ON THE STRUCTURE OF THE DIFFUSED, THE POLYCOTYLEDONARY AND THE ZONARY FORMS OF PLACENTA[1]. By Prof. Turner.

In all inquiries into the anatomy of the Placenta, two series of structures have to be investigated, the one belonging to the fœtus, the fœtal placenta, the other to the mother, the maternal placenta. The placenta is therefore a compound organ, and the complexity of its structure in any given mammal is in proportion to the degree in which, in the course of its development and growth, the originally separable fœtal and maternal portions have become interlaced with each other.

The fœtal placenta and membranes, continuous with and derived from the germinal layers of the embryo, consist of the membranous sacs, known as the umbilical vesicle, the allantois, the amnion, and the secondary or persistent chorion. The persistent chorion, with the villi growing from it, forms the fœtal placenta properly so called. It is the outer envelope of the fœtus and is the medium of connection with the maternal placenta. There are four structures, of which one is developed at the periphery of the ovum, whilst the remaining three ultimately reach the periphery, which from their position may enter into the formation of the persistent chorion: viz. the zona pellucida, the subzonal membrane, the allantois, and the umbilical vesicle. The structureless zona, with its simple structureless villi, which together form the primitive chorion, very early disappears, either by becoming incorporated with the subzonal membrane, so as no longer to be recognised as an independent membrane, or by becoming absorbed. The subzonal membrane, or serous envelope of the ovum of Von Baer, originally continuous with the amniotic folds, and through them with the epiblast layer of the blastoderm, persists, and forms the external or epithelial non-vascular layer of the persistent chorion, and of the villi which grow from it. The allantois

[1] This Memoir contains the substance of a course of three Lectures, on the Comparative Anatomy of the Placenta, delivered June 14th, 15th, 16th, 1875, in the Theatre of the Royal College of Surgeons of England.

grows and expands so as to come into intimate relation with the whole or the greater part of the inner surface of the subzonal membrane, and conveys to it, from the mesoblast layer of the embryo, the connective tissue and blood-vessels, which form the inner or vascular layer of the persistent chorion, and the vascular matrix of the villi. In most mammals the umbilical vesicle takes no part in the formation of the permanent chorion, but in the *Rodentia* it expands, reaches and remains in contact with a limited portion of the subzonal membrane, to which it conveys connective tissue and blood-vessels. The persistent chorion, therefore, is a compound membrane, produced by the union of the subzonal membrane, from which its epithelial layer is derived, with the allantois from which it derives its blood-vessels and connective tissue.

The maternal placenta is formed by the mucous membrane lining the uterus, in which important changes occur during pregnancy. This membrane in the non-gravid state is covered on its free surface by a ciliated columnar epithelium. Beneath the epithelium is the sub-epithelial connective tissue, which contains a very large proportion of fusiform, ovoid and spherical corpuscles. In this tissue the blood-vessels, lymph-vessels, and nerves of the mucosa ramify, and in it lie the utricular glands. The glands of the mucosa are branching tubes, which lie, more or less, perpendicularly to the plane of the surface of the membrane, and are separated from each other by the interglandular corpusculated connective tissue, the proportion of which between any two glands is often not more than equal to the transverse diameter of a gland, though at others its amount is considerably greater. The epithelial lining of the glands, as was first demonstrated by Nylander and Leydig in the pig[1], and as has subsequently been shown by Lott[2] in various other mammals, is columnar and ciliated.

When the fertilized ovum is received into the cavity of the uterus the mucosa undergoes important changes. It swells up, becomes thicker, softer, and more vascular. Its epithelial covering usually, though not always, loses its columnar form; its glands enlarge throughout their entire length: the inter-

[1] Müller's *Archiv*, 1852.
[2] Stricker's *Handbuch*, article *Uterus*.

glandular tissue increases largely and rapidly in quantity, by a multiplication not only of the cells of the surface-epithelium, but by a proliferation of the corpuscles of the sub-epithelial connective tissue, so that the glands are separated from each other by a much greater amount of interglandular tissue than in the non-gravid state; the blood-vessels not only increase in numbers but in size. At the same time the free surface of the mucosa is perforated by multitudes of small openings, easily to be seen with a pocket-lens. Those openings lead into depressions in the swollen mucous membrane, which are usually regarded as the dilated mouths of the tubular glands, but which, as I shall show in this memoir, are the mouths of crypt-like depressions situated in the interglandular part of the mucous membrane. These crypts are for the lodgement of the villi, which project from the outer surface of the persistent chorion. As the area of distribution of the villi on the chorion varies very considerably in extent in different forms of placenta, the distribution of these crypts in the uterine mucosa necessarily also varies; for the crypts and the villi are correlated with each other.

The arrangement and structure of the placenta in those animals in which it is said to be diffused will first engage our attention.

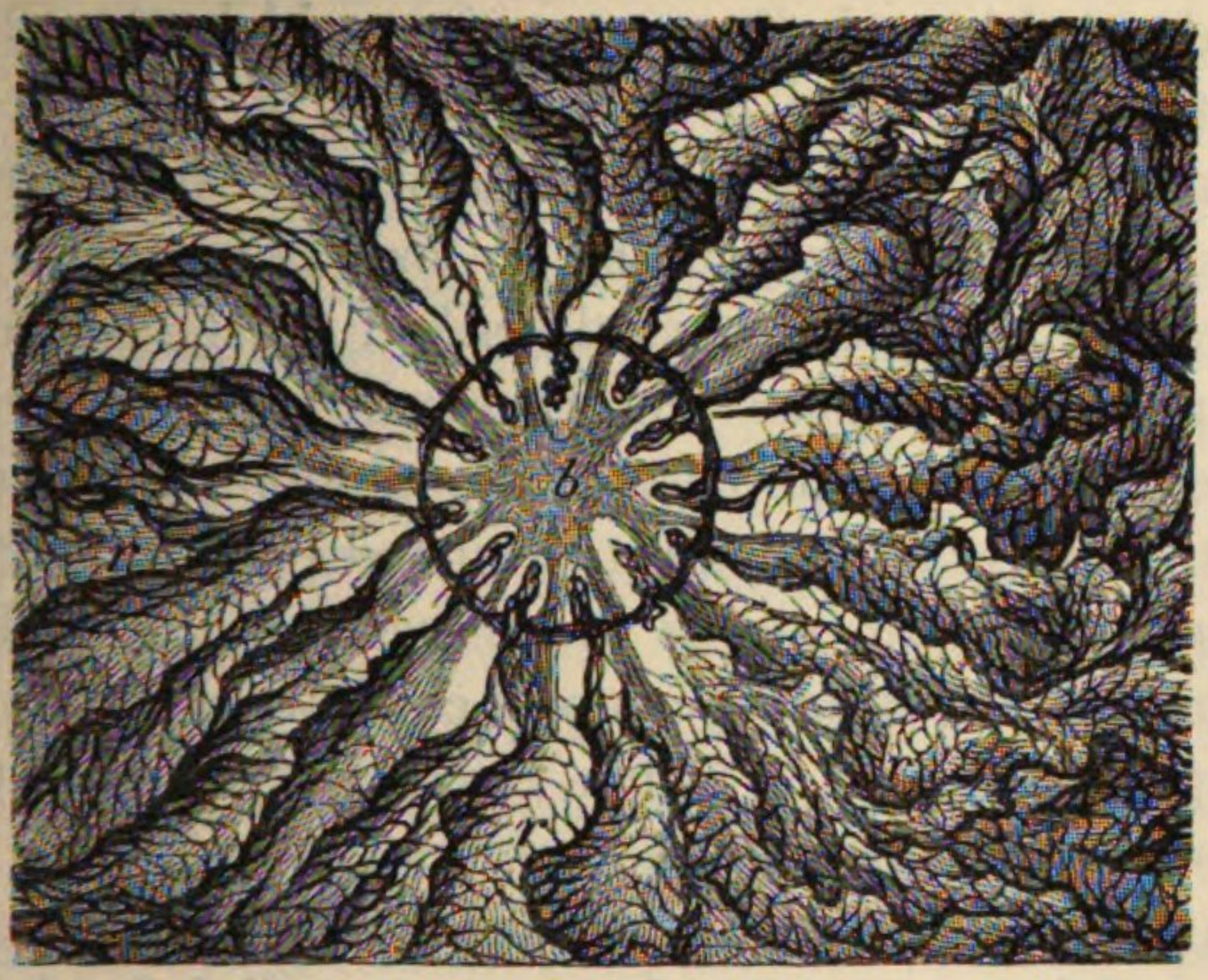
THE DIFFUSED PLACENTA.—In the diffused placenta the villi are distributed over almost the entire outer surface of the chorion, and the uterine crypts exist in a corresponding area of the mucous membrane. This form of placenta is found in the Pigs, the Solipeds, the *Cetacea*, in *Manis*, the *Camelidæ*, the *Tragulidæ*, the Tapir, the Hippopotamus, and, in all probability, the Rhinoceros.

I shall commence by describing the structure of the placenta as I have myself observed it in the common Pig, and shall in the first place speak of the fœtal placenta. The surface of the chorion of a pig, where the embryo was 1·3 inch long, was traversed by multitudes of feeble ridges, visible under low powers of the microscope, but no true villi could be seen. A distinct and compact capillary plexus was present both in the ridges and intermediate parts of the chorion. In the ridges

the plexus was elongated, but it formed a polygonal network in the intermediate areas. The polar ends of the chorion were smooth and free from ridges for about three inches from each pole. A uniform layer of squamous epithelial cells, the nuclei in which were distinct, covered the face of the chorion. In an older specimen, where the fœtus was six inches long, the ridges on the chorion were more strongly elevated, but still requiring a microscope for their examination. The summit of each ridge was broken up into numerous short, simple villi, just as a mountain-ridge may be broken up into short peaks and summits. In injected preparations these ridges and villi were seen to be very vascular[1]. Scattered irregularly over the surface of the chorion were quantities of circular or almost circular slightly elevated spots, which varied in number in a given area. Sometimes as many as 30 were seen in a square inch, in other places not more than 20. The spots varied in diameter from $\frac{1}{20}$th to $\frac{1}{10}$th inch, occasionally one $\frac{1}{5}$th inch in diameter was seen. In most of the red injected specimens these spots were white and free from colour, as if non-vascular, but when the injection was pushed further they became red also, though not so completely as the rest of the chorion. Examined microscopically each spot was observed to have a minute central depression surrounded by villi, which were the terminal villi of a group of ridges, and it was now seen that the villous ridges were arranged on the chorion with especial reference to these spots; for each spot was a centre from which the ridges radiated outwards as the spokes do from the centre of a wheel. After proceeding some distance the ridges not unfrequently branched, and adjacent branches joined together so as to form a network. Hence the villous surface of the chorion may be regarded as mapped out into a number of areas, the centre of each area being a circular spot, from which the villous ridges radiate. Each end of the chorion, for nearly three inches from the pole, had a smooth non-villous surface, and though possessing considerable vascularity was not so vascular as the villous part of the chorion. Hence the chorion of the pig is not uniformly

[1] For valuable aid in injecting this and the other injected placentæ described in this Memoir, I have to express my thanks to my Museum Assistant, Mr A. B. Stirling.

Fig. 1.



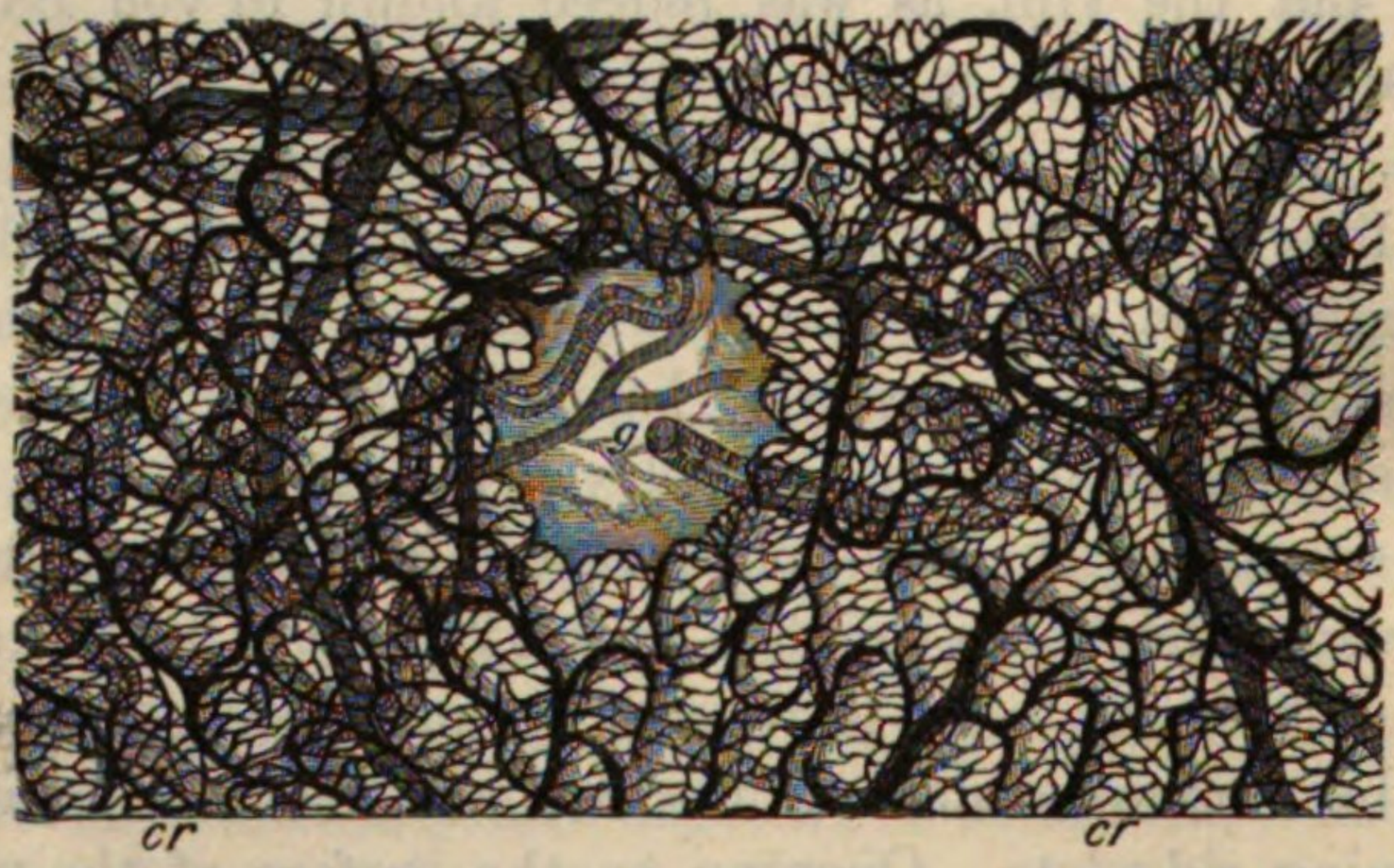
Portion of injected Chorion of Pig, as seen under a low magnifying power, to show the minute spot *b*, enclosed by a vascular ring, from which villous ridges, *r*, *r*, *r*, radiate. Figures 1, 2 and 3 were drawn on wood from my preparations by my assistant Mr A. H. Young.

villous, but the villi, as was indeed known to von Baer, are distributed over the middle and not the polar regions of the chorion. Though the structure of the placenta in the pig is simple like that of the mare and other animals with a diffused placenta, yet, as regards the distribution of the villi, they are arranged as a broadly zonular band which does not reach to within several inches from the poles of the chorion.

