discoid out of the diffused arrangement.

As I described, in my last year's course of lectures on the placenta[1], the various gradations as regards deciduation and non-deciduation during the act of parturition exhibited by the zonary, polycotyledonary, and diffused forms of placenta, I need not dwell further on them on this occasion. With regard to the dome-shaped placenta, in the Sloth it is undoubtedly deciduate, though in the *Myrmecophagidæ* its condition has not yet been precisely ascertained. The several examples of discoid placenta, so far as they have been studied, also furnish well-marked examples of the deciduate placenta.

Though we are enabled, by the study of the structure of the placenta in different mammals, to conceive how, by comparatively slight modifications in the arrangement of the fœtal and maternal parts of the organ, a highly specialized placenta may have been evolved out of a simple and more generalized form, the question of what it was that induced this evolution to take place is one of much greater difficulty, and in the present state of biological science impossible to solve.

There can be little doubt that organisms may become modified by the direct action of surrounding agencies, and

[1] See my published *Lectures on the Comparative Anatomy of the Placenta*, 1st series, Edinburgh, 1876.

further, that, through the operation of these agencies on the organism, actions may be set up which re-act on the matter of the organism itself. Thus changes in climate, food, and the character of the habitat of an organism may induce variations in the tegumentary organs, the teeth and other portions of the digestive apparatus, the limbs and the skeleton, which variations may be perpetuated, in the descendants of the individual in which they may arise, by hereditary transmission, or may even become more and more pronounced in successive generations, if they should prove useful to the life purposes of the individual and of the species.

But the conditions generally under which the placenta is placed in all mammals seem to be so nearly uniform, that it is difficult to see how it can be affected by surrounding agencies. In all mammals the placenta is enclosed in a uterus, situated in the abdominal cavity: it is at a uniform temperature, so that it cannot be affected by variations in the amount of external heat, and it is altogether excluded from the action of light. Whether its form be diffused or concentrated into a more limited area, it has to perform the same function, viz. that of preparing material for the nutrition of the fœtus, and of bringing that material into sufficiently close relation to the fœtal vascular system so that it may be readily absorbed. Although it is possible that the structural modifications, which I have described, may influence the rapidity of transmission of material from mother to fœtus, there can be little doubt that the chemical and osmotic changes which go on in the several forms of placenta are similar in all cases.

It may be of some interest, however, to consider more in detail some of the special conditions in which the placenta is placed, and to enquire if the habits of life of the animal, the duration of gestation, the size of the mother and fœtus, the shape of the uterus, the number of fœtuses produced at a birth, or the relative size and distribution of the allantois, can have exercised any influence in producing modifications in the form and minute structure of the placenta.

As the discoid and zonary forms of placenta occupy a much smaller proportion of the chorion than do the polycotyledonary and diffused, the modification in shape and the consequent concentration of the organ in a more limited area in the disco- and zono-placentalia might be supposed to be correlated with certain habits of life, which rendered it advisable that the placenta in them should be packed in a comparatively small space.

Thus it might be thought that speed was not so compatible with the possession of a large diffused, as with a compact discoid placenta, or that an animal might climb or burrow more readily if its placenta were limited in its area, and occupied a smaller proportion of the abdomen. But a comparison of the habits of the mammalia with their placental characters does not bear out this supposition. The Horse, one of the swiftest of terrestrial mammals, and the *Balænoptera* of aquatic mammals, have the diffused placenta alike with the lumbering Pig and Hippopotamus; whilst the Deer and Antelope with the cotyledonary placenta have an equal, if not greater speed than the zono-placentary Dog or Lion which chases them. The Hedgehog, which rolling itself up into a ball lies torpid for many months of the year, has a discoid placenta, like the Bat, which in its flight flits as rapidly before the eye so as to produce scarcely any image of its form on the retina. The Lemur with its diffused placenta is as arboreal in its habits as the Squirrel or Monkey with their discoid placenta. The Hare which lives and runs on the surface of the ground has a discoid placenta like the Rabbit and Mole which burrow and tunnel out passages under the surface.

