XIV.—*On the Placentation of the Seals.** (Plates XVIII.–XXI).

By Professor TURNER.

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Observations on the form of the Placenta and on the arrangement of the Fœtal membranes in the Seals have been recorded by more than one anatomist. ALESSANDRINI of Bologna† obtained a specimen of the Monk Seal (*Phoca bicolor*) *Monachus albiventer*, in the gravid condition, in which the uterus contained a single fœtus. He recognised the placenta to be zone-like in form, as in the Carnivora. He also described a decidua surrounding the margin of the placenta, and gave many particulars respecting the arrangement of the chorion, the allantois, the amnion, the umbilical vesicle, the umbilical cord, and the general mode of distribution of its blood-vessels. ROSENTHAL stated‡ that in two pregnant seals, which he dissected, the placenta was zone-like, as in the cat and dog, and that each uterus only contained a single fœtus, as is the rule, he believes, in this group of animals. ESCHRICHT considered§ that the examinations which he had made of the membranes of seals preserved in spirit of wine were confirmatory of the correctness of ALESSANDRINI'S observations. BARKOW described|| the dissection of the uterus of the common seal, *Phoca vitulina*, in which he saw a zone-like placenta. Only a single fœtus was present, and that in the left uterine cornu. Although the right horn was far from equalling in size the left, it was considerably larger than in the non-gravid condition, and the uterine glands were strongly developed in its mucous membrane, but there was no extension of the fœtal membranes into it. He also pointed out that the ramifications of the umbilical vessels extended as far as the ends of the chorion.

* The substance of this memoir was communicated orally to the Royal Society of Edinburgh, June 2, 1873, and a brief abstract was published in the "Proceedings" of that date. Through various causes its expansion into a form suitable for the Transactions of the Society has been delayed much longer than was at the time contemplated by the author. (June 1875).

† Opusc. Scientif. vol. iii. 1819, and Meckel's Archiv. vol. v. p. 604.

‡ Zur Anatomie der Seehunde. Nova Acta Caes. Leop. Akademie XV. 1825.

§ De Organis, &c., p. 19. Hafniæ, 1837.

|| Zootomische Bemerkungen. Breslau, 1851.

In all the specimens recorded by these anatomists, as well as in the one I am about to describe, the uterus, although with two cornua, contained only a single foetus; but in a uterus, said to be that of the *Phoca vitulina*, described by A. F. J. C. MAYER,* the left horn is stated to have contained five embryos, and the right four, each embryo being situated in an oval sac-like dilatation of the uterine cornu. The placenta was zonary, and not only the amnion, but the allantois and umbilical vesicle, were present. This specimen of MAYER's differed so materially in the number of embryos which it contained from those examined by all other anatomists, that I am disposed to think it could not have been the gravid uterus of a seal, but must have been derived from some true carnivorous animal.†

Seals, like other uniparous mammals, do, however, occasionally produce twins, and I possess twin fetuses obtained by a former pupil, Mr T. G. KERR, from the uterus of a specimen of *Phoca groenlandica*.

Although most important facts in the naked eye anatomy of the placenta of the seals have been recorded by the anatomists just referred to, yet its minute structure does not seem to have been investigated by any of these observers. This blank in its anatomical history I hope in some measure to supply in this communication.

Uterus and Placenta.

In the month of July 1872 I was invited by my friend Dr JAMES M'BAIN to accompany him on a visit to the "Vigilant," the cruiser to the Board of Fisheries, to see two specimens of the Grey Seal, *Halichoerus gryphus*, which had been shot three days previously by Captain M'DONALD at Sule Skerry, off Cape Wrath. One specimen was a young male, 4 feet 7 inches long, the other a fine female, which measured 6 feet 11 inches from the tip of the nose to the tip of the tail, and 7 feet 10 inches to the end of the hind flippers. From the presence of a white glairy mucus at the orifice of the vagina, and from the distended condition of the abdomen, we were of opinion that the animal was gravid. On opening into the abdominal cavity, the enlarged and pregnant uterus was at once recognised, and through Captain M'DONALD's kindness I was permitted to remove it and several other organs for examination.

The uterus consisted of two horns, a body and a cervix. It was invested by peritoneum, which passed outwards from the horns and the side of the body

* Analecten für Vergleichenden Anatomie, Zweite Sammlung, p. 55. Bonn, 1839.

† Sir EVERARD HOME ("Comparative Anatomy," v. p. 27), refers to a placenta of a seal which had come under his observation, and in vol. vi. plates 26 and 63, gives some figures of the organ. The figures show the villous structure; but they are especially intended by the author to illustrate the "nerves." Professor OWEN ("Comparative Anatomy," iii. p. 745), says that in the seals the placenta is zonular in four or five continuous or connected divisions. In *Phoca vitulina* the diameter of the placental zone, parallel with the long axis of the ovum, is between 2 and 3 inches.

to form the strong broad ligaments, and to be reflected upon the back of the bladder. The horns sprang from the bifurcation of the body. The right contained a large foetus, and measured 2 feet 6 inches along its anterior convex surface from the angle of bifurcation to the tip of the cornu; whilst the left, similarly measured, was only 9 inches; the circumference of the gravid horn at its middle was 20 inches, that of the non-gravid only 4 inches (fig. 1).