On examining the maternal placenta in the gravid uterus of a pig, where the fœtus weighed only 12 grains, the free surface of the mucosa was seen to present an undulating appearance, owing to numerous shallow furrows and fossæ separated by intervening ridgelets. Opening on the surface of the mucosa, the openings being marked by shallow depressions distinct from the furrows above referred to, were the mouths of the utricular glands, and not unfrequently a plug of epithelium projected through the orifice. Each gland-orifice was surrounded by a smooth portion of the mucosa. In a more advanced specimen, where the fœtus was 6 inches long, the mucosa was thrown here and there into transverse folds. When examined with a pocket-lens fine ridges and furrows were seen, which were adapted to furrows and ridges on the surface of the

chorion. When more highly magnified the furrows were seen to be subdivided into shallow crypts into which the villi of the chorion fitted. Scattered over the surface of the mucosa were numerous smooth almost circular depressed spots, free from ridges and crypts, corresponding in size and numbers to the circular, radiating spots already described on the surface of the chorion; and, as von Baer[1] and Eschricht[2] have described, the star-like elevations of the chorion are adapted to these smooth spots on the mucosa when the two surfaces are in contact. In the minutely-injected uterus the ridges and the walls of the crypts were seen to contain a compact capillary plexus, whilst the smooth spots possessed a feeble vascularity, so that they appeared as distinct white spots, surrounded by highly vascular ridges, on the injected mucous surface. Beneath the superficial crypt-layer of the mucous membrane was a well-defined glandular layer, the glands in which were tubular and branched repeatedly, so that each gland-stem or duct had connected with it numerous

Fig. 2.



Surface-view of a portion of the injected Uterine Mucosa of a Pig to show a depressed circular spot in which the mouth of a gland *g*, opens. This spot is surrounded by numerous vascular crypts *cr*, *cr*. The branching glandsof the glandular layer and the larger vessels lie deeper than the crypts. Magnified same scale as Fig. 1.

branching tubes. The depressed circular spots had a special relation to the ducts of these glands, for opening either in the centre of each spot, or near its border, by an obliquely-directed

[1] *Ueber Entwickelungsgeschichte der Thiere*, p. 250, 1837.
[2] *De organis quæ respirationi et nutritioni fœtus mammalium inserviunt.* Hafniæ, 1837.

orifice, was a gland-stem, which could be seen running, somewhat tortuously, from the deeper glandular layer of the mucosa to the spot. Eschricht had in 1837 described the mouths of the utricular glands in the pig as situated in small circular spots (*areolæ*), distinct from the surrounding crypts (*cellulæ*), which circular spots in injected specimens, owing to their feeble vascularity, appeared white, when compared with the highly vascular crypts. These observations of Eschricht seem to have been overlooked by most subsequent observers. In 1871[1] I described a similar arrangement in the uterus of a pig which I examined. In 1873 a description with a characteristic figure of a spot in an uninjected specimen was given by Ercolani[2]. It is clear therefore that in the pig the glands do not open into the crypts of the gravid mucosa, but into special depressions of the mucous membrane distinguished by a difference in form and in the degree of vascularity from the surrounding crypt-like surface. The crypts therefore are interglandular in position, and are produced by modifications in the interglandular part of the mucous membrane, and not by a dilatation of the gland-orifices themselves. The free surface of the mucosa was covered by an epithelium which also lined the crypts. The epithelial cells were columnar in form, finely attenuated at their deeper end; and not unfrequently I saw an appearance as if cilia projected from the broad end of the cell; but the animal had been too long dead to enable me to determine their presence by vibratile movements. Owing to the shallowness of the crypts and the very short villi of the chorion in the pig the uterine and chorionic surfaces separated from each other with great readiness. As the tubular glands did not open into the crypts their secretion did not come into immediate contact with the general villous surface of the chorion. The mucous membrane of the gravid uterus of the pig differs from that of the non-gravid animal in the following characters: in the presence of a layer of crypts, in the increased size and greater obliquity of the glands, and in the much greater vascularity of the membrane generally.

I have not had the opportunity of examining the fœtal

[1] *Trans. Roy. Soc. Edinb.* Vol. xxvi. p. 490.
[2] *Mem. dell' Accad. delle Scienze di Bologna*, Plate 2, Fig. 1.

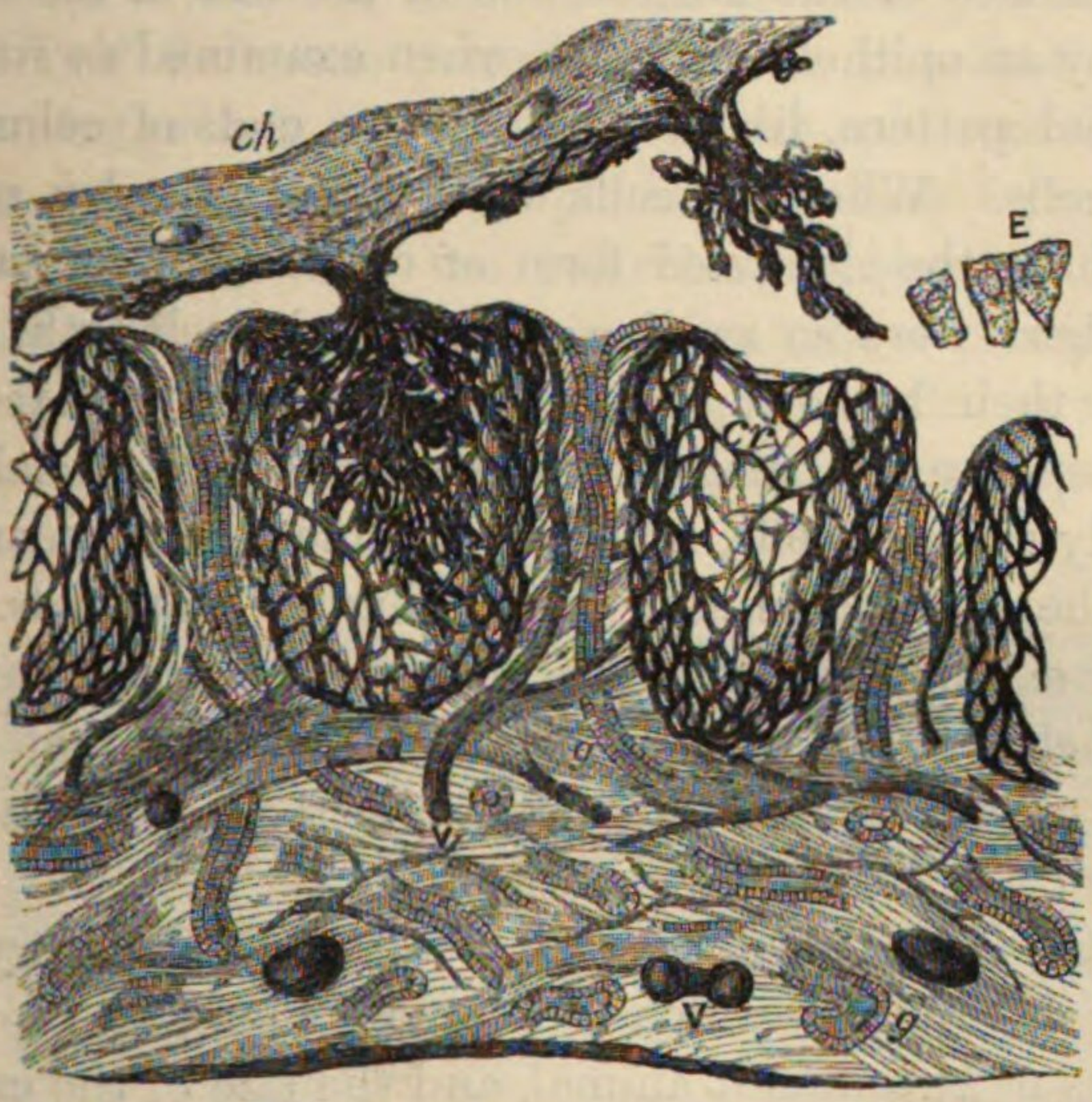
placenta of the Mare in the early period of gestation, but two specimens in advanced stages have come under my observation. In both, the surface of the chorion presented a soft, velvety, vascular appearance, due to its being almost uniformly covered with vascular villi, even up to the poles. But at each pole, where the chorion was in relation to the orifice of the Fallopian tube, a spot, a fraction of an inch in diameter, smooth and bare of villi, was present. Opposite the os uteri internum a well-defined bare patch, which in one specimen was about an inch in diameter, having in its centre a faint papillary elevation, was present. Radiating outwards from this patch were five long branching arms, also free from villi, and immediately beyond these some irregularly-shaped bare patches were seen. The surface of the uterine mucosa was also very vascular, except opposite these bare patches on the chorion, and the folds and depressions radiating from the os uteri corresponding to the radiated patch on the chorion had a comparatively slight vascularity. In the chorion from another mare the bare spot opposite the os uteri measured $2\frac{1}{2}$ inches long by from $\frac{1}{2}$ to $\frac{3}{4}$ inch broad, and had distinct bare radii passing off from it. In each specimen an irregular-shaped non-villous patch, about an inch long, was found on a portion of the chorion not in relation to a uterine orifice. Though in the mare the villi seem to the naked eye to be closely set over the surface of the chorion, yet when examined with low powers of the microscope they are seen to be arranged in brush-like clusters or tufts, separated by narrow non-villous intervals, an arrangement the importance of which will appear when the corresponding surface of the mucosa is described. The tufts are like minute fœtal cotyledons and the villi in each tuft are filamentous in shape and contain a loop of capillary blood-vessels.

I have not yet been able to procure the uterus of the mare in an early period of gestation. But on inspecting with a simple lens the surface of the uterine mucosa of a mare which had reached an advanced stage of pregnancy[1], I found it subdivided into multitudes of irregular polygonal areas, varying in diameter from $\frac{1}{12}$th to $\frac{1}{20}$th inch, by slender ridges,

[1] I am indebted to J. R. W. Dewar, Esq., V. S. of Midmar, Aberdeen, for this specimen.

which anastomosed with each other so as to have a reticulated appearance. In injected preparations the ridges were seen to be less vascular than the areas which they enclosed, and consequently they were more readily recognised in injected than in non-injected portions of the mucosa. But in addition the ridges were smooth on the surface, whilst the enclosed areas possessed a delicate punctated appearance. When more highly magnified each area was seen to be subdivided into multitudes of crypts, which passed more deeply into the mucosa than in the pig. The arteries and veins of the mucosa occupied the ridges, and broke up into small branches which ended in a

Fig. 3.



Vertical section through the injected placenta of the Mare. *Ch.* the chorion with its villi, partly *in situ*, and partly drawn out of the crypts, *cr. g, g*, the utricular glands. *V, V*, the blood-vessels of the mucosa imbedded in the connective tissue. *E* loose epithelial cells which formed the lining cells of a crypt.

compact capillary plexus situated in the walls of the crypts, the artery in each ridge giving off branches to the crypt-areas between which that ridge was situated.

The glandular layer of the mucosa contained numerous branched tubular glands. From each gland a stem or duct proceeded which ascended almost vertically into a ridge be-

tween the crypt-areas, and opened on the summit of the ridge by a circular or oval aperture, which was usually situated at a spot where convergent ridges became continuous with each other. In the mare, therefore, as in the pig, the utricular glands do not open into the crypts; but on definite surfaces of mucous membrane between the crypts, so that the crypts are interglandular in position, and produced by changes in the interglandular part of the mucosa. The demonstration of the want of any communication between the utricular glands and the crypts in the mucosa of the gravid mare, and the consequent interglandular position of the crypts, was made a few years ago by Prof. Ercolani[1] of Bologna.

The surface of the mucosa and of the wall of the crypts was covered by an epithelium, which when examined *in situ* showed a polygonal pattern, like the broad free ends of columnar epithelium-cells. When the cells were teased asunder, some were seen to have the elongated form of ordinary columnar epithelium; others were so swollen out that their length but little exceeded their breadth; whilst others were irregular in shape. The protoplasm was distinctly granular, more especially in the irregularly-shaped cells, which resembled in appearance the cells of the serotina as seen in the higher mammals. Numerous cells exhibiting transitional forms between ordinary columnar epithelium and serotina-cells were seen, so that the large granular cells of the serotina are to be regarded as a modified epithelium.

The filiform villi of the tufts of the chorion occupied the crypts in the mucosa, which represented therefore the maternal cotyledons of a ruminant animal, and the size of the crypt-areas correspond to the size of the tufts. The ridges between the areas filled up the intervals between the tufts. The secretion of the uterine glands was not poured into the crypts so as to come into immediate relation with the villi, but opposite the inter-villous surface of the chorion. The villi of the chorion were so closely fitted into the uterine crypts, that, in the specimen of the gravid uterus near the full time, it required a little force to draw the villi out of the crypts. As in the pig,

[1] See the French translation of his Memoir, and the figures in Plates 3 and 5. Algiers, 1869.

the gravid mucous membrane differed from the non-gravid in the presence of a layer of crypts, in the increased size and greater obliquity of the glands, and in the greater vascularity of the membrane generally.