There are considerable differences in the duration of gestation, and consequently in the rate of development of the tissues and organs in different mammals, and it is a fair subject for enquiry if a short gestation and rapid histological development are invariably associated with one form of placenta, a long gestation and slower development with another; but here also there is no definite relation between the habit and the anatomical arrangement. The disco-placentary Rabbit has a gestation of four weeks, whilst the Human female, also with a discoid placenta, has one of nine months. The zono-placentary Cat has a gestation of eight weeks, the Lion of fourteen weeks, and the Elephant of nearly two years. The

Sheep with its cotyledonary placenta goes twenty-one weeks with young, whilst the Cow with a similar placenta is pregnant for nearly double that period. The Llama, with a diffused placenta, has a gestation of twenty-four weeks, whilst the Mare carries its young for eleven months, and the Camel for thirteen months.

As some mammals are much larger than others, and as the fœtus at the time of birth bears a proportion to the size of the mother, it might be thought that the smaller, more compact placentæ would be found in those animals in which the fœtus attains no great size, and the more diffused placentæ in the bigger species, and to some extent this is undoubtedly the case. Thus many of the smaller mammals, as the Rodents, Bats and *Insectivora* have a discoid placenta, and a zonary placenta is found in the smaller *Carnivora.* But the zonary placenta is also present in the larger *Carnivora,* and in the Elephant, the biggest of all existing terrestrial mammals, whilst a discoid placenta occurs in the Human female. Although a diffused placenta is met with in the huge *Balæna* and *Balænoptera* amongst the *Cetacea,* and in the Hippopotamus, Tapirs and Camels amongst land mammals, whilst the Giraffe, Oxen and Deer have the polycotyledonary form; yet in these groups also smaller species are found with similarly formed placentæ; thus the Chevrotains and Peccaries have a diffused placenta, and the little Musk deer a cotyledonary.

Another point which needs consideration in the discussion of this question is the relation between the shape of the uterus and the form of the placenta. To some extent there does seem to be a relation, although exceptional arrangements occur. Uteri, as is well known, are either simple, *i. e.* possess a single cavity, or are divided into two horns. Now it would appear that the diffused, polycotyledonary and zonary forms of placenta never occur in a simple uterus, but the discoid placenta is met with both in simple and bicornuous uteri.

There is also no definite relation between the form of the placenta and the number of fœtuses produced at a birth. The Mare, the *Cetacea,* the Lemurs, the *Manis* amongst the mammals with a diffused placenta are uniparous, but the Pig, also with a diffused placenta, may produce at a birth ten or a dozen or even more. The *Carnivora* as a rule have several young at a birth, but the zono-placentary Seals and Elephant carry only a single fœtus. The disco-placental Rabbit, Mole, and Hedgehog are pluriparous, whilst the Hare, Monkey and Human female are uniparous. In a uniparous mammal, with a diffused or polycotyledonary placenta, the chorion is not limited to the horn of the uterus in which the fœtus is lodged, but extends to the tip of the opposite horn: in the zono-placental uniparous Seal, with a two-horned uterus, the chorion is limited to the fecundated cornu; in the disco-placental uniparous Hare the chorion extends into the non-fecundated horn. But, for the purposes of the placenta, one of the compartments of the uterus in a pluriparous mammal may be regarded as the equivalent of the entire uterus of a uniparous mammal.

As the chorion derives its vascularity from the allantois, and as the distribution of the allantois over the inner surface of the chorion determines the extent of the vascularity of that membrane, it might have been thought that the villi would persist over the whole of the chorion to which the allantois proceeded, so that the form of the placenta would be regulated by the arrangement of the allantois; that in the diffused placenta, for example, the allantois would be much more extensively distributed than in the discoid, and that the disappearance of villi from the surface of the chorion would be associated with an atrophy of the vessels of the allantois. The Human placenta would indeed seem to give support to this view, for at an early stage of development the vascular allantois is distributed over the whole inner surface of the villous chorion, though in the later stages its vessels disappear over an extensive area, the villi of which also atrophy. But the comparative examination of the placenta shows this to be by no means the general rule, for in the diffused placenta of the Pig the poles of the chorion are vascular, though they are non-villous; in the polycotyledonary placenta the intercotyledonary parts of the chorion, though non-villous, are yet highly vascular, and in the zonary placenta the poles, though free from villi, have an abundant capillary plexus distributed in them. Neither can the persistence of the sac of the allantois have any influence in determining the persistence of the villi on the surface of the chorion, for the *Cetacea*, though with the villi diffused over almost the entire outer surface of the chorion, have the sac of the allantois restricted to that part of the chorion which lies opposite the belly of the fœtus.