A well-marked "ligamentum rotundum" arose from each horn about one and three-quarter inch from the tip, and extended between the layers of the broad ligament. A strong muscular diaphragmatic band passed from the tip of each horn. A short Fallopian tube also curved outwards and opened by a very wide fimbriated mouth on the inner face of a deep "pavilion," in which the ovary was lodged. The right ovary, about the size of the human testicle, contained a large corpus luteum. The left ovary was scarcely half the size of the right. Tortuous veins and arteries were distributed in the broad ligaments in immediate proximity to the ovaries. Numerous muscular fasciculi extended almost transversely outwards from the body of the uterus into the broad ligament on each side between its two layers. Tortuous veins and elongated serpentine arteries ascended beneath the peritoneal investment of the body of the uterus, and within the right broad ligament, to the gravid right horn. An injecting-pipe was introduced into one of these arteries, and another into a vein, and a transparent injection of carmine suspended in gelatine was passed into these vessels. The cavities of the left horn, of the left side of the body, and of the vagina were then opened by a longitudinal incision. The fore part of the left horn was occupied by a very viscid brown mucus, and was nine inches in length. It was prolonged for nine inches and a half into the left side of the body of the uterus, and the calibre at this part was twice as great as that of the free part of the horn. This portion of the horn contained no appreciable quantity of mucus, and there was no prolongation of the foetal membranes into it from the gravid side. The cavity of the left horn entering into the corpus uteri was separated from the corresponding portion of the right horn by a broad septum, which terminated in a free sickle-shaped border immediately in front of the os uteri internum. The cervix uteri was $2\frac{1}{2}$ inches in length, and projected into the vagina, where it formed two very prominent lips which surrounded the os externum. Its mucous lining was thrown into longitudinal folds. The vagina was 6 inches in length, and its mucous lining possessed several strongly marked transverse folds. Both the vagina and cervix uteri contained a glairy whitish-brown mucus.

An incision was then made into the gravid right horn where it entered into the formation of the corpus uteri, which was found to be widely dilated, and this incision was prolonged for a short distance into the free part of the horn. A similar incision was also made for a few inches through the uterine wall at the

outer end of this cornu. The presence of a large zonary placenta was then recognised, and the outer envelope of the foetus, the chorion, was seen to extend from the orifice of the right Fallopian tube as far as the extremity of this cornu, close up to the os uteri internum. A small quantity of reddish-brown fluid, obviously situated between the mucous membrane of the uterus and the outermost foetal envelope, escaped when the wall of the uterus was cut through. The foetus lay within its membranes with its snout directed towards the os internum, its tail and hind flippers towards the free end of the horn, its back in relation to the anterior convex border of the uterine cornu, and its abdominal aspect opposite the posterior concave border. The foetal membranes were then punctured to allow of the escape of a quantity of reddish allantoic fluid, and on slitting them up still further, the foetus, with its umbilical cord, a little more than two inches in length, was exposed. The umbilical vein was opened into, and a quantity of a transparent blue injection was thrown into the foetal part of the placenta. Into one of the umbilical arteries some red injection was then passed. The cord was now cut through, and the foetus removed.

The zonary placenta formed a broad belt, 0·3 to 0·4 inch in thickness, which lay about midway between the tip of the gravid horn and the septum between it and the left cornu. Its transverse diameter was not uniform, for it measured 9 inches in breadth opposite the anterior convex surface of the horn, and not more than 4 inches at the concave posterior surface. Each lateral border of the placenta was free, but continuous with the non-placental part of the chorion. Its uterine surface next this free border, for a breadth of from $\frac{3}{4}$ inch to $1\frac{1}{4}$ inch, varying in different localities, was not adherent to the uterine wall like the great mass of the placenta, but was covered by a prolongation of the mucous lining of the non-placental part of the uterus, which was reflected on to it so as to form a distinct band of decidua reflexa, which was not, however, continued on to the non-placental part of the chorion. This reflected decidua was delicate, and tore down so readily, more especially at its free edge, that portions were stripped away in the act of handling the placenta during its examination. In this manner the foetal villi were exposed, and formed a fringe around the free border of the placenta. Except in the placental area, the outer surface of the chorion was perfectly smooth.

The foetal membranes and placenta were then everted, in order to obtain a more complete view of the general disposition of the membranes and of the inner face of the placenta.

The sac of the allantois was co-equal in length with the chorion, to the inner surface of which its membrane was so closely adherent that it was difficult to separate it from the chorion without tearing one or other of the two membranes. The allantois was prolonged over the inner face of the placenta, except at the part opposite the abdominal aspect of the foetus, where the

umbilical vesicle was in contact with the placenta. The allantois conducted the umbilical vessels to the placenta, and enclosed them in folds, which formed meso-vascular bands, extending for a considerable distance around the inner face of the placenta. Folds of this membrane, also enclosing branches of the umbilical vessels, extended for some distance beyond the margins of the placenta, where they were so arranged as to form the walls of pouch-like recesses, which communicated with the general sac of the allantois. When this sac was first examined it seemed as if it was perfectly closed, and all communication between it and the urachus was cut off. But on dissecting the abdominal end of the cord I found a very slender tubular urachus, which was prolonged as a fine tube to open into the sac of the allantois. This tube possessed thin, semi-transparent walls, and was so fine that it barely admitted a pig's bristle. It extended for $1\frac{3}{4}$ inch between the walls of the amnion and umbilical vesicle, and then for about the same distance between the apposed surfaces of the amnion and allantois, before it opened into the sac of the latter by a narrow funnel-shaped orifice, which was directed so obliquely as to form a valve-like arrangement.

The amnion formed a large elongated bag, in which the foetus and liquor amnii were contained. It lay in relation to the concave aspect of the uterine horn, and the allantois was reflected around the greater part of its outer surface. Its sac was not equal in extent to the sac of the allantois, and the end which contained the tail of the foetus was considerably smaller than the part in which the body and head were lodged. It was reflected in the usual way on to the umbilical cord, by which it was conveyed to the belly of the foetus.

The short funis was cylindrical at its abdominal end, and contained a single vein, two arteries, and the tubular urachus. Two inches from its origin the vein bifurcated, and the cord became flattened, as the branches of the vein, each accompanied by an artery, diverged from each other. The arterial and venous trunks then subdivided into branches to reach the placenta, invested by folds of the allantois as already described. In their course these branches passed between the allantoic membrane and the wall of the umbilical vesicle, and some even were suspended in the cavity of the vesicle. Branches both of the artery and vein ramified between the conjoined chorion and wall of the sac of the allantois, as far as the poles of the chorion.

The umbilical vesicle, though very much smaller than the amnion, formed a well-defined sac which lay between the amnion and placenta, and was elongated laterally into two small horn-like prolongations, which ran parallel and in close relation to the narrower part of the placenta. Its outer surface was in part in contact with the allantois. A funnel-shaped prolongation passed up to the umbilical cord, as far as the angle of bifurcation of the two primary

branches of the umbilical vein from each other, where it terminated in a pointed *cul-de-sac*.