The diffused distribution of the villi over the surface of the chorion in the *Cetacea*, and the velvety appearance due to this arrangement, have been recognised by several anatomists, from observations made more especially on the common porpoise. In 1869 I examined several square feet of the chorion of *Balænoptera Sibbaldii*[1], and showed that the whalebone whales agreed with the toothed whales in the diffused distribution of the villi. But in the *Cetacea*, as in the pig and mare, patches of chorion bare of villi are also present. Some years ago Prof. Rolleston pointed out[2] that in a specimen (species unknown), which he examined, a bare spot was situated at each pole. In a gravid *Orca gladiator*, which I examined in 1871[3], I found not only the polar bald spots, but a stellate non-villous surface, nearly the size of a crown piece, and with several bare lines radiating from it opposite the os uteri; the arrangement corresponding very closely with that just described

Fig. 4.

Stellate non-villous portion of the Chorion of *Orca*, opposite the os uteri. About half the size of nature.

in the chorion of the mare in the same locality. These large radiating bare spots in the mare and cetacean are exaggerated

[1] *Trans. Roy. Soc. Edinburgh*, 1870.
[2] *Trans. Zool. Soc.* p. 307, 1866.
[3] *Trans. Roy. Soc. Edinb.* 1871.

representations of the small radiating spots, so abundantly distributed over the chorion of the pig.

When the chorion of *Orca* was examined microscopically the villi were seen to vary in number and in arrangement in different parts. Sometimes they were set in rows and formed parallel ridges: at others they were collected into tufts, irregular in form and size, which sometimes consisted of two, three or four villi, but frequently of a larger number. Solitary villi were also met with in the irregular intervals between the tufts and ridges; and it was not uncommon, as Eschricht had observed in *Phocæna*[1], to see short stunted simple villi projecting from the general plane of the chorion. The tufts not unfrequently swelled out into a branching crown, which, to adopt Eschricht's description of the shape of the villi in *Phocæna*, formed a miniature representation of the head of a cauliflower. The secondary villi of a tuft, as well as the simple villi, were club-shaped.

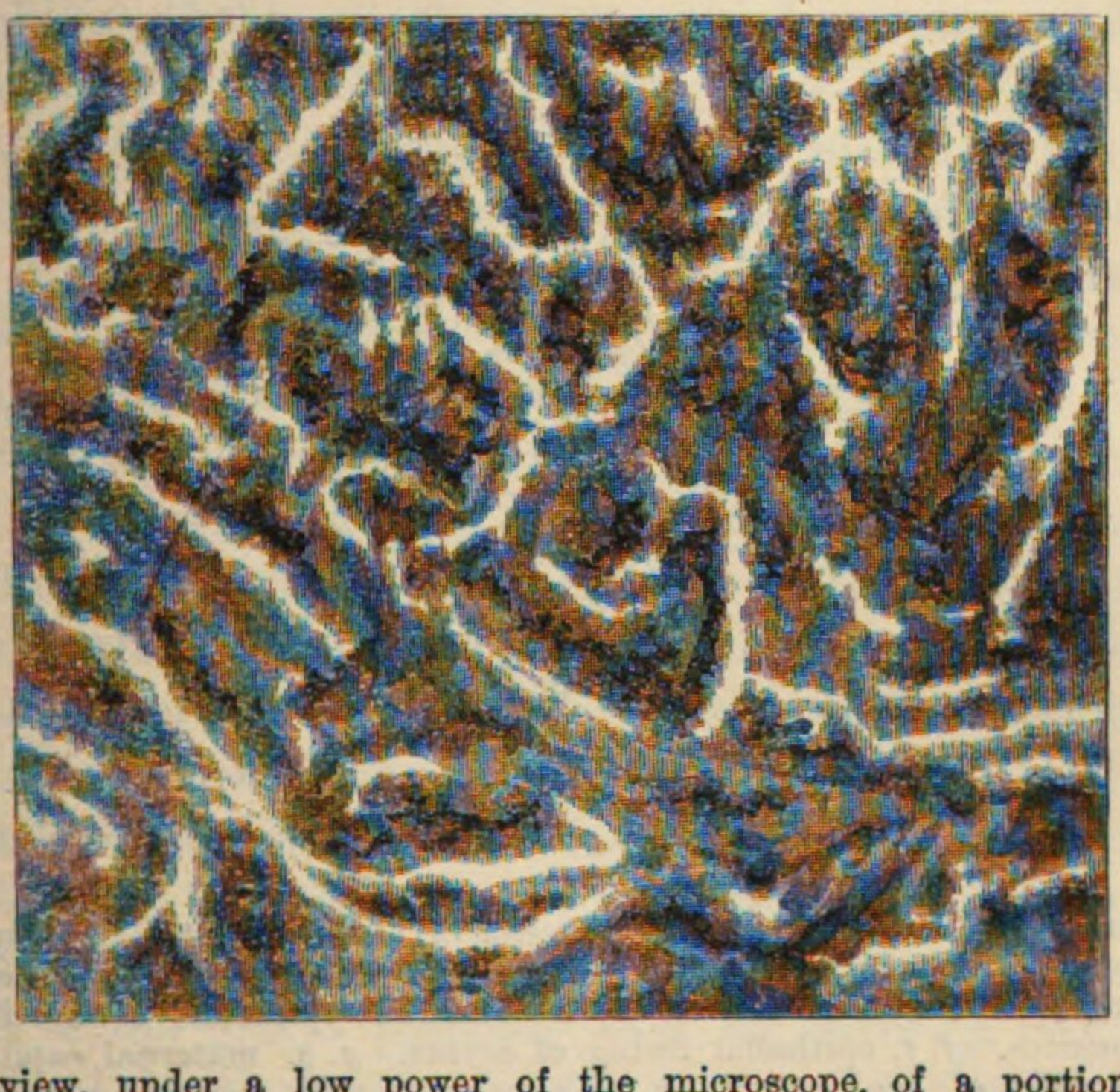
A layer of spherical or ovoid corpuscles was situated immediately within the free surface of each villus, and not unfrequently the periphery of the villus was slightly elevated immediately above the individual corpuscles, so that the outline of the villus had a gently undulating appearance. These corpuscles I have named from their position the sub-epithelial corpuscles of the villus. In their form and appearance they are not unlike the white corpuscles of the blood, and it is possible that they may have migrated out of the blood-vessels into the connective tissue of the villus. The villi contained a distinct capillary network. Not only in the *Orca*, but in the pig and mare, the capillaries of the chorion were not limited to the villi, but an extra-villous capillary network, which freely anastomosed with the intra-villous capillaries, was situated beneath the general plane of the chorion. The blood in its passage from the terminal twigs of the umbilical artery to the umbilical vein had to flow not only through the capillaries within the villi, but through the extra-villous network, from which the rootlets of the vein arose.

Eschricht in 1837[2] and Stannius in 1848[3] described the

[1] *De Organis*, &c., p. 6. [2] *De Organis*, &c.
[3] Müller's *Archiv*, p. 402, 1848.

presence of numerous little recesses on the free surface of the uterine mucosa of the gravid porpoise, in which the villi of the chorion were lodged. In 1871[1] I had the opportunity of dissecting the gravid uterus of *Orca gladiator*, and of determining much more minutely, than had previously been done, the structure of the gravid uterine mucosa in this order of mammals. The free surface of the mucosa had a delicate reticulated appearance, due to an anastomosing arrangement of slender bands of the membrane. Sometimes a subdivision of the surface into irregular polygonal areas was seen, at others its surface was traversed by an elongated ridge and furrow

Fig. 5.



Surface-view, under a low power of the microscope, of a portion of the uninjected uterine mucous membrane of *Orca gladiator*.

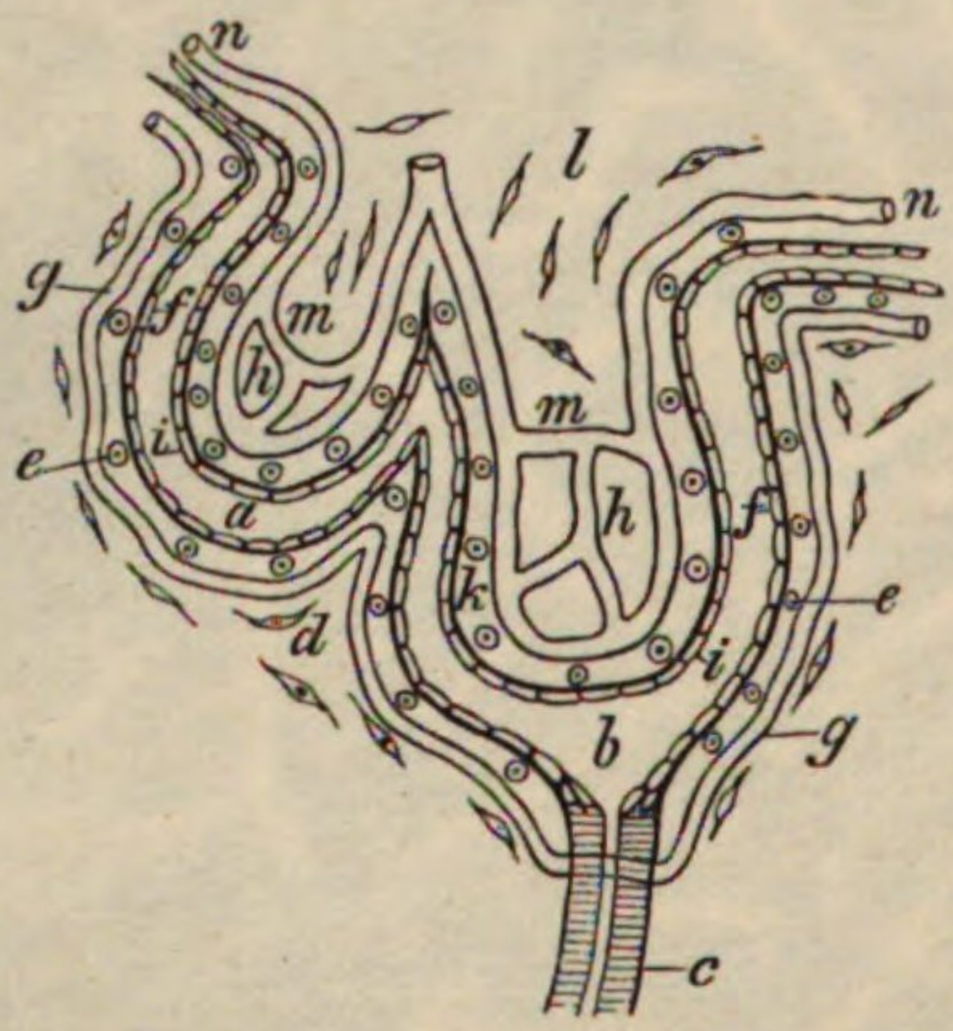
arrangement. The polygonal areas and the furrows were subdivided by more delicate bands into small crypt-like compartments, and the intermediate ridges and bands of the mucous membrane were not unfrequently covered by similar crypts.

Beneath the crypt-layer was the glandular layer of the mucous membrane. The glands, as in the pig and mare, were

[1] *Trans. Roy. Soc. Edinburgh*, p. 467, 1871.

tortuous tubes and branched repeatedly. The mode of termination of the glands on the surface of the mucosa was more difficult to determine than in the pig and mare, but after repeated examinations, both of vertical sections through the membrane, as well as of surface-views, I came to the conclusion that the tubular glands opened into the bottom of some of the crypts[1]. But as the crypts were very much more numerous than the ducts of the glands, and as those crypts into which tubular glands opened were deeper and more funnel-shaped than those into which glands did not open, I was led to divide the crypts into two groups, non-glandular cup-shaped crypts, and glandular funnel-shaped crypts. The relation of the glands

Fig. 6.



Diagrammatic section through the placenta of *Orca gladiator*. *a*. cup-shaped crypt. *b*. funnel-shaped crypt. *c*. tubular gland-stem with its epithelial lining. *d*. fusiform and *e*. spheroidal sub-epithelial connective-tissue corpuscles. *f. f*. epithelial lining of crypts. *g. g*. maternal capillaries in the walls of the crypts. *h. h*. chorionic villi occupying the crypts. *i. i*. epithelial covering of the villi. *k*. spheroidal and *l*. fusiform corpuscles of the villi. *m. m*. intra-villous fœtal capillaries continuous with *n. n*. extra-villous capillaries. The space represented between the fœtal epithelium *i. i*. and the maternal epithelium *f. f*. is to give distinctness to the diagram, for in the placenta itself the two epithelial surfaces are in close apposition.

[1] I am not prepared to say that on a surface so extensive as the mucous membrane of the gravid uterus in *Orca* there may not be here and there a spot free from crypts at which a tubular gland may open, but should this be so, it would have to be regarded as the exception and not the rule. For in a portion of mucosa about half an inch square I found several gland-openings at the bottom of a corresponding number of funnel-shaped crypts.

to the funnel-shaped crypts seemed to justify the inference that these pouch-like depressions in the mucosa were (as was stated, by Dr Sharpey, to be the case in the pits or "cells" on the surface of the uterine mucosa in the gravid bitch) the mouths of the glands somewhat enlarged and widened. But however this might be the case with the funnel-shaped crypts it obviously could not be so with the cup-shaped crypts, which were interglandular in position, and, as in the pig and mare, could only have been produced by changes in the interglandular part of the mucous membrane. I guarded myself however against too absolute an acceptance of the view that the funnel-shaped crypts were merely the widened mouths of the glands by stating (p. 501) that they, like the cup-shaped crypts, may be formed by a folding of the greatly hypertrophied mucous membrane: only in the one case the hypertrophy and folding take place between the glands, in the other at the mouth of the gland itself. The difference between the mode of opening of the glands in *Orca* on the one hand, and in the pig and mare on the other, seemed to be this: that in *Orca* the free surface of the mucosa was much more uniformly crypt-like than in the pig and mare, so that there were no intermediate surfaces destitute of crypts on which the glands could open, whilst in the pig and mare the crypts were collected into definite areas, with distinct smooth surfaces intermediate to them. This more compact arrangement of the crypts in *Orca* corresponds with the more crowded condition of the villi on the surface of the chorion. That the whole series of crypts however in the cetacean uterus, as in the pig and mare, are to be regarded as interglandular formations, is supported by the observations of Eschricht on the mucosa of the gravid porpoise. For he states (p. 35) that in this animal the glands open on the surface of the mucous membrane, not into the "cells" in which the villi are lodged, but into separate shallow areolæ; that in the porpoise, as in the pig, these *areolæ* are much less vascular than the surrounding crypts; and that for so great a multitude of gland-ramifications there are not more openings on the surface of the mucous coat than in the pig.