No one of these several conditions can in itself be regarded as furnishing a sufficient determining cause capable of accounting for the production of the different forms of placenta, and as two or more do not occur together in a sufficiently definite manner to permit us to say that in combination they may produce the variations met with, we are, so far as these agencies are concerned, still ignorant of the true causes of the modifications in the placenta. That some advantage in the economy of the organ has resulted to the animals possessing a discoid or zonary placenta from their concentration in a limited area, over those mammals which retain the less highly specialized diffused and polycotyledonary forms, is very probable. The dilatation of the maternal vessels into colossal capillaries or into sinuses, which seems to be general in the zono-placentary mammals, which exists also in the lobes of the dome-shaped placenta of the Sloth, and in Man and Monkeys amongst the disco-placentalia, modifies the relation of the maternal vessels, with their investing epithelium, to the fœtal villi. In the diffused and polycotyledonary placentæ, which possess a maternal network of ordinary capillaries, only one aspect of the maternal vessel is in relation to the maternal epithelium and the fœtal villi; but, in the other placentæ referred to, the entire circumference of the maternal vessel is surrounded by maternal epithelium and fœtal villi, which would seem to permit of a more rapid interchange of material between the mother and the fœtus; just as in the lungs of birds and mammals the pulmonary capillaries are arranged so as to have their wall more completely in relation to the air in the air-sacs than is the case in the lungs of reptiles.

We have no definite information before us for determining if the surface of the chorion covered by villi varies in its extent inversely with the length, absolute number and complexity of the villi springing from it. We certainly do know that in the diffused placenta the villi though numerous are short and simple, whilst in the more concentrated forms, though fewer in number, they have increased in length or breadth, and in the complexity of their ramifications; but we cannot say if the increase in their length, breadth and complexity bears a precise relation to the diminution in the extent of the horizontal area of the chorion from which they spring. It is possible that the concentration of the villi within a disc or zone may, by limiting the horizontal area of the organ, require the expenditure of a smaller amount of force in the placental circulation than when the placenta is diffused over an extensive surface, and that the flow of the blood, through dilated capillaries, or irregular sinuses, may be accompanied by a smaller amount of friction than when it flows through an ordinary capillary plexus. Should this be the case, then the physics of placental nutrition and circulation would undoubtedly gain something by these modifications in arrangement; and their production, at some remote epoch, as a variation arising in some animal or animals, may, through an advantage in the economy of the organ, have led to their perpetuation by hereditary transmission.

We do not and indeed cannot expect ever to know anything of the placentation of extinct mammals, for the rocks have borne no testimony to the shape and structure of this organ. We may assume, perhaps, as a matter of speculation, that the extinct mammalia, which in their osteological characters so far resembled existing animals as to be referred to the same families and genera, possessed a placenta similar in form and structure to that present in the allied existing animals.

It does not appear that any of the existing genera of mammals have been traced further back in geological time than the miocene division of the tertiary period, though many can only be followed into the pliocene[1].