The inner or foetal face of the placenta possessed a convoluted appearance, with intermediate depressions or sulci, which may be called the primary fissures, and the placental substance was continuous across the bottom of each sulcus from one convolution to the other. The convolutions ran parallel to each other from the narrower to the broader part of the placenta, and were most strongly marked in its median portion. When a vertical section was made through the placenta and adjacent part of the uterine wall, and the placenta gently drawn away from the uterus, its uterine face was also seen to be convoluted, with the convolutions and sulci in reverse order to those seen on its chorionic aspect. A well-defined layer of mucous membrane, which, from its position, represented the serotina, intervened between the muscular coat of the uterus and the placenta, and followed closely the windings of the convolutions, dipping down into the primary fissures in the form of broad laminae, just as the pia mater dips between the convolutions of the cerebrum. Each convolution was split up into elongated plates by secondary fissures, into which processes of the mucosa, derived not only from the broad laminae just referred to, but from that in contact with the uterine face of the convolutions, penetrated (figs. 4, 9). Each plate was again subdivided by tertiary fissures into small polygonal lobules, into which more delicate processes of the mucosa entered, and these could be traced through the thickness of the placenta up to the chorion.

The mucosa could readily be peeled off the uterine face of the placenta, and when this was done the laminae were drawn out of the primary fissures, just as one can draw the pia mater out of the cerebral sulci when the grey matter on the surface of the cerebrum is exposed. The more delicate processes, however, which entered the secondary and tertiary fissures were torn through in the act of peeling, and remained in the substance of the placenta entangled between the foetal villi. When these processes were seized with a pair of fine forceps, and gentle traction employed, they could be withdrawn without much difficulty from the substance of the placenta. From the ease with which the processes lying in the secondary and tertiary fissures tore across in the act of peeling off the placenta, there could be little doubt that a similar disruption occurs in the separation of the placenta during normal parturition. This opinion was confirmed by an examination of the placenta of a *Phoca vitulina*, shed at the full time, which through the kindness of Professor FLOWER I had an opportunity of inspecting in July 1874, in the Museum of the Royal College of Surgeons of England.* The part of the mucosa, therefore, which is shed

* The birth in the Zoological Gardens of the young seal to which this placenta belonged, is recorded by Mr A. D. BARTLETT in the Proceedings of the Zoological Society of London, June 11, 1868. In his description it is named *Phoca foetida*, but I believe that the species was *vitulina*, as stated in the text.

along with the placenta consists of the delicate easily torn processes which dip into the secondary and tertiary fissures, and are entangled between the placental lobules and amidst the foetal villi. The uterine face of the separated placenta is not covered by a continuous layer of decidua, for the greater part of the mucosa is not shed when the placenta is expelled, but remains as a layer of membrane of considerable thickness on the inner surface of the muscular coat, and presents on its placental aspect numerous irregular pits or trenches into which the convolutions of the placenta are received when the organ is *in situ*.

Before describing the minute structure of the serotina, I shall relate some observations on the structure of the mucosa in the non-gravid uteri of some seals, which I have had the opportunity of examining, and also the structure of the uterine mucosa in the gravid uterus of *H. gryphus*, both in the non-gravid horn and in the non-placental area of the gravid horn.

In the non-impregnated uterus of a young seal (species unknown) elongated, tubular, utricular glands were very numerous, and closely packed together in the mucosa. The glands lay perpendicular to the plane of the surface, were tortuous, and apparently branched at their deeper ends; by their opposite extremities they opened by funnel-shaped mouths on the free surface of the mucosa. They were lined by a columnar epithelium, and possessed a central lumen. The interglandular connective tissue contained multitudes of corpuscles.

I obtained in 1870 the non-gravid uterus of an adult grey seal (*H. gryphus*) from a specimen captured in that year off the coast of Fife.* The uterus was empty, and the cavities of its horns contracted, but as the uterine veins were dilated, and a large vascular corpus luteum was present in the left ovary, I concluded that the animal had been delivered of a foetus not long before her capture. When the uterus was opened the mucous membrane was seen to form strong folds extending in the longitudinal direction. By its deep surface this membrane was connected to the muscular coat by a lax connective tissue. Vertical sections through the mucosa, examined microscopically, displayed numerous tubular glands, which opened freely on the surface. Their main stems lay almost perpendicular to the plane of the surface, but as the glands were somewhat tortuous, and gave off lateral offshoots, they were not unfrequently transversely or obliquely divided. The epithelium did not fill up the gland tubes, but left a central lumen. The exact form of the epithelium cells could not definitely be made out, but the end which lay next the lumen was rounded or somewhat polygonal, like the broad free end of a columnar epithelium cell. The interglandular connective tissue was vascular, and a well-marked capillary plexus ramified immediately beneath the surface of the mucosa around the mouths of the glands.

* The capture of this specimen is recorded in the "Journal of Anatomy and Physiology," vol. iv. 1870.

In the uterus of a *Cystophora cristata*, which died in the Zoological Gardens, London, May 19th, 1874, about three and a half months after the birth of a cub, and for which I am indebted to Dr JOHN ANDERSON, I was able to confirm the observations previously made on the uterus of *H. gryphus*. On the free surface of the mucosa was placed a layer of columnar epithelium, the cells of which were large and well formed. The mouths of the utricular glands were seen without difficulty opening on the summits and sides of the longitudinal folds of the mucous membrane; their orifices were circular, closely set together, and each was surrounded by a capillary vascular ring (fig. 19). The free surface of the mucosa was studded with multitudes of minute orifices—the mouths of the glands. The glands were comparatively short both in *H. gryphus* and *C. cristata*, and the capillaries of the mucosa formed a closely-set network around them. The corpus luteum of *C. cristata*, was in the right ovary, which was not more than about half the size of the ovary of *H. gryphus*.