The walls of the crypts and the interglandular connective tissue in *Orca* contained numerous nucleated corpuscles. In

the interglandular tissue they were mostly fusiform, but in the walls of the crypts a distinct layer of globular lymphoid-looking corpuscles was seen close to the free surface, which was not unfrequently elevated, in a sinuous outline, immediately superficial to these corpuscles, which may, from their position, be called the sub-epithelial corpuscles of the crypts. It is not improbable that these corpuscles may have migrated through the walls of the adjacent capillaries. The walls of the crypts were very vascular and contained a compact capillary network. Owing to the closer arrangement of the crypts, the surface of the mucosa generally presented a more uniform vascularity than in either the pig or mare. In all these animals indeed the great vascularity of the crypts was one of the most striking features in the structure. The capillaries in the walls of all the crypts belonging to the same group formed a continuous network, and in the *Orca*, owing to the more uniform crypt-formation, the capillaries of one group freely anastomosed with those of adjacent groups. The capillaries in the crypt-walls in each animal formed a series of anastomosing festoons, and usually a distinct capillary ring surrounded the mouth of each crypt. Moreover there was a great difference between the vascularity of the crypts and that of the deep layer of the mucosa in which the glands were situated, for the vascularity of the latter was not more than may be seen in connection with the tubular glands of the intestine. The crypts in *Orca* were lined by a well-defined layer of epithelium-cells, which closely followed the various irregularities of the mucous surface. The free ends of the cells were polygonal, often hexagons, or pentagons, though sometimes elongated into a pyriform shape. In my original memoir on the placentation in *Orca*, I stated that they had the appearance of a pavement-epithelium, though they were not larger than the broad free ends of the cylindrical epithelium lining the glands. I have since re-examined this layer of cells, and have now come to the conclusion that they cannot be associated with either the pavement-epithelium (*i.e.* if we employ the term as equivalent to squamous), or with the cylindrical epithelium. The cells are neither sufficiently elongated for the one, nor flattened for the other, but have an intermediate or transitional form.

The villi of the chorion fitted into the crypts, but were easily extracted from them. Only those villi which occupied the funnel-shaped crypts were brought into immediate contact with the secretion of the tubular glands, but in all the crypts the villi were in contact with the epithelial lining.

In *Manis*, as was pointed out by Dr Sharpey[1], the chorion was studded with villous ridges, but a bare band free from villi ran longitudinally along the concavity of the chorion, and there was a corresponding bald space on the surface of the uterine mucous membrane. The ridges of the chorion started from the margins of the bald stripe and ran round the ovum. The mucous membrane of the uterus possessed a finely reticulated appearance on the surface, and was punctated with the orifices of numerous shallow crypts in which the villi had been lodged. Branched cylindriform glands were very abundant in the deeper layer of the mucosa, but their mode of opening on the surface could not be satisfactorily ascertained, owing to the condition of the specimen.

The *Camelidæ*, unlike the ordinary Ruminant mammals, possess, as has for many years been recognised, a diffused placenta. I have recently, through the courtesy of Prof. Flower, had the opportunity of examining a considerable part of the chorion of a Dromedary, preserved in the Museum of the Royal College of Surgeons, London. The free surface of the chorion was thickly studded with short villi, but at one spot a bare patch about $1\frac{1}{2}$ inch long was seen; the relation of which to the wall of the uterus could not be ascertained. The villi were not arranged in tufts but arose singly from the chorion, having a somewhat constricted base, and expanding at the free end in a club-shaped manner. The villi varied in length from about the $\frac{1}{20}$ th to $\frac{1}{12}$ th inch. The larger proportion were unbranched, but some of the longer villi were divided into two or three short offshoots at the free end. The vessels of the chorion had been injected with size and vermilion, and a beautiful intra-villous network of capillaries was displayed. An extra-villous plexus of capillaries, not unlike that which I have described in

[1] Quoted in Huxley's *Elements of Comparative Anatomy*, p. 112, 1864; and with additional details in my Memoir on the Placentation of the Sloths in *Trans. Roy. Soc. Edinb.* 1873.

the mare and in *Orca*, was also seen. Although the gravid uterus itself was not in the museum for examination, yet there can be no doubt that its free surface must have been thickly studded with crypts for the reception of the villi.

In the *Tragulidæ* also, as has been described and figured by M. A. Milne-Edwards in *Tragulus Stanleyanus*[1], the villi are not collected into cotyledons, but are uniformly diffused over the surface of the chorion.

In the Tapir, as was shown by Sir Everard Home[2], the chorion is villous as in the mare. In *Tapirus Malayanus*, I am told by my friend Dr John Anderson, there is "a long bare area as in *Manis*, *Platanista* and *Orcella*, but proportionally of much greater size. The uterus also has the general characters of that organ in the gravid *Platanista*[3]." In the Hippopotamus M. H. Milne-Edwards has described[4] large villi disseminated over the whole surface of the chorion, except at the poles, where the membrane is smooth. Mr A. H. Garrod has also seen[5] the uniformly villous covering of the chorion in the placenta of this animal.

THE POLYCOTYLEDONARY PLACENTA.—This form of Placenta is characteristic of animals belonging to the order *Ruminantia*. It consists of a number of thick tuft-like masses of villi—the fœtal cotyledons, which are lodged in crypts situated in an equal number of thick, spongy elevations of the uterine mucous membrane—the maternal cotyledons. The fœtal cotyledons are separated from each other by considerable areas of smooth chorion, and the maternal cotyledons have equally large areas of smooth mucous membrane between them. Each cotyledon is complete when the fœtal are lodged within the maternal cotyledons, and each when complete forms a miniature placenta.

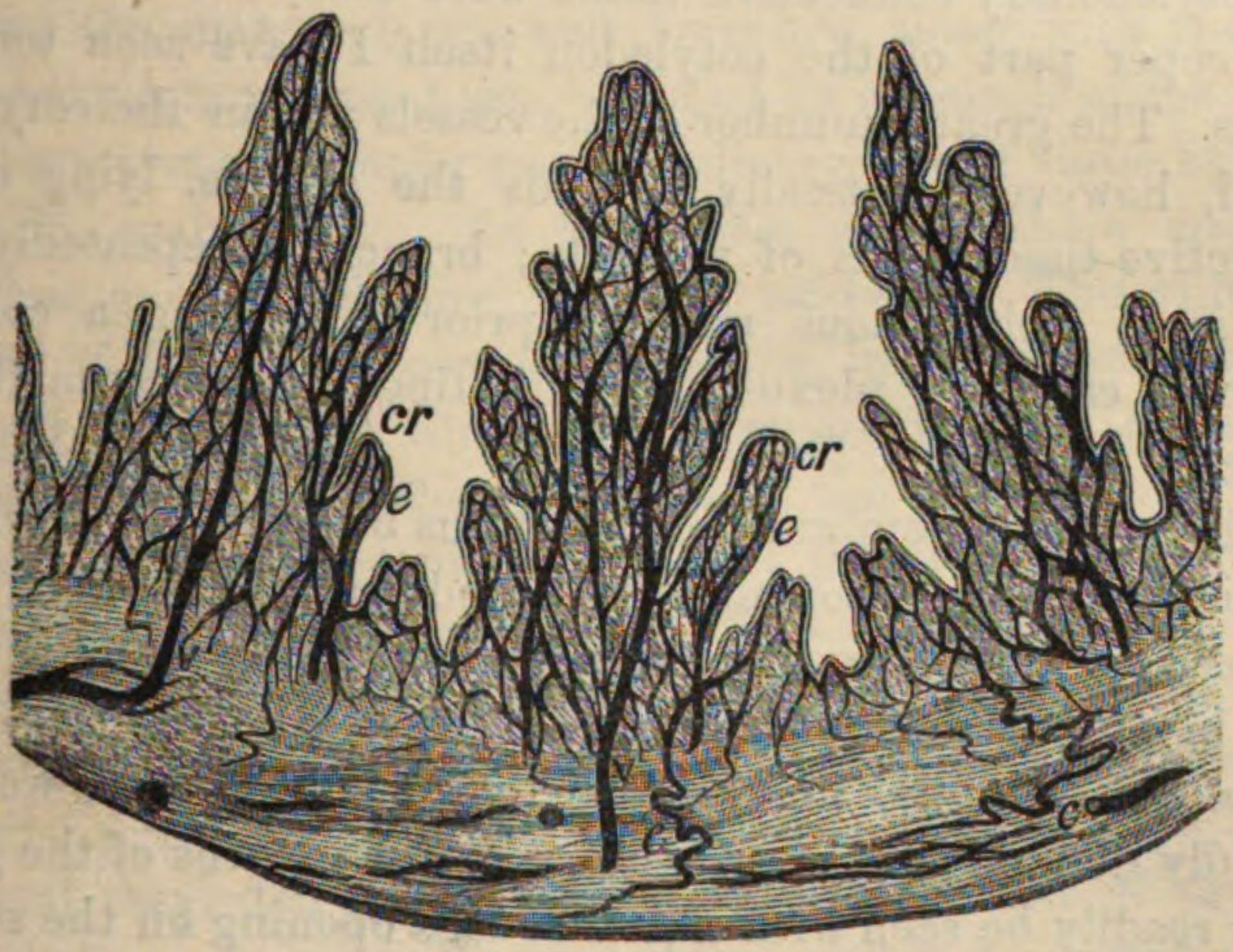
The first indication of the formation of a maternal cotyledon,

[1] *Ann. des Sciences Naturelles*, p. 101, Vol. II. 1864.
[2] *Lectures on Comp. Anatomy*, v. p. 328, and Plate 27.
[3] The characters of the gravid uterus in the rare Cetacean genera, *Platanista* and *Orcella*, have been specially studied by Dr Anderson, and will be described by him in a memoir to be shortly published.
[4] *Leçons sur la Physiologie*, IX. p. 562, 1870.
[5] *Proc. Zool. Soc.* Nov. 19, 1872.

as has been pointed out by Ercolani[1], is an elevation of the mucosa, which presents an irregular undulating surface. As the development proceeds this irregularity increases, until well-defined depressions or crypts are formed. The walls of the crypts continue to grow in length, and the crypts are not only deepened, but smaller compartments branch off from them. In the course of time they assume the appearance of deep pits, subdivided into numerous crypt-like compartments, into which the villi of the chorion closely fit. The shape of the fully formed cotyledons and the disposition of the pits vary in different Ruminants. I shall especially describe what I have seen in the Sheep and Cow.

In the Sheep the maternal cotyledons projected as cup-shaped mounds from the uterine wall. They were covered on the outer convex surface by the uterine mucosa, which was prolonged as far as the free inverted edge of the cup. The inner surface of the cotyledon was composed of a soft, spongy material, containing numerous pits, which extended almost

Fig. 7.



Semi-diagrammatic vertical section through a portion of a maternal cotyledon of a Sheep. *cr. cr.* pit-like crypts, with *e. e.* the epithelial lining. *v. v.* the veins, and *c. c.* the curling arteries of the sub-epithelial connective tissue.

[1] *Mem. dell' Accad. delle Scienze di Bologna*, 1870, Plate I. and 1873, Plate II.

vertically, and divided as they passed deeper into its substance into smaller crypt-like compartments, which radiated towards the outer wall of the cotyledon, without diverging much from each other. The pits were lined by well-marked cells, most of which were irregular in shape, polygonal, ovoid, or even somewhat caudate, and of considerable size, though some appeared like modified columnar cells. They consisted of granular protoplasm, in which one, two, or sometimes three, well-defined ovoid or elliptical nuclei were imbedded, but without a cell-wall. Not unfrequently the outline of the individual cells was very indistinct, and they seemed as if composed of a layer of protoplasm studded with nuclei.

The cells rested on a highly vascular sub-epithelial connective tissue, which formed the proper wall of the pits. The mucous membrane investing the cotyledon was continuous at the mouth of the cup with the walls of the pits in the spongy tissue, so that the cells lining the pits were in the same morphological plane as the epithelium covering the mucosa. The cotyledons were highly vascular. Some of the arteries in the sub-cotyledonary connective tissue were corkscrew-like; and in the deeper part of the cotyledon itself I have seen tortuous vessels. The greater number of the vessels within the cotyledon passed, however, vertically towards the surface, lying in the connective-tissue walls of the pits; branching repeatedly, as a rule, in a dichotomous manner, prior to forming a compact maternal capillary plexus,—not dilating into maternal blood-sinuses.

The mucous membrane of the uterus between the cotyledons contained numerous tortuous, branched, tubular glands. Some of these extended almost vertically to the surface, and could be seen in almost their entire length in vertical sections—others ran more obliquely, and, owing to their tortuosity, were repeatedly divided in vertical sections. The mouths of the glands could readily be seen with a pocket-lens opening on the surface, the orifice being partially surrounded by a minute elevation of the mucosa. In the mucosa around the base of the cotyledons a ring-like series of gland-openings was seen. In the mucosa covering the cotyledons, glands were also present, but their orifices were much stretched, as if by the pressure due to the

great growth of the subjacent spongy tissue of the cotyledon. The sub-epithelial connective tissue, in which the glands lay, was not by any means so vascular as that which formed the walls of the pits within the cotyledons. In some sections through the cotyledons and adjacent mucosa no glands were to be seen in the connective tissue intervening between the cotyledon and muscular wall, but they were collected in considerable numbers around the cotyledon, as if pushed outwards by its rapid growth. In other sections, however, tubular glands were seen in the sub-cotyledonary connective tissue; but they seemed to be the deep ends of branching glands, the stems of which had inclined obliquely, so as to open on the surface of the mucous membrane covering the cotyledon. None of these subjacent glands, or those situated on the surface of the cotyledon, were seen to open into, or in any way to communicate with, the pits within the cotyledon itself.