Amongst the *Perissodactyla*, for example, remains of the Horse have been found in pliocene formations, together with those of certain horse-like animals, which have been named *Protohippus*, *Merychippus* and *Hipparion*; whilst the North American genera *Mesohippus* and *Miohippus* prolong the line

[1] I may refer to the excellent Lectures of Professor Flower for much valuable information on the antiquity and the affinities of the extinct mammalia, as deducible from a comparison of their osteological characters. See *Proceedings of Royal Institution of Great Britain*, April 25, 1873, and March 10th, 1876; also *Nature*, Feb. 17th to May 4th, 1876.

back through the miocene to the *Orohippus* of the eocene period. The Rhinoceroses go back to the pliocene and through the American genera *Diceratherium* and *Hyracodon* to the miocene; whilst the Tapirs have also been met with in the miocene. But in the early miocene and eocene the remains of animals are found, which in their skeletons combined the characters of the existing genera of *Perissodactyla*. Thus the *Anchitherium* possessed both horse and tapir-like characters, the *Palæotherium* had arrangements suggestive of the rhinoceros, horse and tapir, whilst the *Lophiodontidæ* of the early eocene formed apparently a more generalized ungulate type.

Now as existing horses, tapirs, and probably rhinoceroses have a diffused placenta, and on the assumption that the diffused placenta is the least specialized form, it is not unlikely that the extinct *Perissodactyla* had also a diffused placenta, though in the *Lophiodontidæ* it may have closely approximated to the generalized type of placenta.

Amongst the *Artiodactyla* the tubercular-toothed division, or Bunodonts, possess considerable antiquity. The pigs go back to the later miocene and the hippopotamus to the pliocene. The existing genera have, and the extinct forms probably also possessed, a diffused placenta. The Selenodont, or ruminant *Artiodactyla*, have been found in the pliocene and later miocene. The more typical existing ruminants have, as is so well known, the polycotyledonary placenta, a form which was probably possessed by their miocene and pliocene ancestors. In the North American miocenes the family *Oreodontidæ*, and in the later eocenes the genera *Anoplotherium*, *Dichobune*, *Chæropotamus* and *Hyopotamus* are found, which partake of the characters of both pigs and ruminants. These genera are also allied to the true pigs through the transitional forms *Chærotherium* and *Palæochærus;* so that genera at one time existed which combined the characters of those families of Artiodactyles, some of which we now know to possess a diffused, others a polycotyledonary placenta. It is probable that in these extinct forms the placenta was diffused, though beginning, it may be, to put on the cotyledonary arrangement. But amongst existing ruminants two aberrant forms, the Chevrotains and Camels, possess the diffused placenta. Through the Chevrotains the

Ruminants gravitate towards the Bunodonts or pigs, whilst through the Camels they incline, through the extinct genus *Macrauchenia,* to the *Perissodactyla.* Not only therefore do extinct forms supply transitional links between the true ruminants and those extinct genera in which presumably the diffused type of placenta was present, but amongst existing ruminants are found genera, which, possessing the diffused type of placenta, are allied in the one case to the diffused placental Perissodactyles, in the other to the Bunodonts. Hence it seems to me that the palæontological evidence supports the argument which I had previously based on a consideration of their structural characters, that the polycotyledonary placenta, which is only a little more specialized than the diffused placenta, may have been evolved out of a more generalized diffused form.

The diffused placenta is not however limited to the *Ungulata,* but, as we have already seen, is found in the *Cetacea* and Lemurs. The palæontological history of the *Cetacea* carries them back to pliocene and miocene times, and if *Zeuglodon* is to be regarded as an ancestral form of the order, even to the eocene. There is distinct evidence that Lemurs existed in the early miocene, and possibly even in eocene times. Presumably the *Cetacea* and Lemurs have preserved the simple diffused placenta through all these ages; though the concentration of the gland-openings in large areas in the uterine mucosa of existing Lemurs marks a greater degree of specialization, than if each gland had opened independently in its own area, as is the case for example in the common pig, and as may perhaps have been the arrangement in the more ancient forms of Lemurs.