The free surface of the non-gravid horn of the uterus of the pregnant *H. gryphus* possessed no longitudinal folds of its mucous membrane such as were observed in the non-gravid uteri of *H. gryphus* and *C. cristata*. The surface of its mucosa was to the naked eye almost perfectly smooth, but when examined with a simple lens, slight irregularities were seen, partly due to the presence of minute ridges with intervening depressions, and partly owing to a granulated condition of the membrane. When examined with higher powers of the microscope the tubular utricular glands were readily seen. They were more elongated, and less tortuous than in the unimpregnated uterus; the branches at their deeper ends were much more distinctly seen, and they were much less closely crowded together, owing to the increase in the amount of the interglandular connective tissue. The glandular epithelium was abundant, the cells being elongated, though I could not satisfactorily determine that they possessed a precise columnar form. The granulated appearance of the mucosa seemed to some extent due to the presence of these glands in the membrane.

The free surface of the mucous membrane of the non-placental area of the gravid horn of the same uterus was smooth in appearance, both to the naked eye and under a simple lens. With higher powers the tubular utricular glands were also seen without difficulty, but they were more elongated, so slightly tortuous as in many instances to be almost straight, and separated by greater intervals, occupied by the interglandular connective tissue, than in the non-gravid horn. In some of the glands the columnar form of the cells was distinctly recognised, and the almost circular form of the gland orifice on the free surface of the mucosa was in many preparations readily seen. The mucous membrane of the septum between the two horns was smooth on the aspect directed both to the gravid and non-gravid horn. The appearance and form of

the glands, and the proportion of interglandular connective tissue was almost alike on both aspects.

From a comparison of the mucosa of the gravid with the non-gravid horn of the pregnant uterus, and of these with the unimpregnated uteri in these seals, it is evident that the changes which take place in the mucous membrane, in connection with the great distension of the uterus during pregnancy, consist in an obliteration of the strong longitudinal folds of the mucosa; in a large increase in the absolute and relative amount of the interglandular part of the mucous membrane; in an elongation of the tubular glands, which elongation is in great part due to an untwisting of the glands, so that they become much less tortuous, though from the very considerable length which some of these glands possessed, it is possible that they and their branches may have actually grown in length. The similarity in the appearance of the septal mucous membrane on its two aspects was evidently due to the growth of this partition being equal for the non-gravid as for the gravid horn.

The band of mucous membrane reflected on to the border of the placenta was smooth on its free surface like the adjacent part of the uterine mucosa with which it was continuous. When peeled off the placenta, and placed under the microscope, utricular glands were seen in it, which in form and relative numbers closely corresponded with the arrangement just described in the mucosa of the non-placental area of the gravid horn. Many of the glands, however, displayed an appearance such as I had not previously observed; for their lumen, instead of being empty, was occupied by a bright yellow material. It is not improbable that this yellow substance was the secretion of the gland confined within the lumen through some obstruction near the mouth of the gland, which prevented its excretion.

I then proceeded to examine the structure of the mucosa, the general arrangement of which, and relations to the uterine wall and placenta, have already been described. In the non-deciduous serotina, *i.e.*, in the layer of mucous membrane left on the wall of the uterus, after the placenta was peeled off, utricular glands were seen, but they were much more sparingly distributed even than in the mucosa of the non-placental area of the gravid horn. In various of these glands an appearance was observed, indications of which had also been seen in some of the glands both in the mucosa of the non-placental area and in the reflexa, of a breaking up within the gland-tubes of the epithelium into scattered masses, separated by intermediate irregular intervals.

On that surface of the non-deciduous mucosa, which was exposed by peeling off the placenta, irregular scattered patches of cells were seen when examined with a magnifying power of 300 diameters. In some places the patches were so close together that they gave the impression of being portions of the originally continuous epithelial layer of the mucosa, which had become broken up

into patches by the removal of some of the cells in the act of peeling off the placenta. In other localities much wider intervals between the patches existed, so that their probable original continuity with each other was not at first sight so apparent. It was observed that the cells remained in position on those parts of the mucosa immediately superficial to its larger blood-vessels, whilst they were frequently absent from the surface of the membrane situated between these vascular trunks. The cells in a patch were in close contact with each other. They were short columnar cells; their free ends being either circular, or ovoid, or polygonal, and in many cases having the diameter of a white blood corpuscle, though others were somewhat larger (fig. 10).

Both the non-deciduous serotina and the decidua reflexa were much more vascular than the mucosa of the non-placental area of the uterus. The increased vascularity was due to the blood-vessels being larger, and apparently more numerous in a given area. In all these localities vessels of capillary size were present, but the veins and arteries of the serotina and reflexa were considerably larger than those of the non-placental mucosa. This increase in size was not due to the formation of varicosities on limited portions of their walls, but to a general expansion of the vascular tube. No curling or cork-screw like arteries were seen, and the veins presented no unusual tortuosity. In the sub-epithelial layer of the non-deciduous serotina nerves were distinctly seen. The slender nerve trunks gave off fine branches, which ramified in the surrounding connective tissue until the finest branches consisted of but one or two fibres. The sub-epithelial connective tissue contained multitudes of well-marked connective tissue corpuscles.

The broad laminae of mucosa which dipped into the primary fissures between the convolutions of the placenta had an interrupted layer of epithelial cells on their free surface, similar in shape but somewhat bigger than those of the non-deciduous mucosa just described. The arrangement and relative size of the blood-vessels were also the same, and utricular glands were present, though sparingly distributed in the sub-epithelial connective tissue.