The fœtal cotyledons consisted of numerous villi, which collectively formed a ball-like mass, occupying the concavity of the maternal cotyledon. Each villus consisted of a main stem, which gave off a tuft or cluster of spatulate branches. The villi entered the maternal pits and branched along with them, so that every compartment was occupied by a branch of the villus; but there was necessarily no great divergence of these branches from the main stem. At their deeper end these spatulate branches gave off slender terminal offshoots. The villi were formed of gelatinous connective tissue, in which very distinct fusiform and stellate corpuscles were arranged in an anastomosing network. At the periphery of the villus was a layer of flattened cells, with small but distinct nuclei arranged so as to form an epithelial-like investment. The umbilical vessels ramified within the villi and formed networks of capillaries. The villi were in close contact with the epithelial cells lining the maternal pits. Owing to the inversion of the free edge of the maternal cotyledon and the radiated arrangement of the pits, with their contained villi, it was impossible to disengage the maternal and fœtal cotyledons from each other without drawing away with the fœtal villi portions of the maternal cotyledon. I invariably found that, in drawing the fœtal villi out of their compartments, flakes of epithelial cells accompanied them, which

showed how readily this element of the maternal issue is shed. During parturition, however, when the parts are relaxed, the disengagement of the two structures can necessarily be more easily accomplished.

In the Cow the maternal cotyledons differed in form from those in the sheep. They were fungiform or umbrella-shaped, and were connected to the uterine wall by a broad neck, around which the uterine mucosa was prolonged as far as the border of the umbrella. The whole convex surface of the cotyledon was riddled with pits, which passed vertically into its spongy substance, and divided into smaller compartments in the deeper part of the cotyledon. Projecting from the wall of each pit were delicate bands, visible to the naked eye, arranged as a rule in a vertical direction, and in the intervals between these bands the wall was perforated by numerous orifices, easily seen with a pocket-lens, which were the mouths of depressions or crypts in the wall of the pit, some lying almost at right angles, others obliquely to the wall of the pit itself. The pits, with their numerous crypts, were lined by cells, similar in character to those of the sheep. But I should state that a larger proportion of these cells had preserved the columnar form of the epithelium of the non-gravid uterine mucosa. They rested on a highly vascular connective tissue, in which the maternal capillaries formed a compact network.

The surface of the uterine mucosa between the cotyledons presented the mouths of the tubular, branched, utricular glands, which extended more obliquely to the surface than in the sheep, so that in vertical sections through the membrane they were frequently cut through and divided; segments of each gland were, as a rule seen, though sometimes the stem of a gland mounted to the surface to open by an obliquely-directed orifice. Glands were also present in the connective tissue forming the neck of the cotyledon, but none were seen to communicate with the pits.

The fœtal cotyledons were situated on the umbrella-shaped maternal cotyledons, and their numerous villi occupied the pits. The stems of the villi were comparatively large, and studded with multitudes of minute tufts, which, arising obliquely or almost at right angles to the main stem, entered and occupied

the crypts. The minute villi forming these tufts were so slender and filiform that each terminal offshot contained only a single capillary loop. The villi were in contact with the epithelium-cells, and in drawing them out of the pits, more especially in drawing the tufts out of the crypts, multitudes of cells of the lining epithelium came away with them. From the differences in shape of the maternal cotyledon in the cow and in the sheep, there is not the same difficulty in unlocking the fœtal from the maternal placenta in the former animal as in the latter.

In the Red-deer the general form of the cotyledons is not unlike what I have described in the Cow. The form and to some extent the structure of the cotyledons in the Roe-deer have been described by Bischoff[1]. Prof. Owen has given some beautiful figures of the fœtal cotyledons of the Giraffe[2], and has pointed out that some of large size were arranged in longitudinal rows, whilst numerous smaller ones, of irregular form and unequal dimensions, projected from the outer surface of the chorion in the inter-space of the normal larger cotyledons. I have examined microscopically the villi of this specimen as preserved in the Museum of the Royal College of Surgeons, London, and have found them to possess some variations in form. Some were filiform and almost cylindrical, others broader and more flattened. Some were unbranched except at the free end, where they gave origin to two or three short bud-like offshoots: others were much more deeply cleft, but none could be said to have an arborescent form. The cotyledons were very vascular, and each villus contained a compact capillary network. Although the uterine mucosa of the gravid Giraffe has not apparently been examined, there can be no doubt that maternal cotyledons containing pits for the reception of the fœtal villi must exist, and Owen has shown that, even in the non-gravid state, elevations are to be seen in the uterine wall, which correspond in position to the future cotyledons.

It is necessary that we should now consider whether the pits and crypts in the maternal cotyledons of the ruminant placenta, in which the villi of the chorion are lodged, are merely the greatly enlarged mouths of the utricular glands of the

[1] *Entwicklungsgeschichte des Rehes*, Giessen, 1854.
[2] *Trans. Zool. Soc.* Vol. III.

mucosa, or are structures specially formed during pregnancy, by great hypertrophy and folding of the inter-glandular part of the mucous membrane, as in the diffused forms of placenta. Prof. Spiegelberg[1] was of opinion, from some observations which he had made, that they were only remarkable dilatations of the utricular glands, and Bischoff was at one time disposed to regard them as the largely developed glands of the uterus. Subsequently however Bischoff figured in the cotyledons of the Roe-deer[2], the utricular glands ascending to open on the surface of the uterus, not in the cotyledons, but around its circumference. Eschricht however had previously stated that in the cow the glands open, not into the cotyledons, but on the surface of the uterus between them. Ercolani also has figured and described[3] both in the sheep and cow the glands as situated around the cotyledons, and not communicating with the cavities within them. In the description which I have given of the cotyledons in the sheep and cow, I have stated that I was unable to detect any communications between the glands and crypts: the glands indeed appeared as if they had been pressed to the periphery of the cotyledons by the great development of its spongy substance. Hence it would appear that in the polycotyledonary, as in the diffused placenta, the crypts in which the fœtal villi are lodged are not produced by an enlargement and dilatation of the tubular glands of the mucosa; but are new structures formed, during pregnancy, by a great hypertrophy and folding of the interglandular part of the mucous membrane.

THE ZONARY PLACENTA.—The Zonary or Annular placenta is found in its most characteristic form in the *Carnivora* and *Pinnepedia*, though it is present also in *Hyrax* and in the Elephant.

The gravid uterus of the dog, cat, and other pluriparous *Carnivora* possesses a moniliform appearance. Each dilatation is a compartment of the uterus containing an embryo, with its membranes, and between adjacent compartments the uterine

[1] *Henle and Pfeuffer's Zeitschrift*, XXI. quoted by Ercolani, p. 17, of the French translation of his Memoir.

[2] *Entwicklungsgeschichte des Rehes*, Plate VIII. 1854.

[3] *Memoir of* 1873, Plate 2.

cavity forms a narrow tube. If one of these compartments be opened, in a well-advanced stage of development of the embryo, the chorion will be seen to be smooth and bare of villi, except in about its middle third, where the villi are arranged as a zonular band around the transverse circumference of the ovum. The uterine mucosa possesses a similar zone closely blended with the zonular band of the chorion. The mucous membrane on each side of the zone is smooth and vascular: it lies in apposition with the smooth part of the chorion, but has no attachment to it. Where the zonary and smooth parts of the mucosa are continuous with each other a narrow strip of mucous membrane is reflected on the margin of the zonular band of the chorion, and forms a rudimentary decidua reflexa. In the true carnivora the decidua reflexa is so very narrow that it has often been overlooked; but in the grey seal, where the placenta is large, the reflexa is from $\frac{3}{4}$ to $1\frac{1}{4}$ inch broad. As the zonary placenta is much more complex in structure than either the diffused or polycotyledonary forms, it is necessary, in order to understand the arrangements, that it should be examined in different stages of development. I shall first describe what I have seen in the domestic cat.

In the earliest impregnated Cat's uterus, which I have examined, the compartments were ovoid, and the long diameter of each, measured along the arc, did not exceed $\frac{8}{10}$th inch. When a compartment was opened the chorion readily separated from the mucous lining. At each pole of the compartment an area of mucosa $\frac{1}{10}$th inch in its long diameter was smooth; but the rest of the membrane was hypertrophied, spongy, swollen, and elevated above the smooth polar portions, and formed the placental area. The placental area possessed on its surface an extremely delicate reticulation, many of the strands of which had a sinuous direction. It was thickly studded with minute orifices barely visible to the naked eye, but easily seen with a pocket-lens. These orifices were the mouths of the pits or crypts in which the villi of the chorion had been lodged. A few of these openings were two or three times larger than the rest. The appearance which I saw in the cat is evidently similar to that figured by Dr Sharpey in the bitch (Fig. 211)[1], and

[1] Baly's Translation of *Müller's Physiology*, note p. 1576.

by Bischoff in the same animal (Fig. 48, A)[1], though, as will be seen further on, I interpret its mode of production in a different manner from those anatomists. The crypts passed vertically into the spongy substance, and when vertical sections were made through it, they were seen to be separated from each other by trabeculæ; the chief beams of which lay vertically, and when they reached the free surface formed the strands of the reticulum already described. The vertical trabeculæ were connected together by others directed obliquely or in a sinuous manner, and these lateral connections were especially seen about midway in their length. Hence not only on the surface, but when horizontal sections were made through the placental area, a reticulated arrangement was seen, and the crypts constituted the interstices of the reticulum. As these trabeculæ were formed of the thickened mucous membrane of the placental area, they were necessarily composed of the somewhat modified tissues of that membrane. On the surface was a definite layer of epithelium, the cells of which were short columns, with distinct, circular or ovoid, brightly-refracting nuclei. These cells rested on a delicate sub-epithelial connective tissue in which the maternal capillaries ramified.

The trabeculæ and the sub-mucous connective tissue were carefully examined with the object of ascertaining their relations to the tubular glands. In vertical sections the glands were distinctly seen, transversely or obliquely divided, lying in a definite layer of connective tissue situated deeper than the crypts. Sometimes the divided glands were separated by comparatively broad bands of connective tissue from the crypts and trabecular structure, but in other places they were immediately subjacent. They were lined by a well-defined columnar epithelial layer. I looked for the stems of the glands to see if I could ascertain whether they opened into the crypts or passed along the trabeculæ to open on the free surface of the mucosa, but did not succeed in tracing them to their orifices.

As it was important however to ascertain if the crypts equalled in number in a given area the glands of the mucosa in the same area, or if the crypts much exceeded in number the glands, I submitted different parts of the mucosa of the

[1] *Entwicklungsgeschichte des Hunde-Eies*, 1845.

gravid uterus of this cat to microscopic examination, and compared the appearances seen with those presented by the mucosa of the non-impregnated uterus. In the non-gravid cat the stems of the glands were almost perpendicular to the free surface of the mucosa. They were so tortuous at their deeper ends as to be repeatedly cut across in a vertical section through the membrane. The interglandular connective tissue, containing numerous corpuscles, formed well-marked bands between the glands. Vertical sections made through the mucosa lining the constrictions between the compartments of the uterus of this gravid cat showed the tubular glands to be on the average $\frac{1}{4}$th wider than in the non-gravid condition, the interglandular connective tissue was much smaller in quantity, so that the glands were more closely crowded together; but in the placental area of the mucosa of the same cat the interglandular tissue was greatly increased in quantity, so that the glands were much further apart. The glands themselves were, as in the non-placental area, dilated, but the number of glands seen in the sections did not nearly equal the number of crypts.

In a cat's ovum, which had reached a somewhat more advanced stage of development, where the long diameter of the uterine compartment, measured along the arc, was $1\frac{1}{2}$ inch, I found that the villi of the chorion readily disengaged from the uterine crypts. By far the larger part of the chorion was still villous, not more than $\frac{2}{10}$ths inch at each pole being smooth. The line of demarcation between the placental and non-placental polar areas of the mucosa was very distinct. The placental area, or the hypertrophied and spongy mucosa, possessed a reticulated appearance, the principal strands of which were sinuous, and gave off numerous collateral branching offshoots, which joined adjacent branches to form the walls of the numerous pits or crypts which opened on the surface. The strands and branches were larger and the pits and crypts were more dilated than in the younger ovum already described, and on looking down the larger pits, their subdivision into smaller crypts could be seen. The crypts were lined by an epithelium, numbers of the cells of which possessed a columnar form, though others were swollen and otherwise altered in shape, so as to be irregularly polygonal. The cell-protoplasm was

granular and the nucleus was distinct. The sub-epithelial connective tissue was vascular. When vertical sections were made through the placental area the more dilated size of the crypts and pits than in the younger specimen was distinctly recognised, being thus in conformity with the larger size of the chorionic villi. Between the deeper closed end of the crypts and the muscular coat was a definite layer in which portions of gland-tubes, lined by an epithelium, some of which were transversely, others obliquely divided, could be seen. The glands were dilated as in the younger specimen, and not so numerous as the crypts, neither could I obtain satisfactory evidence of the communication of the mouths of the glands with the crypts. I am led therefore to the conclusion that the crypts formed in the early period of gestation in the placental area of the cat are not due to a mere widening of the mouths of the tubular glands; but are produced, as in the pig and mare, by a great increase in the amount of the interglandular part of the mucosa, which becomes folded so as to form the crypt-like arrangement which I have just described. In this respect, therefore, my observations agree with those of Ercolani on the same animal[1]. The interpretation, therefore, which Ercolani and I have put on the appearances seen in the placental area of the cat in the early stage of gestation differs from that given by Dr Sharpey on the appearance seen in the uterine mucosa of the bitch at a similar stage. As is so well known, Dr Sharpey held that the pits and "cells" (crypts) seen on the inner surface of the uterus, which receive the villi of the chorion, are the mouths of the utricular glands enlarged and widened. It is possible that in the cat, as in the *Orca*, the utricular glands may open into some of the crypts, so as to seem to justify the inference that they were formed by a widening of the mouths of the pre-existing glands. But this interpretation obviously cannot be given of the formation of those crypts which are interglandular in position. Hence it seems to be more in conformity with the structural arrangements of the organ to conclude, that the crypts which arise in the uterine mucosa during pregnancy are new formations,

[1] *Mem. dell' Accad. delle Scienze di Bologna*, 1870, Plates 2, 3, 4.

produced by a great hypertrophy and folding of the surface of the mucous membrane.