Of the zono-placental mammals the *Proboscidea, Canidæ, Viverridæ* and *Felidæ* can be traced through the pliocene to the miocene period, whilst the remains of Bears and Otters do not appear to have been found older than the pliocene. When the process of specialization of a zonary placenta first began we have no evidence. But the differentiation as regards the *Proboscidea* may perhaps have originated in some of those gigantic forms included under the name of *Dinocerata,* which have recently been discovered in the American eocenes, and which as Professor Flower has stated seem to bridge over the gulf between the modern orders of *Proboscidea* and Perissodactyle Ungulates. And in support of this view I may recall attention to the observation made twenty years ago by Prof. Owen on the placenta of the Elephant, in which he saw not only the zonary equatorial band, but a patch of villi diffused over the chorion at each of its poles. These diffused patches preserve in the placental structure evidences of the perissodactyle affinities of the modern *Proboscidea.*

The remains of mammals exhibiting affinities with existing *Carnivora* have been found in the eocene, as the *Arctocyon primævus,* the different species of *Hyænodon,* and the genera *Synoplotherium* and *Mesonyx,* whilst the miocene has yielded certain generalized types, as the *Amphicyon,* which seems to combine the characters of modern dogs and bears, and the *Machærodus,* which is allied to the *Felidæ.* It is possible that in these extinct genera, the differentiation into a zonary placenta may have occurred; though the affinities of the extinct *Zeuglodon,* on the one hand with the Seals, and on the other with the *Cetacea,* may indicate that to be the line through which the differentiation has been effected. On the other hand, such genera as *Hyænodon, Synoplotherium* and *Mesonyx,* which possess affinities in some of their skeletal characters with the *Insectivora;* or those genera, which Professor Marsh has grouped together in the order *Tillodontia,* and which combine the characters of Carnivores, Ungulates and Rodents, may indicate the direction along which the discoid form of placenta may have originated.

Of the disco-placental mammals, existing families of *Rodentia, Insectivora* and *Cheiroptera* have been found in the miocene, but remains allied to these orders have been described from eocene strata. No very reliable evidence of the remains of true Monkeys has been obtained older than the miocene. Whether the differentiation of the discoid placenta took place in miocene times, or at some earlier period in connection with then existing genera, it is of course impossible definitely to state; though from the fact that the osteological and dental characters of these orders were distinctly differentiated, the placental characters were in all probability likewise differentiated in the miocene period, so that the production of the discoid placenta had presumably taken place at an earlier epoch.

From the description which has been given in these lectures of the form and structure of the placenta it will have been seen that in the genera constituting several of the orders and sub-orders of mammals the placenta has an uniform shape, and within certain limits a close correspondence in internal structure, so that their placental affinities correspond with affinities in the other organic systems. Thus the *Perissodactyla* possess a diffused placenta, the typical Ruminants a polycotyledonary placenta, the *Carnivora*, including the *Pinnipedia*, a zonary placenta, the *Rodentia*, *Insectivora*, *Cheiroptera*, Monkeys and Man each a discoid placenta. On these grounds a classification of the Mammalia on the basis of the placenta has been proposed and adopted by many zoologists. But with this system of classification, as with other systems, which have been based on the characters of a single organ, though it may be found applicable to many genera, yet exceptions occur in such numbers, and of so much importance—exceptions so difficult to reconcile with the general basis of the system—that in my opinion the placental system of classification can no longer be sustained.

Thus in the order *Artiodactyla*, whilst the bunodont Pigs and Hippopotamus have a diffused placenta, the typical Ruminants have a polycotyledonary placenta; though in the aberrant Camels and Chevrotains the placenta is as diffused as in the bunodonts; whilst in the Giraffe, the placenta, though chiefly cotyledonary, yet has to some extent villi diffused over the surface of the chorion. But in the order *Edentata*, as at present constructed, a more remarkable diversity in placental form is met with. In *Manis* the placenta is diffused. In the Hairy Ant-Eaters and Sloths it is dome-like; a similar arrangement, judging from Kölliker's[1] description, is met with in the Armadilloes, though Owen describes the placenta in *Dasypus* as a single, thin, oblong, disc[2]; whilst in *Orycteropus*, as I have recently shown, the placenta is broadly zonular[3], so that the *Edentata*, so far as their placentation has been up to this time studied, furnish examples of all the known group-forms of placenta, except the polycotyledonary. It may, however, be said that the *Edentata* form an order constituted on no very definite basis; that they are animals associated together on the ground of possessing certain negative characters in common, rather than from any positive affinities, and that no

[1] *Entwicklungsgeschichte des Menschen*, 2nd ed. p. 362, Leipzig, 1876.
[2] *Comp. Anat. Vertebrates*, III. p. 731. 1868.
[3] This *Journal*, July, 1876, p. 693.

argument of any weight, as against the placental system of classification, can be based on the diversities of placental form and structure which they exhibit.