The structure of the delicate bands of deciduous mucosa which passed into the secondary and tertiary fissures in the substance of the convolutions was then examined. The free surface of these bands was covered by an epithelial layer, the cells of which were columnar like those of the non-deciduous mucosa; but their contents were more opaque and yellow, as if in process of fatty degeneration. Flake-like layers of cells were not unfrequently seen lying loose in the fluid in which these specimens were examined, as if they had become detached from the free surface of the decidua. In one or two instances rows of cells, as if the cellular contents of utricular glands, were observed, but no glands were seen in these delicate processes. The bands of decidua, lying in the secondary and tertiary fissures, consisted of a delicate membranous connective tissue, into which the blood-vessels of the non-deciduous mucosa were prolonged. These

decidual bands dipped between the lobules of the placenta, almost up to the chorion, and the maternal vessels branched and formed in them a capillary network. From these bands slender processes passed into the interior of the placental lobules, where they formed a lattice-like arrangement of very slender trabeculæ, winding in a sinuous manner through the lobule. These trabecles could be pulled out of a lobule with a pair of fine forceps, and in many specimens the bud-like processes of the chorionic villi lodged in the interstices between the trabecles were drawn out along with them. Each trabecle was formed of a capillary blood-vessel, surrounded by a thin layer of connective tissue, which again was invested by a layer of columnar epithelial cells similar to those already described on the free surface of the bands of decidua (fig. 7). These cells were very easily detached from the surface of the trabeculæ, and quantities of loose cells floated about the fluid in which the specimens were examined. The deep attached end of a cell was often attenuated into a fine process. The trabecles were therefore delicate bands of the uterine mucosa, and were composed of its several constituents *minus* the utricular glands.

When the uterine face of the placenta, from which the non-deciduous mucosa had been peeled off, was examined, a greyish membrane was seen, which at first sight seemed as if it might have been a portion of the decidua remaining adherent to the surface of the placenta, and the exact nature of which required some care to determine. It lay in contact with the uterine face of the placental lobules; but instead of being prolonged from the uterine surface of one lobule to the corresponding surface of the adjacent lobules, so as to form a continuous layer over the whole uterine surface of the placenta, it was continued for some distance down the side of each lobule into the substance of the placenta, and formed an investment for the individual lobules. Hence the uterine face of the placenta was broken up into polygonal areas, each of which corresponded to a placental lobule, and the areas were separated from each other by the bands of decidua which dipped into the secondary and tertiary fissures of the placenta (fig. 6). I then satisfied myself that the greyish membrane belonged to the foetal and not to the maternal part of the placenta; for whilst the decidua readily peeled off from the one surface of the grey membrane, the other surface was not only in immediate contact with the chorionic villi, but was continuous with their substance, so that it could not be separated from them without tearing through not only the small blood-vessels which passed from the villi into the greyish layer, but its proper connective tissue substance.

The greyish layer consisted of a tough membrane. When stripped off a placental lobule, and examined microscopically, the surface next the villi was seen to possess many longitudinal folds, often lying parallel to each other, separated by intermediate shallow depressions. This membrane was composed of bundles of the white fibres of connective tissue, the fasciculi of which were

best marked in the longitudinal folds. The corpuscles of the connective tissue were ovoid and fusiform, relatively large in size and granular. Ramifying in the membrane were the small blood-vessels derived from those of the chorionic villi, which had been torn through when the grey membrane was stripped off; hence this membrane derived its vascular supply from the chorionic and not from the maternal system of blood-vessels, and must be regarded as a foetal and not a maternal structure. On that surface of the greyish membrane which lay next the non-deciduous mucosa, patches of epithelial cells similar to those previously described on the free surface of the mucosa were seen. I believe that these cells, though adhering to the membrane, did not properly belong to it; but to the mucosa, from which they had separated in peeling off the placenta; and in this manner one may explain why the epithelial covering of the mucosa seemed to form an interrupted and not a continuous layer.

Numerous vertical sections were now made through the entire thickness of the placental lobes, and examined with the view of determining the arrangement and structure of the villi of the chorion, their more exact connection with the greyish layer, and their relations to the intra-lobular parts of the deciduous mucosa (fig. 5). The stems of numerous large villi arose at frequent intervals from the placental surface of the chorion, and passed through the placental lobules almost perpendicular to the plane of the chorion and branched in a highly arborescent manner. From the sides of the stems of the villi, from the sides of their branches, and from the extremities of the greater number of these branches much smaller branched villous processes arose which gave origin to multitudes of villous tufts. Some of the larger branches from the parent stem had, however, a different mode of termination: they reached the periphery of the lobule and blended with the greyish layer already described. This layer, therefore, was obviously formed by the junction with each other of the ends of those branches of the villi which reached the periphery of the lobule; by their union a continuous layer of foetal tissue was formed, not only on the uterine surface of each lobule, but reaching for some distance down its sides. From the placental surface of the chorion, in the intervals between the origins of the stems of the large arborescent villi, numbers of short branching villi arose, which soon subdivided into terminal branching tufts. The terminal branching tufts were, as a rule, slender elongated structures, but some were shorter and more club-shaped.

The matrix substance of the villi consisted of a delicate connective tissue containing multitudes of distinct corpuscles. Where this tissue formed the terminal tufts the corpuscles were very numerous, and appeared in some cases not only imbedded in the substance of the tuft, but as if arranged, after the manner of an epithelium, on the free surface. In some of my preparations the more superficial cells were detached, and were seen to have the form of delicate

scales of nucleated protoplasm. The blood-vessels of the villi were derived from the umbilical vessels. The large trunks lay in the stems of the villi and branched in an arborescent manner, ending in a capillary plexus in the terminal villous tufts (fig. 8). In some of the larger branches a vessel ran parallel and close to the surface of the villus which communicated with the capillaries of the tufts arising directly from the sides of the branches. Those villi which entered into the formation of the greyish membrane conveyed the vessels which formed the capillary plexus situated in it.

The intra-lobular prolongations of the maternal mucosa did not pass directly from the non-deciduous layer of mucosa, investing the muscular coat of the uterus, into the lobules, for the greyish membrane situated on their uterine surface, and on the adjacent part of the sides of the lobule, prevented a direct entrance. The intra-lobular decidua was therefore derived from those processes of the decidua which dipped into the secondary and tertiary fissures. These processes, in the form of slender bands and laminae, penetrated up to the chorion, and then branched off laterally into the lobules where they formed the sides of the fissures, when they at once broke up into the reticulated lattice-like arrangement of sinuous trabeculae already described. In sections made through the lobules, where no displacement of the relative position of the foetal and maternal structures had taken place, the meshes of the reticulum were seen to be occupied by the villous tufts, and not unfrequently the tufts were surrounded by a ring-like arrangement of trabecles. In this manner, throughout the entire lobule, the maternal and foetal parts of the placenta were so closely intertwined that the two systems of blood-vessels were brought into close juxtaposition with each other: the structures which intervened being, on the maternal side, the epithelial investment of the trabeculae, and on the foetal, the flattened scale-like superficial cells of the villi. The greyish membrane also contributed to the production of the juxtaposition, for not only were the folds on its deeper surface vascular, and projected into the lobule so as to have the maternal trabeculae in contact with them, but it is not improbable that others of the capillaries which it contained were, when the placenta was in position, in relation with the capillary blood-vessels of the non-deciduous mucosa forming the irregular pits or trenches into which the placental convolutions fitted. In the non-deciduous as in the intra-lobular mucosa, a layer of epithelium covered the free surface of the maternal membrane.