When the ovum of a cat, which had completed about one-half the period of gestation was examined, a most important advance in placental formation was observed. The zonary villous band on the chorion was restricted to its middle third, and an equally large smooth surface was found at each pole. The zone on the chorion was now so completely interlocked with the corresponding zone in the uterine mucosa, that the two surfaces could not be detached from each other. The placenta could only be separated by rupturing the slender marginal band of decidua reflexa, and tearing through, or altogether pulling off, the placental area of the mucosa, which area was intermediate between the placenta proper and the muscular coat of the uterus, and formed a well-defined decidua serotina.

The villi of the chorion had the form of broad sinuous leaflets, which became attenuated at their uterine ends and gave off bud-like offsets from the free border. When vertical sections were made through the placenta the villi were seen to pass vertically through the organ up to its uterine aspect. The trabeculæ of maternal tissue, which formed the walls of the pits or crypts in which the villi were lodged, passed between the villi up to the chorion, and closely followed the sinuosities of the villi, so as to form an intimate investment for them, and in horizontal sections through the organ they were seen to be arranged as a series of laminæ, winding in a sinuous manner between the leaf-like villi. Between the placenta proper and the muscular coat was a well-defined layer of serotina, equal in thickness to the muscular coat itself. It was traversed by the numerous blood-vessels which passed into and out of the placenta, and which formed not unfrequent anastomoses with each other. The decidua serotina consisted not only of the vascular connective tissue, but of the epithelial cells of this part of the mucosa, which were similar in character to those described in the preceding stage of development. In thin sections, tubes, lined by an epithelium, were seen cut transversely or obliquely; they were about equal in diameter to the gland-tubes seen in the serotina in a less advanced stage of gestation, and were without doubt the dilated glands of this

portion of the mucosa. It may here be stated, that in the non-placental area of the same uterus the tubular glands were distinctly seen separated from each other by comparatively wide intervals of interglandular tissue. The chorionic villi dipped into depressions in the decidua serotina, and were in contact with its epithelium. The trabeculæ and laminæ situated in the substance of the placenta were also continuous with the serotina and were invested by an epithelial layer, the cells of which were modified columns, like the cells of the decidua serotina. The blood-vessels of the serotina entered the laminæ and trabeculæ and ramified in them throughout the maternal part of the placenta. In the placenta of one of the embryos, where the maternal vessels were injected, they formed a network of capillaries of ordinary magnitude. In the other placentæ from the same uterus the maternal capillaries when injected with red gelatine were dilated to two or three times the size of the capillaries in the fœtal villi, and ascended almost vertically in the trabeculæ. Not unfrequently near the chorionic surface they dilated into sinus-like enlargements, which were crowded with blood-corpuscles. It is possible that these dilatations may, to some extent, have been due to the force employed in filling the maternal vessels with injection, but this will not, I think, account for the whole extent of the dilatation[1]. The vessels of the capillary network of the fœtal villi were injected with a blue colour and showed no dilatations; and the contrast between the two systems of vessels within the organ was well seen both in horizontal and vertical sections.

The placenta of a cat, shed in the ordinary course of parturition, was covered on its uterine surface by a layer of soft yellowish-white tissue, which was smooth and uniform in character, and was without any flocculent, ragged processes projecting from it. This layer was the deciduous serotina, and from it laminæ and trabeculæ passed into the substance of the placenta, which had a similar sinuous arrangement and relation to the fœtal villi as in the placenta at half time. Examined microscopically, the vascular connective tissue of the serotina

[1] The dilatation of the maternal vessels in the feline placenta has also been referred to by Eschricht and other observers.

with its epithelial investment was recognised, but as it was not possible in a detached placenta to inject the maternal blood-vessels their disposition could not be made out. I examined thin sections through the serotina for the presence of utricular glands. I saw indistinct appearances of tubes transversely or obliquely divided, which might be interpreted as tubular glands, but the aggregation of cells within and around them was so great that it was difficult to speak positively on this point. The chorionic system of fœtal blood-vessels was injected, and the leaf-like villi, with their remarkable compact capillary plexus, were readily seen. On examining with a pocket-lens the uterine surface of the serotina, many minute, rounded, scattered holes were seen in it, through each of which a terminal bud of a leaf-like villus projected so as to reach the uterine surface of the placenta. These buds were often clavate in form, and contained a capillary plexus, continuous with that of the body of the villus. It is clear, therefore, that when the placenta of the cat is shed at the time of parturition, a continuous layer of serotina, interrupted only by these minute orifices, is shed along with it.

The presence of a layer investing the uterine surface of the cat's placenta, analogous to the caducous layer of the human placenta, was distinctly recognised by Eschricht; who also described the thin, perpendicular, flexuose laminæ of maternal structure passing through the entire thickness of the organ and investing the fœtal villi as if with sheaths[1]. Though Eschricht was at first inclined to the view that the layer investing the uterine surface of the placenta was nothing else than the mucous tissue of the uterus, further consideration led him to state that it altogether differed from that tunic. But he also came to the conclusion that the mucous tunic was left entire in the placental zone, exhibiting only torn and broken-off vessels.

There can be no doubt however, from its position and structure, that this layer is the mucosa of that part of the uterus which corresponds to the placental zone, for it and the intra-placental laminæ and trabeculæ are merely a more advanced condition of the crypt-like modification of the mucosa, which I have described in the earlier stages of placental formation in

[1] *De Organis*, &c., pp. 14, 18.

this animal. Is the whole thickness of the mucosa corresponding to the placental zone shed along with the placenta? or is this layer merely the superficial part of the membrane? are questions which may now be asked. These of course can only be satisfactorily answered after the uterus of a cat killed immediately after parturition has been examined. But I may state that, in the uterus of the cat in the mid-period of gestation, I found, on peeling off the placenta, that the serotina did not split into two layers, the one, a deciduous serotina attached to the placenta, the other, a non-deciduous serotina remaining connected to the uterine wall, but that the whole thickness of the serotina came away with the placenta, leaving the muscular coat exposed; moreover, the uterine surface of the placenta presented a smooth surface precisely similar to that exhibited by the organ when shed at the full time. A similar separation also took place more than once in the process of injecting the vessels of the gravid uterus.

Though the placenta in the Bitch, as in the cat, possesses the zonary form, yet its minute structure in the two animals presents sufficient differences to enable the anatomist readily to distinguish the one from the other. If the description and figures by Sharpey and Bischoff of the early stages of formation in the bitch be compared with the corresponding stages in the cat, a close resemblance is seen; but in the more advanced stages characteristic differences can be recognised.

In the Bitch, both at half and full time, when the placenta was stripped off the uterine zone, a distinct mucous membrane was left on the uterus, which was continuous at the margins of the zone with the narrow band of decidua reflexa and through it, with the mucosa covering the non-placental area. This zonary mucous membrane was subdivided into numerous, irregularly polygonal pits or trenches, bounded by folds of the mucous membrane. These folds had a ragged, flocculent appearance. The membrane was very vascular, and at the ragged edges of the fold numerous torn blood-vessels were seen. When examined microscopically the free surface not only of the pits and trenches, but of the folds, was seen to be covered by a layer of cells—the epithelium of the mucous membrane—which rested on the vascular sub-epithelial connective tissue. When this

epithelium was looked at from the surface, a pattern of polygonal cells was seen like the free ends of columnar epithelium; but the cells were bigger than one usually finds this form of epithelium to be, and had, more especially in the uterus at full time, a distinct yellow colour, as if the cells were undergoing fatty degeneration. When the cells were scraped off, so as to be seen in profile, their columnar form was easily recognised. As this mucous membrane was not detached from the uterus along with the placenta it is to be regarded as a non-deciduous serotina.

The uterine surface of the placenta also had a ragged appearance, for the numerous folds of the mucous membrane had entered the placenta, and, when it was stripped off, their torn ends were seen on its outer surface, but the flocculent appearance was still further increased by the free ends of the chorionic villi, which reached the surface. The prolongations of the mucous folds entered the placenta at a multitude of points in the interspaces between the villi, and as they ascended to the chorion they branched repeatedly, so as to give investments to the branches of the villi of the chorion. These intra-placental prolongations of the mucosa consisted of sub-epithelial connective tissue, in which the maternal vessels ramified, and of an epithelium composed partly of columnar cells, and partly of cells the regular columnar form of which had been modified into irregular polygons. These cells were larger and more distinct than the cells on the corresponding structures in the cat, and their protoplasm was so very granular as in many cases to obscure the nucleus. These prolongations of maternal tissue constituted a deciduous serotina. The shed placenta of the bitch, whilst possessing in its substance numerous prolongations of maternal tissue not unlike those previously described in the cat, yet differs from the latter animal, as has also been pointed out by Prof. Rolleston[1], in the absence of a continuous layer of deciduous serotina on its uterine aspect.

The chorionic villi in the bitch were arborescent and not leaf-like as in the cat. They terminated in short villous tufts. The umbilical arteries ended in a compact capillary plexus.

[1] *Trans. Zool. Soc.* v. 1863.

The villi were in close contact with the epithelial cells investing the intra-placental prolongations of the mucous membrane.

I may now relate some observations which I have made on the glands in the non-gravid uterine mucous membrane of the bitch. It is well known that two kinds of glands were described by Dr Sharpey[1] in the uterine mucous membrane of this animal, viz. short; simple, unbranched tubes, and compound tubes having a long duct dividing into convoluted branches, both kinds opening close together on the surface of the mucosa. These observations were supported by Weber and Bischoff, and generally accepted by anatomists and physiologists; but Prof. Ercolani of Bologna, in his first memoir on the Structure of the Placenta[2], stated his inability to distinguish more than one kind of gland, and concluded that only the long tubular glands were present. I have felt it necessary therefore carefully to examine the uterine mucous membrane of the unimpregnated bitch with reference to this question. On a surface view the mouths of the glands could be distinctly seen closely crowded together, as is so well represented in Dr Sharpey's figure (fig. 209), and in Bischoff's memoir (*Entwicklungsgeschichte des Hunde-Eies*, Plate XIV. Fig. 47). When horizontal sections were made through the membrane near its surface the glands were seen to be transversely divided, and so closely set together that the interval between any two adjacent glands was in some cases not equal to, in other cases about equal to, the transverse diameter of a gland-tube; further, all the gland-tubes in any given transverse section exhibited the same structural characters. When vertical sections through the membrane were examined, long compound tubular glands were readily seen passing into the deeper part of the mucosa, and between these, short and simple tubes were also recognised, so that, under low magnifying powers, at first sight these sections seemed to confirm the observations of Sharpey, Bischoff and Weber, which were made under magnifying powers of 10 and 12 diameters. When magnified more highly these apparently short simple glands were seen to vary considerably in length, some dipping for only a short distance

[1] Baly's Translation of *Müller's Physiology*, Note, p. 1576.
[2] *Mémoire sur les Glandes Utriculaires de l'Uterus*, p. 22, French Translation, Algiers, 1869.

from the surface of the mucosa, others for a greater distance, and exhibiting indeed every gradation in length up to the branched tubular glands themselves. But in the connective tissue, immediately below the short glands, portions of tubes were seen extending in line with the short tubes though apparently not continuous with them, but often with careful focussing a continuity could be traced, though obscured by overlying connective tissue. I am therefore of opinion that the utricular glands in the bitch, as in so many other mammals, lie in the mucosa, some almost vertically, others in various degrees of obliquity, so that, when vertical sections are made, some are cut short across, others longer, whilst others again may be seen in almost their entire length. I conclude therefore that all the glands belong to the type of compound tubular glands, that the apparent differences in length are simply due to the mode in which the glands are cut across in making the section, and that the physiological division proposed by Bischoff into simple mucous crypts and proper tubular glands cannot be supported.

From a dissection which I have made of the gravid uterus of a Fox at about the mid-period of gestation, I have satisfied myself that it corresponds in many respects with the bitch, though with specific differences. The uterine mucosa remained on the uterus when the placenta was stripped off, and possessed pits or trenches with intermediate ragged folds. The uterine face of the placenta was flocculent, owing to the prolongations of the folds into the substance of the placenta being torn across in the process of separation. These prolongations entered the placenta at a number of points, and passed with a sinuous course up to the chorion, and gave off many branches, which not unfrequently were arranged as an anastomosing reticulum, in the meshes of which the lateral offshoots of the villi were lodged. They were very vascular and their vessels were larger than ordinary capillaries. Compared with the capillaries of the fœtal villi they were from twice to four times as big, so that they may be regarded as indicating the early stage of a dilatation into maternal sinuses, such as is still more clearly seen in the sloth, and reaches its maximum development in the human placenta. Many of these vessels ran vertically through the placenta, so that when horizontal sections were made through

the organ, they were seen in transverse section. In many cases these transversely divided vessels were surrounded by a ring of cells—the epithelial investment of the process of maternal tissue in which the vessel lay—which showed that the process only contained a single dilated capillary. The epithelial cells investing the intra-placental prolongations of the decidua were remarkably large and distinct, and on the average about $\frac{1}{4}$th or even $\frac{1}{3}$rd as large as the corresponding cells in the bitch. The fox therefore, like the bitch, has no continuous layer of modified mucosa, such as is seen in the cat, on the uterine face of the separated placenta. The villi of the chorion had an arborescent arrangement, and gave off both lateral and terminal offshoots in which a network of capillaries ramified.

I have studied the zonary placenta of the *Pinnepedia* in the Grey Seal, *Halichœrus gryphus*, a specimen of which, in the sixth month of gestation, I examined, in 1872. In this animal, as in the dog and fox, when the placenta was peeled off the uterus, a well-defined layer of mucous membrane was left on the muscular coat, which layer presented on its placental aspect numerous irregular pits and trenches, in which the convoluted folds of the placenta had fitted. From this layer numerous broad laminæ of the mucosa were prolonged into the placenta, not however, as in the dog and fox, irregularly over its uterine surface, but by means of a definite series of fissures. The laminæ dipped into the substance of the placenta, as the pia mater dips between the convolutions of the cerebrum, and the fissures, which they entered, may from their size be called primary. Each convoluted fold of the placenta was split up into elongated plates by secondary fissures, into which processes of the mucosa, derived not only from the broad laminæ, but from the mucosa in contact with the uterine face of the convolutions, penetrated. Each plate was again subdivided into polygonal lobules by tertiary fissures, into which more delicate processes of the mucosa entered, which could be traced through the thickness of the placenta up to the chorion. In drawing the placenta away from the uterus the laminæ were drawn out of the primary fissures, but the more delicate processes, which entered the secondary and tertiary fissures, were torn through, and remained in the substance of the placenta, entangled

between the placental lobules and amidst the fœtal villi. The placenta of the seal when removed from the uterus had not on its uterine face a continuous layer of mucosa, as is seen in the cat.