But the differences in the *Edentata* and *Artiodactyla* are not the only obstacles to accepting the placental system of classification. The genus *Hyrax*, for example, presents an organisation so remarkable, that whilst some zoologists have referred it to the *Rodentia*, others have regarded it as allied to the *Ungulata;* others have looked on it as intermediate between Ungulates and Rodents; others have made it the type of a distinct order *Hyracoidea*, having affinities on the one hand with the *Ungulata*, on the other with the *Rodentia* and *Insectivora*. But this animal, as indeed has long been known, has a placenta which is neither diffused, nor polycotyledonary as in the *Ungulata*, nor disc oid as in the *Rodentia* and *Insectivora*, but zonary as in the *Carnivora*. Moreover, as I ascertained from the examination of a specimen a few months ago[1], the minute structure of the placenta of *Hyrax* is so like that of the domestic cat, that it is difficult to distinguish the one from the other. In its placental, though not in its other affinities, *Hyrax* approaches so closely to the *Felidæ*, that, if the placenta is to be regarded as the dominant character in classification, it ought to be associated with the Cats, a position in which no zoologist has ventured to place it.

Again, if the form of the placenta in the genus *Elephas* were alone to be taken into consideration, the great preponderance of its equatorial zone would, on the placental system of classification, require this animal to be approximated to the *Carnivora*, an alliance which is not supported by the examination of other features of its structure.

But the Lemurs throw yet greater difficulties in the way of accepting the placental system of classification. The external form of these animals, more especially the configuration of the hands and feet, and the characters of the skeleton and teeth, have led zoologists to associate them with the higher mammalia. Linnæus grouped them with Man, Apes, and Bats in the order *Primates*, and although the Bats have by common consent been since referred to a separate order, yet many eminent zoologists retain the Lemurs with Man and Apes amongst the *Primates*.

[1] *Proc. Roy. Soc. London*, Dec. 16th, 1875.

Blumenbach and Cuvier constructed the order *Quadrumana* for the Apes and Lemurs, an arrangement which has also met with much acceptance. Gratiolet, Gervais, Haeckel, and Carus have placed the Lemurs in a separate order, one however which they regard as allied to the Apes and *Insectivora*. By all zoologists, therefore, they are considered to have close affinities with those mammals which have a discoid placenta; so close indeed has this affinity been supposed to be, that the Lemurs have been erroneously assumed to possess a disc-shaped placenta.

But the figures published by Professor Alphonse Milne Edwards[1] and the examination made by myself[2] of the gravid uteri of several genera of Lemurs have shown that in these animals the placenta is diffused, so that in their placental form and structure, as well as in the large and persistent sac of the allantois, they correspond closely with the *Perissodactyla*, bunodont *Artiodactyla*, and *Cetacea*.

Hence, if the placental characters are to out-weigh those presented by other organs, the position of the Lemurs in the class Mammalia must be completely reversed. Instead of being grouped in more or less close relationship with the Apes and *Insectivora*, they must be placed alongside of the Whales and *Ungulata*. But this is a position which will, I think, scarcely be accepted by zoologists.

From a consideration therefore of the form and structure of the placenta in the several orders of mammals, so far as we have as yet had an opportunity of studying it, one is led to the conclusion that, for purposes of Classification, the placenta cannot be accepted as a dominant organ; but that in the present state of science, where our acquaintance with the genealogical relations of animals is insufficient for the construction of a definite pedigree, the presence of a combination of similar characters drawn from more than one system of organs gives a safer guide to the affinities of an animal, than the existence, in only a single organ or system, of even a very close resemblance in form and structure.

[1] *Histoire Naturelle des Mammifères de Madagascar.* Vol. IX. Tome IV. Atlas I. Plates 113 to 121. No description of these plates has yet been published. Paris, 1875.

[2] *Trans. Roy. Soc. London*, 1876.