From the mode in which the placental lobules were walled in on the uterine aspect by the greyish membrane of foetal tissue, from the processes of decidua having to penetrate up to the chorion before their capillaries entered the lobules, and from the recurrent course which so large a proportion of the intra-lobular trabeculae had to take in order to reach the villi situated nearest to the greyish membrane; the maternal blood-vascular system penetrated throughout the entire

lobule, and was brought into relation with the numerous offshoots of the villi. In the separation of the placenta during parturition a quantity of maternal vascular tissue comes away therefore with the placenta.

The Fœtus.

The fœtus, a male, was well grown. It measured, from the tip of the nose to the end of the tail, 19 inches, and to the end of the hind flipper, $20\frac{1}{2}$ inches. Its girth immediately behind the pectoral flippers was 15 inches. The bladder and urachus were pervious up to the root of the umbilical cord, but I could not pass a bristle from the intra-abdominal urachus into the fine tubular urachus in the cord itself. The umbilical vein did not divide until it reached the under surface of the liver. The umbilical arteries had the usual relation to the side of the bladder. The teeth had not cut the gum, but the outlines of the crowns of the canines and molars could be distinctly felt through the mucous membrane. The palpebral fissure was not closed in by a membrane. The third eyelid was large. Vibrissæ about one inch in length projected from the muzzle and eyebrows.

The fœtus was covered with straight stiffish hairs, the longest of which were about half an inch in length, and neither woolly nor fur-like. The hairy coat was yellowish fawn-coloured, streaked with dark gray bands and spots. The hairs were firmly adherent to the skin, and no loose hairs were found in the bag of membranes. When the hairs were pulled out of the skin no under coat of wool was to be seen. The hairy coat of the mother was lead-grey in colour on the back of the body and head, but on the back of the fore and hind limbs, and at the sides of the neck the general tint was white, with black spots. The belly also was white, and marked with numerous irregular black spots. The young male, shot at the same time, had a different coloration of the hair. The top of the head and back of the body were brown, interspersed with gray irregular patches; down the middle of the forehead was a dark-brown stripe, with a lighter brown stripe on each side. The belly was ash-coloured, with brownish spots at the sides and anal end.

Several observers have directed attention to the shedding of the hairy coat of the fœtus of some species of seal, either *in utero*, or immediately after birth. WRIGHT states* that the young of the *Phoca variegata* of NILLSON (*Phoca vitulina*) change the first hair (which is whitish-yellow, long, and as it were curly or woolly) in the uterus in the first half of June, and the hairs of the new-born animals have then the same colour and quality as the hairs of the mother. The moulted woolly hair is found in the uterus alongside of the young animal. This, he says, is consistent with the mode of life of this species of seal, the young of

* Förhand. vid de Skandin. Naturforsk. i Stockholm, July 1842. Abstract by Hannover in Müller's Archiv, p. 38, 1844. I am indebted to Sir James Paget for this reference.

which at once pass into the water. Mr BARTLETT points out that the young seal (*P. vitulina*?) born in the Zoological Gardens, June 8, 1868, a few minutes after its birth rolled and turned about, so as completely to divest itself of the outer covering of fur and hair which formed a complete mat upon which the young animal lay for the first hour or two after its birth. When born it was very active, and within three hours afterwards was swimming and diving about in the water like an adult animal. This young seal was 32 inches long, and weighed 20 lbs. at its birth. The young of *Halichærus gryphus*, on the other hand, according to WRIGHT, are born with yellowish-white woolly hairs, and cannot even swim; the mother suckles them on the land for three weeks, and then, when they have changed their woolly hairs, they take to the water.

Captain M'DONALD, who has for many years observed the habits of the Grey Seal (*H. gryphus*) on the west coast of Scotland, has kindly given me some interesting information about this animal. When just born, he says, the hair on the back and belly is yellowish-white, streaked with some faint grey stripes down the back. At the end of a week the hair is whiter than when newly born. When about fourteen days old the hair begins to fall off, and the first coat is entirely shed at the end of twenty-eight days. I saw a young male, nearly five months old, which Captain M'DONALD had alive on board the "Vigilant," to be slate-grey coloured on the back, with scattered black spots irregular both in size and shape. When the skin was wet the slate-grey tint was darker than when dry. The muzzle was a lighter shade of grey. The belly was whitish-yellow, with irregular black spots. The grey colour of the back and the whitish-yellow of the belly shaded into each other along the sides of the animal, where the black spots were more numerous than on the back or belly.

The period of the year in which the seals produce their young varies very considerably in the different species. *Cystophora cristata* gives birth to its young in the month of February, though some writers say about the month of April; *Phoca groenlandica* about the end of March and the beginning of April; *Phoca vitulina* in the month of June; *Halichærus gryphus* again does not, as Captain M'DONALD informs me, bring forth its young until the month of October. On October 1st, 1874, he landed on the Eastern Hysker, a rocky islet near Canna, and found four young grey seals which had just been born. On the 12th October he again landed and found fifteen young animals, all of which had been pupped since his former visit. He has never seen more than one pup to each female. The mother suckles its young about ten weeks, and, if not disturbed, the young animals do not take to the water until the mother ceases to give suck, when the males and females begin again to copulate. There appears to be one adult male to three or even more females. The foetus described in this memoir was therefore about three months from the completion of its term of intra-uterine life. The period of gestation is about nine months.