The layer of membrane left on the surface of the uterine zone had all the structural characters of a mucous membrane. The free surface was covered by a layer of short columnar epithelial cells; the sub-epithelial connective tissue was very vascular and contained scattered, branched, tubular glands. The vascularity of the membrane was considerably greater than that of the mucosa of the non-placental area. The broad laminæ of this membrane had a similar structure. The more delicate secondary and tertiary processes consisted of a vascular connective tissue covered by a columnar epithelium, but without glands.

The villi of the chorion were long and very arborescent, and formed the polygonal lobules already described. The larger branches of a villus reached the periphery of a lobule, and instead of terminating in a cluster of bud-like off-shoots, the ends of many of the branches derived from the same parent stem were joined together so as to form a continuous layer of grey membrane, situated not only on the uterine surface of the lobule, but reaching for some distance down its sides. From the sides of the stem of the villus, as well as from its branches, multitudes of villous tufts arose. The prolongations of the maternal mucosa which passed into the lobules so as to come in contact with the villous tufts, were not derived directly from the non-deciduous layer of mucosa investing the muscular coat, for the greyish membrane situated on the uterine face of the lobule prevented a direct entrance. The intralobular maternal tissue arose from the processes which entered the secondary and tertiary fissures, which gave off lateral branches into the lobules. Within the lobules these branches subdivided into a reticulated lattice-like arrangement of sinuous trabeculæ, and the meshes of this reticulum were occupied by the villous buds. The trabeculæ had the same structure as the processes of the mucosa from which they were derived. The seal therefore in the reticulated arrangement of those portions of its mucosa, which are in direct contact with the

terminal villi, presents a general correspondence with the fox, but the subdivision of the mucosa is more complete, and the cells of the epithelial investment are not so big as in the fox[1].

Although the zonary form of the placenta in *Hyrax capensis* was pointed out many years ago by Sir Everard Home[2], and although its structure has been examined by several anatomists, there is by no means an agreement on the exact relations of its fœtal and maternal portions. Prof. Huxley is convinced from his investigations[3] that the placenta in *Hyrax* has such an interblending of the fœtal and maternal portions that it is as truly deciduate as that of a Rodent. Prof. Owen states[4] that the villi are imbedded in a decidual substance, and the surface of attachment to the uterus is less limited than in the Elephant. On the other hand, M. H. Milne-Edwards describes[5] the placenta as only adhering very feebly to the walls of the uterus. Its villi, he says, are simple, very analogous to those of an ordinary pachyderm. In the midst of the zone there are vascular vegetations engaged in corresponding uterine cavities, but they adhere no more, than do the analogous prolongations in the ruminant, to the crypts in which they are included: they can be detached with the same facility without tearing through anything and without carrying away any portion of uterine tissue. There is nothing, he concludes, to indicate the presence of a caduca, and the allantois does not overstep the limits of the placental zone[6].

No observations have been recorded on the structure of the uterine mucosa in the gravid Elephant, but Prof. Owen has described and figured[7] the fœtal membranes. The chorion was encompassed at its middle by an annular placenta, 2 ft. 6 in. in circumference, varying from 3 to 5 in. in breadth, and from 1 to 2 in. in thickness:

[1] I have given a detailed description of the placenta of this Seal in the *Trans. Roy. Soc. Edinburgh*, 1875, and have figured not only its structure, but that of the cat and fox.

[2] *Lectures on Comparative Anatomy*, v. 325, Pl. 61.

[3] *Lectures on Comparative Anatomy*, 1864, p. 111.

[4] *Comparative Anatomy of Vertebrates*, III. 742.

[5] *Considérations sur la Classification des Mammifères*, Paris, 18 8.

[6] In the June number for 1875 of the *Annales des Sciences Naturelles*, M. George figures not only the placenta of Hyrax, but the gravid uterus. He says nothing however of its structure.

[7] *Phil. Trans.* 1857, p. 347.

"The placenta presents the same spongy texture and vascularity as does the annular placenta of the *Hyrax* and of the *Carnivora;* but the capillary filaments or villosities enclosing the fœtal vessels enter into its formation in a larger proportion, and are of a relatively coarser character. The greater part of the outer convex surface of the placenta is smooth: the rough surface, which had been torn from the maternal or uterine placenta, exposed the fœtal capillaries, and occupied chiefly a narrow tract near the middle line of the outer surface. A thin brown deciduous layer is continued from the borders of the placenta, for a distance varying from one to three inches, upon the outer surface of the chorion. In addition at each of the poles of the chorion was a villous and vascular subcircular patch, between two and three inches in diameter, the villi being short, $\frac{1}{6}$th of a line in diameter, or less."

This specimen is preserved in the Museum of the College of Surgeons, London, and through the courtesy of Prof. Flower I have been permitted to obtain a slice for microscopic examination. Notwithstanding the number of years the placenta had been in spirit, I succeeded in passing some injection into the vessels of the chorion and the larger trunks in the stems of the villi, so that I was able to follow the villi more precisely into the substance of the placenta than I should otherwise have been able to do. The placenta was very compact and was clearly composed both of a fœtal and a maternal portion closely interlaced with each other. Many of the villi were of large size and passed through the entire thickness of the organ, branching repeatedly in an arborescent manner. Others again were of smaller size, and did not pass more than one-third through the organ, but, like the longer villi, branched repeatedly. The tissue of the villi was delicately fibrillated, and in it ran the branches of the umbilical vessels.

Interlocked between the villi was a tissue, which contained a very distinct network of minute tubes, obviously capillary blood-vessels, and on the surface of this tissue a layer of cells was seen with some difficulty. I succeeded more than once in isolating a few of these cells, and found them to be rounded or ovoid, with definite nuclei and with granular protoplasm. I believe these cells to be the epithelial covering of the laminæ of maternal mucosa, forming the walls of the highly-developed crypts in which the villi were lodged, whilst the capillary network subjacent to these cells, belonged to the intra-placental

maternal vascular system. Several times I saw an appearance as if the intra-placental mucosa was split up into a reticulated arrangement of trabeculæ, similar to what I have described in the seal, but from the condition of the specimen it was difficult to speak positively on this point. There could be no doubt however that in this separated placenta of the elephant a large amount of uterine mucosa was inextricably locked in between the fœtal villi.

General Morphology of the Placenta.—In the study of the morphology of the placenta in any mammal the presence of two parts, a fœtal and a maternal, originally quite distinct and separable from each other, must be clearly kept in view.

The morphology of the fœtal part presents no difficulty. It consists simply of a vascular villous membrane covered by an epithelium. The sub-epithelial part of the membrane is composed of a delicate connective tissue, containing numerous corpuscles in which the terminal branches of the umbilical vessels, with their capillary network, are distributed. The vascular villi may be either simple or branched, and in some of the mammals, whose placentation has just been described, *e.g.* the seal, the branching may assume a highly arborescent arrangement.

The morphology of the maternal part of the placenta presents greater difficulty, not only because the uterine mucous membrane, out of which it is produced, is more complex in structure than the chorion, but because this membrane becomes greatly modified in the course of placental development, and not unfrequently becomes so interlocked between the fœtal villi as to be separated from them with great difficulty.

In all the forms of placenta, along with the growth of the villi from the surface of the chorion, depressions or crypts arise in the uterine mucosa for their reception, and the walls of these crypts are formed by foldings of the hypertrophied mucosa.

In the diffused placenta the changes in the uterine mucosa are less complicated than in the other forms. The villi of the chorion are short, and branch but slightly. The crypts in the uterine mucosa are consequently shallow, so that the relations of the fœtal and maternal parts can be easily seen. Two free

surfaces are in close apposition, the villi of the chorion fit into the crypts of the mucosa, but they can be drawn asunder without difficulty, so that the compound nature of the placenta can be at once demonstrated.

In the polycotyledonary placenta the villi are longer and more branched. The pits or crypts for their reception are consequently deeper and divided into smaller compartments, and the maternal mucosa in the site of the cotyledons is more hypertrophied, thicker, and more spongy. Two free surfaces are here also in apposition; but the length and branching of the villi, and the depth and subdivision of the crypts, render it somewhat more difficult to draw the two surfaces asunder than in the diffused placenta.

In the zonary placenta as seen in the *Carnivora*, *Pinnepedia* and *Elephas*, the villi are long and usually arborescent, though in the cat they are leaf-like and very sinuous. The foldings of the uterine mucosa, which have led to the production of the crypts, are more complicated, so much so indeed in the fox and seal, as to give rise to a remarkable subdivision of the membrane into a microscopic network. The two surfaces in apposition have become so interlocked that it is almost impossible to disengage them from each other. Hence in the process of parturition more or less of the uterine mucosa in the placental area is separated and shed in the substance of the placenta.

The morphological elements in the gravid mucosa of all mammals, are, as in the non-gravid membrane, epithelium, sub-epithelial connective tissue, blood- and lymph-vessels, glands and nerves. Of the arrangement of the lymph-vessels and nerves in the placenta we have no precise information. The epithelium, the sub-epithelial connective tissue, and the blood-vessels form the walls of the crypts in which the villi are lodged. The glands have no necessary relation to the crypts. In the pig, as has been shewn by Eschricht, myself, and Ercolani; in the mare, as has been pointed out by Ercolani and myself; and in the porpoise, as has been described by Eschricht, the mouths of the glands can be distinctly seen opening on the surface of the mucosa, in smooth areas intermediate to and quite distinct from the crypts. In *Orca gladiator*, though at first

sight the funnel-shaped crypts seemed to be the dilated mouths of glands, yet further consideration has satisfied me that neither they nor the cup-shaped crypts are derived from the glands. In the *Ruminantia,* Eschricht, Bischoff, Ercolani and I have been unable to see any communication between the glands and the pit-like crypts of the cotyledons. In the *Carnivora,* though, as was interpreted by Sharpey, Weber, and Bischoff, the crypts seen in the placental area in the early stage of gestation may seem to be merely the mouths of the glands enlarged and widened, yet a more minute analysis of the structure shows that, though some of the glands may, as in *Orca,* open into crypts, yet that the crypts are much more numerous than the glands, and are consequently not derived from them. Hence in all these, and I believe in other placental mammals, the crypts are not modified glands, but are interglandular in position. The crypts do not exist in the non-gravid uterus, but, as was first definitely shown by Prof. Ercolani, are formed during pregnancy by a folding on itself of the mucous membrane.

The crypts are lined by an epithelium, which is derived from the epithelial lining of the uterus: the increase in the number of epithelial cells, owing to the greater magnitude of the mucous surface, being effected by proliferation of the pre-existing epithelial cells. In many mammals the cells lining the crypts have the columnar form, like the epithelium of the non-gravid mucosa, and in the pig the cells are apparently ciliated: but in some mammals the columnar form is not preserved, and the cells are rounded, or polygonal, and with granulated protoplasm. These cells form the cells of the decidua serotina, and they are homologous with the rounded, or polygonal, colossal, granulated cells of the decidua serotina in the human placenta.

The connective tissue in the walls of the crypts is derived from the sub-epithelial connective tissue of the non-gravid mucosa, through a rapid increase in the number of its corpuscles, though it is possible that there may also be a migration of white blood-corpuscles into it. The blood-vessels in the walls are continuous with the vessels of the mucosa, and are greatly increased in numbers. In the diffused and polycotyle-

donary forms of the placenta they are arranged as a capillary network, but in the zonary placenta they exhibit a tendency to dilate into colossal capillaries, which are the first indications of a maternal intra-placental blood-vascular sinus system, such as attains much greater development in the sloth, and acquires its maximum size in the quadrumana, and the human female. The vascular connective tissue forming the walls of the crypts constitutes the vascular part of the decidua serotina, by which term is signified the maternal mucous membrane situated between the fœtal placenta and the muscular wall of the uterus; or, in other words, the maternal part of the placenta. In the diffused form of placenta the serotina consists of the whole of the mucous surface in which the crypts are met with. In the polycotyledonary it forms the maternal cotyledons. In the zonary placenta it consists of the annular band of mucosa, with the intra-placental laminæ and trabeculæ.

As is well known, the form of the placenta, the arrangement of the fœtal membranes, and the behaviour of the uterine mucosa at the time of parturition, have been taken by many zoologists as affording a basis of classification of the placental mammals. In 1828 von Baer[1] published a classification of animals based on their development. He divided the placental mammals into groups according to the size of the umbilical vesicle and allantois, and pointed out diversities in the form of the placenta in the different genera. In 1835 Prof. Weber communicated to a meeting of German Naturalists[2] a classification of the placental mammals based on the presence or absence of maternal parts in the separated placenta. Where the vascular folds or "cells" of the uterus are so closely attached to the vascular folds or villi of the chorion, that they fall away at the birth of the placenta they are, he says, "*hinfällig, organa caduca;*" whilst in mammals, where the uterine and fœtal parts are so loosely attached that the surface remains uninjured at birth, there are no "*zufällige organe.*" Eschricht in his essay published in 1837[3] employs a similar classification, and divides placental mammals into two families, in one of which

[1] *Ueber Entwickelungsgeschichte der Thiere*, p. 225, Königsberg.
[2] Froriep's *Notizen*, Oct. 1835, p. 90.
[3] *De Organis*, p. 30.

the uterine placenta is caducous, in the other non-caducous. M. H. Milne-Edwards published a system of classification in 1844[1], in which he attached great weight to the size and disposition of the allantois and the form of the placenta. In a subsequent memoir published in 1868[2] he lays stress upon the presence of a caduca uterina in mammals with a zonary or discoid placenta, and as these animals lose blood at the time of birth he groups them together under the common term *Hématogénètes*. In 1864 Prof. Huxley, in a Lecture on Classification[3], suggested that the terms deciduate and non-deciduate were to be preferred to caducous and non-caducous, and arranged the placental mammals into the groups Deciduata and Non-deciduata; an arrangement which has been adopted by several subsequent writers. By the term Deciduata is meant those mammals which shed, along with the fœtal placenta, more or less of the vascular constituents of the maternal mucosa in the placental area, whilst the Non-deciduata do not part with any of the mucosa in the act of parturition. A sharp line of demarcation therefore is drawn between these two groups of mammals. In employing these terms it should be distinctly kept in mind that the same anatomical elements exist in both types of placenta, and that the shedding or non-shedding of maternal tissue is determined by the degree of interlacement of the fœtal and maternal parts of the organ, and not from the presence in the deciduata of structures which do not exist in the non-deciduata.