Comparison of the Placentation of the Seals with that of the Carnivora.

As the Seals possess, like the true *Carnivora*, a zonary placenta, and as the development of the placenta in the seal, at least in the early stages, is in all probability similar to that in the *Carnivora*, it may not be out of place to examine the placenta in some genera of the latter order, and to compare its structure with that of the seals. I have examined, with this object, the structure of the placenta and gravid uterus in the Cat, Bitch, and Fox, and as I have observed it at various periods of gestation in the cat, I shall commence by describing the placenta in that animal.

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 $\frac{8}{10}$ ths inch. When a compartment was opened the chorion separated from the uterus with great readiness, and exposed the uterine mucosa. At each pole of the compartment an area $\frac{1}{10}$ th inch in its long diameter was smooth, but the rest of the mucosa 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),* and by BISCHOFF in the same animal (fig. 48, A),† 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 (fig. 11). 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 (fig. 12). 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.

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

† Entwicklungs-geschichte des Hunde Eies, 1845.

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 under 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 (fig. 11). 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 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 inter-glandular 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 inter-glandular 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 inter-glandular tissue was greatly increased in quantity, so that the glands were further apart, and, 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 ends 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 in the same manner in this animal as I have satisfied myself to be the case in the gravid uterus of 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 Professor ERCOLANI on the same animal.*

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 of the appearances 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, 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

* Mem. dell Acad. delle Scienze di Bologna, 1870. Plates 2, 3, 4.

† See my Memoir in Trans. Roy. Soc. Edinburgh, 1871.

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 very sinuous manner between the leaf-like villi (fig. 14). 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 placenta 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 foetal villi, and ascended almost vertically in the trabeculæ (fig. 13). 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 have been to some extent 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. The vessels of the capillary network of the foetal villi were injected with a blue colour and showed no dilatation; and the contrast between the two systems of vessels within the organ was well seen both in horizontal and vertical sections (figs. 13, 14).

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 laminae and trabeculae passed into the substance of the placenta, which had a similar sinuous arrangement and relation to the foetal villi as in the placenta at half-time. Examined microscopically, the vascular connective tissue of the serotina, 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 foetal 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, flexuous laminae of maternal structure passing through the entire thickness of the organ, and investing the foetal villi as if with sheaths.* 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 tissue. But he also came to the conclusion that the mucous tissue was left entire in the placental zone, exhibiting only torn and broken-off vessels.

* De Organis, &c., pp. 14, 18.

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 laminae and trabeculae 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 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,—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 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; which folds had a ragged, flocculent appearance. The membrane was very vascular, and at the ragged edges of the folds 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 Professor ROLLESTON* 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. 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† 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 Professor ERCOLANI, of Bologna, in his first memoir on the structure of the placenta,‡ 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

* Trans. Zool. Soc. v. 1863.

† BALY'S Translation of Müller's Physiology, note, p. 1576.

‡ Memoire sur les Glandes Utriculaires de l'Uterus, p. 22. French Translation. Algiers, 1869.

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, these sections at first sight 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 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 deeper than 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 (fig. 17). I am therefore of opinion that the utricular glands in the bitch, as in so many other animals, 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 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 they 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 sustained.

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 foetal villi they were from twice to four times as big, so that they may be regarded as indicating an 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 (fig. 16). 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 $\frac{1}{3}$ d 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.

The placenta of the Seal has a closer affinity in its arrangement and structure to that organ in the canine, than in the feline *Carnivora*. In the seal, as in the dog and 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 on the uterine zone itself, when the placenta is shed, 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 separation, so that the only portions of the maternal tissue which are shed in the act of parturition, are the intra-placental prolongations of the mucous membrane. That the membrane left on the inner surface of the uterus in the placental zone is the mucous membrane, is proved by its vascular structure, by the layer of columnar epithelial cells on its free surface, and by the presence of utricular glands. But the intra-placental prolongations, whilst consisting of the columnar epithelium, and of vascular sub-epithelial connective tissue, contain no utricular glands. The serotina, therefore, both in its deciduous and non-deciduous portions, is nothing more than the modified mucous membrane. In the feline *Carnivora*, again, as illustrated by the common cat, the mucosa not only sends prolongations into the substance of the placenta, but forms a continuous layer on the uterine face of the shed placenta, and there is a consequent deficiency in the corresponding zone in 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 decidualation 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 subdivision of the placenta of the seal into definite minute lobules. The higher grade of decidualation 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 foetal part of the placenta a "grip," if I may so term it, over the maternal part, so 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 separation. For, as I have already pointed out in a previous memoir,* the shedding or non-shedding of maternal tissue, along with the foetal, during the act of parturition is determined by the degree of interlocking of the foetal and maternal portions of the organ with each other, and not from the presence in the deciduata of a structure or structures which do not exist in the non-deciduata.

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 a *Phoca vitulina* in the Museum of the Royal College of Surgeons of England, it appeared to me that a similar membrane existed also in that 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, and that these crypts are formed, quite independently of the utricular glands, by a great growth and folding of the interglandular tissue. In the grey seal, the villi of the

* Trans. Roy. Soc. Edin. 1871, p. 426.

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 described in this memoir, in the meshes of the network of which the villous tufts are lodged. That the increased area of the uterine mucosa during pregnancy 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 uterus of *H. gryphus*, as compared with the non-gravid uterus.