All anatomists agree in regarding the diffused placenta as non-deciduate, for the uterine crypts are so shallow that the chorionic villi can be drawn out of them with great ease; and the fœtal membranes are shed in the act of parturition, without entangling and drawing away maternal mucosa.

The polycotyledonary placenta is also regarded as non-deciduate. But from observations made on the shed membranes of the sheep and cow, I recently ascertained[4] that intermingled with the villi of the fœtal cotyledons were quantities

[1] *Ann. des Sciences Naturelles*, 1844, p. 92.
[2] *Considérations sur la Classification des Mammifères*, Paris, 1868, p. 22.
[3] *Elements of Comparative Anatomy*, London, 1864, p. 103.
[4] *Proc. Roy. Soc. Edinburgh*, May, 1875.

of cells, which possessed the characters of the epithelial cells of the pits and crypts of the maternal cotyledons; so that the fœtal cotyledons carried away with them during parturition portions of the epithelial lining of the crypts, and in so far therefore these animals are undoubtedly deciduate. But from the bloody state of the external parts of the ewe, for some hours after the birth of the lamb, I think it not improbable that the disruption of some, if not all, of the maternal cotyledons had been deeper than an epithelial shedding; that the maternal vessels had, in some places at least, been torn across, so as to have occasioned hæmorrhage.

There is no difference of opinion as to the deciduate nature of the zonary placenta. But it has not been sufficiently recognised that considerable variations occur in the relative proportion of maternal tissue which is shed along with the fœtal placenta. In the seal, the dog and the fox the decidua serotina, or mucous membrane of the placental zone, does not form a continuous layer on the uterine face of the separated organ. A definite layer is however left, when the placenta is shed, on the uterine zone itself, which is subdivided into pits or trenches by projecting folds. When the organ is *in situ* these folds dip into the substance of the placenta, but are torn through in the process of parturition, so that the only portions of maternal tissue which are shed are the intra-placental prolongations. That the membrane left on the uterus in the placental zone is the mucosa is proved by its vascularity, the layer of columnar epithelium on its free surface, and the utricular glands; which structures, the glands excepted, are also in the intra-placental prolongations. In the feline *Carnivora*, again, as illustrated by the common cat, the mucosa not only sends prolongations into the substance of the shed placenta, but forms a continuous layer on its uterine surface, so that there is a corresponding deficiency on the uterus itself. Hence though all the *Carnivora* part with a considerable portion of the maternal mucosa in the separation of the placenta, yet they exhibit differences in the degree in which the shedding takes place. The *Felidæ* have a higher grade of deciduation than the *Canidæ*, and with the latter the *Phocidæ* correspond. Hence the dogs and seals, in their placental affinities, are less removed from the *Cetacea*, the

Suidæ and the *Solipedia* than are the cats. The pits and trenches of the mucosa, which one sees on the uterine zone, after the separation of the placenta in a seal, a fox, or a dog, are obviously similar in their morphological characters to the crypts of the mucosa of a mare, a cetacean, or other animals with a diffused placenta. In the seal the pits and trenches possess a precision of form more than is seen in the dog and fox, a circumstance which is undoubtedly due to the sub-division of the placenta of the seal into definite minute lobules. The higher grade of deciduation in a cat may perhaps be accounted for by the broadly laminated villi, their very sinuous form, and the depth in the mucosa to which their terminal bud-like offshoots penetrate, giving to the fœtal part of the placenta a "grip," if I may so term it, over the maternal part, as to interlock the latter more firmly with the villi, and thus to cause the mucosa to be more completely shed in the process of parturition.

In the fox and seal the intra-placental prolongations of the mucosa are subdivided into a reticulated arrangement of slender trabeculæ, each bar of which contains only a single dilated capillary; but in the seal this subdivision is carried out to a greater extent than in the fox. In the seal occurs that very remarkable anastomosis of the distal ends of the primary branches of the chorionic villi, which gives to the placenta its precise lobular subdivision, and walls in each lobule at its uterine periphery with the greyish membrane. From a somewhat cursory examination of the placenta of the *Phoca vitulina*, in the Museum of the Royal College of Surgeons of England, it appeared to me that a similar membrane existed also in this animal; so that I am disposed to consider the arrangement as one which is of more than generic, indeed of ordinal value.

From the general correspondence in shape and structure between the placenta of the *Pinnepedia* and that of the true *Carnivora*, there can be no doubt, that, in both orders, the early stage of formation is marked by the production of crypts in the placental area of the uterine mucosa. In the grey seal the villi of the chorion, which are lodged in these crypts, acquire, not only a considerable length, but a highly arborescent form, and give origin to multitudes of villous tufts. As the

branching and growth of the villi proceed in the course of development, the crypts will necessarily become divided into smaller compartments; and as the villous tufts increase in number and size, the walls of the crypts will become no doubt thinned, until at length they will lose their uniformly continuous surface, and become subdivided into the reticulated arrangement already described, in the meshes of the network of which the villous tufts are lodged. That the increased area of the uterine mucosa in the pregnant seal is due to a great increase in the interglandular part of the membrane, is proved by the much wider separation of the glands seen in both the non-placental and placental areas of the gravid as compared with the non-gravid uterus of *H. Gryphus*.

It has been customary to regard a placenta as deciduate only when the *vascular* constituents of the uterine mucosa are shed with the fœtal membranes. This acceptation of the term seems to me, however, to be too limited, and does not cover all the cases in which maternal tissue is shed in the separated placenta. I suggest therefore that the definition should be enlarged so as to embrace those cases in which epithelium alone is parted with, as well as those in which both the epithelium and the sub-epithelial vascular uterine tissue come away in the separated placenta. In studying the types of placenta which have formed the subject of this Memoir we have passed by successive gradations from the diffused placenta, which is apparently non-deciduate, to the polycotyledonary placenta in which the epithelial layer of the mucosa only has been found; then to the zonary placenta of the *Canidæ* and *Phocidæ*, where the entire constituents of the intra-placental prolongations of the mucosa are shed, but where a well-marked layer of mucous membrane is left on the uterine zone; and lastly to the *Felidæ*, where apparently the entire mucosa in the uterine zone is shed as a part of the placenta. It follows therefore that the line of demarcation between a diffused non-deciduate, and a zonary deciduate placenta, is not so sharp as has usually been supposed, but is graded over by the ruminant polycotyledonary placenta, in which the epithelial layer is the preponderating if not the only element of the mucosa which deciduates during parturition. But to prevent misconception

it should be stated, as indeed has been already done by Owen[1], Ercolani[2], and myself, if not during parturition, at least afterwards, all placental mammals are deciduate, for in the pig, mare, and cetacean, "during the period of involution which follows parturition, it is obvious that great changes, either from actual shedding of portions of its substance, or from degeneration and interstitial absorption, must take place in the constituents of the crypt-layer before it can be restored to its proper non-gravid condition[3]." In the ruminants also, the thick, vascular, spongy tissue of the maternal cotyledon must disappear before the uterus can assume its normal unimpregnated aspect.

PHYSIOLOGICAL REMARKS.—The fœtal placenta possesses an absorbing surface; the maternal placenta a secreting surface. The fœtus is a parasite, which is nourished by the juices of the mother.

The absorbing structures of the fœtal placenta are the villi of the chorion, and the vessels they contain are the structures which transmit the materials absorbed to the fœtus. In the diffused placenta the smooth inter-villous part of the chorion is probably engaged in absorption as well as the villi themselves, for in both a capillary network is present. As the smooth intercotyledonary part of the ruminant chorion, and the smooth extra-zonary part of the zonary chorion are feebly vascular, they are probably little, if at all, engaged in absorption. Though the villi in the cotyledonary and zonary placenta are much fewer in relation to the extent of the chorion than in the diffused placenta, they are longer, more branched, or more sinuous, so that the surface for absorption is probably as great.

The illustrious Harvey distinctly recognised that the placenta prepared for the fœtus alimentary matters derived from the mother; that in the deer, for example, the pits in the cotyledons were

"filled with a muco-albuminous fluid (a circumstance already observed by Galen), and that from this source the ramifications of

[1] *The Anatomy of Vertebrates*, Vol. III. p. 727, 1868.
[2] *Sur les Glandes utriculaires de l'Uterus*, &c. Algiers, 1869.
[3] *Trans. Roy. Soc. Edinburgh*, 1871, and *Proceedings*, May, 1875.

the umbilical vessels absorbed the nutriment and carried it to the fœtus; just as, in animals after their birth, the extremities of the mesenteric vessels are spread over the coats of the intestines, and thence take up chyle[1]."

Haller applied to this fluid the name of uterine milk; a term which has been adopted by many subsequent writers, and the cotyledons themselves have been regarded as uterine mammæ.

By what structures in the maternal placenta can this fluid be secreted? Weber stated that in the ruminants it was in part separated from the capillaries of the "cells" (crypts), but that in addition there were uterine glands. Eschricht looked upon the utricular glands as the sources of the secretion of this nutrient albuminous fluid, whilst he apparently regarded the "cells" (crypts) as the places of formation of ordinary mucus, and this conclusion, at least as regards the function of the glands, has been adopted by various anatomists. Signor Ercolani, in his important memoirs on the placenta, has given a new aspect to this question. He admits the presence of utricular glands in the mucosa, and their increase in size during pregnancy, but conceives that their chief function is to furnish nutritive materials during only the early stage of gestation; and that as soon as the crypts (or follicles as he terms them) are formed, a new glandular organ is produced, which prepares a secretion that supersedes that of the utricular glands.

On this important subject a few words will now be said. There can be no doubt that the utricular glands are secreting structures, and that they enlarge during pregnancy. In the diffused form of placenta they have the appearance of being structurally perfect up to the completion of gestation; and in the examples described in this memoir, *Orca* excepted, their secretion is poured out so as to be brought into direct relation with the inter-villous, and not with the villous portion of the chorion; but as the whole free surface of the chorion is provided with capillaries, the one is no doubt as capable of absorption as the other, and the glands are presumably active throughout intra-uterine life. In the polycotyledonary placenta the utricular glands are not situated in the cotyledons, so that the uterine milk cannot be formed by them. They exist abundantly in the

[1] *The Works of Harvey, translated by Dr Willis*, p. 562.

intercotyledonary parts of the mucosa, and their secretion is brought in contact with non-villous, feebly vascular areas of the chorion, where the power of absorption of the chorion is probably feeble. In the zonary placenta the glands are altered, and degenerated in the placental zone. In the non-placental area they also show a want of structural completeness, and if any secretion is formed by them, it is poured out in relation to the smooth feebly vascular parts of the chorion. Both in the cotyledonary and zonary forms this secretion is therefore of little or no importance in fœtal nutrition, when the placenta itself is formed.

The crypts possess the structural characters of secreting organs. Each crypt is lined by an epithelium, descended from the epithelial lining of the uterine mucosa; which from the size and appearance of the cells is obviously endowed with great functional activity. This epithelium rests upon a highly-vascular, sub-epithelial tissue, the vascularity of which is doubtless proportioned to the amount of secretion formed by the epithelial cells. The arrangements of the diffused and zonary forms of placentæ are not such as to permit the secretion of the crypts to be collected and examined free from mixture with the secretion of the utricular glands. In the polycotyledonary placenta, where the spongy tissue of the maternal cotyledons consists exclusively of crypts, the secretion of uterine milk can not only be shown to be derived from the crypts, but can be collected and analysed. From the researches of Professors Prevost[1], Schlossberger[2] and Arthur Gamgee[3], it has been proved to contain fatty, saline and albuminous materials dissolved in water, so that from its composition it is well suited to act as a nutrient material. The appearance of these crypts in the early stages of placental formation, and their persistence throughout intra-uterine life, though in the zonary form they may become somewhat difficult to recognise, owing to complexities arising during growth, furnish evidence of their importance. The intimate relation which they bear to the villi, which, in the whole series of placentæ

[1] *Ann. des Sc. Nat.*, 1829, xvi. p. 157, and in conjunction with M. Morin in *Mém de la Soc. de physique de Genève*, 1841, ix. p. 235.
[2] *Ann. der Chemie und Pharm.*, 1855.
[3] *Brit. and For. Medico-Chir. Review*, 1864, xxxiii. p. 180.

described in this Memoir, are lodged within the crypts, shows that the secretion they form is in a position best fitted for being absorbed by the villi.

Under the stimulus imparted by the presence of the fertilized ovum the uterus undergoes enormous development and growth. The muscular coat increases so as to provide an arrangement capable of expelling by its contraction the fœtus, when its period of intra-uterine development is completed. In the mucous coat are developed multitudes of crypts, in which is produced a secretion capable of nourishing the fœtus during its intra-uterine life.

But the placenta is regarded as an organ, which not only provides nutriment for the fœtus, but serves as its respiratory apparatus, and it is believed that an interchange of gases takes place between the fœtal and maternal blood-vessels. Undoubtedly there are many facts on record which seem to show that the *fœtus in utero* needs to respire, and that the placenta is the organ where respiration goes on. But there is no evidence that the respiratory changes during intra-uterine life are actively carried on. The experiments of Wm. Edwards indeed show that new-born dogs and cats can resist asphyxia for more than half an hour. The interposition of a layer of secreting cells between the two systems of vessels necessarily throws difficulties in the way of the ready passage of gases from one set of vessels to the other.

The consideration of the structure of the human and the discoid form of placenta generally, will be deferred until a subsequent memoir.