Neither in the true *Carnivora* nor in the *Pinnepedia* do the utricular glands appear to play an important part in foetal nutrition in the fully formed placenta. Not only is the number of glands small in relation to the size of the placental area, but their epithelial lining has obviously undergone changes which do not seem to be consistent with the possession of functional vigour. In the cat, indeed, the lumen of the gland tube seems to be quite occluded. But whilst these changes have taken place in the utricular glands, other cells have been developed in the gravid mucous membrane, which have all the characters of functionally active structures. I refer to the columnar epithelium cells lining the crypts, and investing the free surface of the laminae and trabeculae, with which the chorionic villi are in opposition. On the theory that the walls of the crypts, the laminae, and trabeculae, are produced by a great growth of the interglandular part of the mucosa, these cells would be descended from the epithelial covering of the non-gravid mucous membrane. Professor ERCOLANI, who has described the arrangement in the cat, considers that by the great growth and folding of the mucous membrane during pregnancy, multitudes of glandular follicles (crypts) are formed, of which these cells are the epithelial lining; and there can be no doubt that the same conclusion must be come to respecting the similar cells which I have found in the placenta of the bitch, the fox, and the seal. The crypts or follicles are therefore to be regarded as secreting structures, which in the *Pinnepedia* and *Carnivora* have replaced the utricular glands. From the maternal blood-vessels which lie immediately subjacent to this epithelial layer the cells elaborate a secretion to be poured into the follicles or crypts, where it is absorbed by the villi, and applied to the nutrition of the foetus. It would appear, therefore, as has been suggested by ERCOLANI, that in these and in all other mammals in which a similar glandular organ is produced, the nutrition of the foetus is effected, not by a direct interchange of materials between the maternal and foetal

systems of the blood-vessels, but by the production of a secretion in the maternal placenta which is absorbed by the foetal placenta. The great vascularity of the maternal placenta is in relation therefore to the activity of this new formed glandular organ, and to the amount of the pabulum required for the production of the secretion.

EXPLANATION OF PLATES.

Figures 1, 2, and 3 were drawn from nature under my superintendence by Mr PETER THOMSON; Figures 4 and 9 by Mr JOHN R. REID. For the series of beautiful microscopic drawings from which the remaining figures have been engraved, I am indebted to my former assistant, Mr J. C. Ewart, M.B.

PLATE XVIII.

- Figure 1. Gravid uterus, vagina, broad and round ligaments, ovaries, and bladder of *Halichoerus gryphus*. *Ut*, uterus; *V*, vagina; *O*, left ovary; *B*, bladder. Figures 1, 2, 3 much reduced.
- Figure 2. Gravid uterus of the same animal, the cavities of which and of the vagina have been opened into. *Ut*, the wall of the uterus in the region of the zonary placenta; the shaded fringe on each side is to represent the free edge of the placenta. *Ch, ch*, the non-placental part of the chorion; *n*, the non-gravid horn of the uterus, into which the foetal membranes do not extend; *V*, the vagina, into the cavity of which the cervix uteri may be seen projecting.
- Figure 3. A view of the foetal membranes which have been everted. *Pl*, the inner convoluted surface of the placenta, which is traversed by folds of the allantois, containing branches of the umbilical vessels; *al, al*, the inner surface of the allantois; *am*, the sac of the amnion opened into, out of which the foetus has been removed; *u*, the short umbilical cord; *uv*, one of the two horns of the umbilical vesicle, the opposite horn is concealed between the right pole of the amnion and the placenta.
- Figure 4. Vertical section through the wall of the uterus and placenta at and near the margin of the latter. *Ut*, wall of the uterus, in which the large uterine vessels may be seen; *Pl*, the placenta; *ds*, decidua serotina, passing from the inner surface of the uterus into the sulci between the convolutions of the placenta; *m*, the mucous membrane of the uterus in its non-placental area; *dr*, the mucous membrane reflected on to the placenta at its free border, —the shaded band to the left of the letters represents the line where the placental villi, through tearing down of the reflected decidua have been exposed; *ch*, the non-placental part of the chorion. Natural size.

PLATE XIX.

- Figure 5. Vertical section through one lobule and a portion of an adjacent lobule of the placenta of the Grey Seal. *Ch*, chorion; *VV*, stems of the large arborescent villi; *V'*, smaller villi arising directly from the chorion. The blue-coloured vessels in the chorion and villi are the ramifications of the umbilical vein. *g.g.*, greyish membrane at the periphery of the lobule in which the blue-coloured vessels of the villi ramify; *b.b.*, bud-like offshoots of the finer branches of the villi; *ds*, uterine mucosa forming the non-deciduous serotina in relation with the placental lobules; *gl*, utricular gland; *uv*, uterine blood-vessels, coloured red, passing into *f*, a tertiary fissure between the two lobules. At the upper end of this fissure these vessels form a network continuous with the intra-lobular maternal capillaries. At *tr* the intra-placental trabecular arrangement of the mucosa is shown isolated and drawn away from the finer branches of the villi. In the greater part of this figure the maternal trabeculae are shown *in situ* intertwined amidst the foetal villi. $\times 40$.
- Figure 6. Uterine surface of four of the lobules of the placenta. *g.g.*, greyish membrane forming the periphery of the lobules; at *g'* the membrane has been dissected off; the blue-coloured vessels are branches of the umbilical vein; *t*, processes of the uterine mucosa, with the vessels coloured red, dipping into the tertiary fissures between the lobules. $\times 4$.

Figure 7. Intra-placental maternal trabeculae, *tr*. At *ep*, *ep* the columnar epithelial covering is seen *in situ*; at *ep'*, *ep'* partially shed. Elsewhere the epithelium has been entirely removed, so as to show the sub-epithelial tissue with its corpuscles, and the single capillary *c*, in each trabecula. $\times 200$.

Figure 8. Branch of a villus, *V*, with its terminal bud-like offshoots. The vascularity of the villus is shown in the upper part of the figure, whilst at the lower end its cellular structure is represented. $\times 200$.

PLATE XX.

Figure 9. Portion of placenta, *Pl*, of the Grey Seal partially dissected off the uterus. *mm*, the uterine mucosa forming the non-deciduous part of the serotina; folds of this membrane may be seen entering the sulci or primary fissures, *s,s*, between the convolutions of the placenta. The broader red lines on the exposed surface of the placenta are intended to represent the secondary fissures of the placenta, and the finer lines the tertiary fissures, by which it is subdivided into the ultimate lobules, *l*. *np*, *np*, non-placental portions of the mucous membrane. Natural size.

Figure 10. Surface view of the uterine mucosa forming the non-deciduous serotina. At *e*, *e* the broad ends of the columnar epithelium cells, still *in situ*, are represented. In the rest of the figure the epithelium has been removed. *uv*, larger trunks of the blood-vessels of the mucosa; *c*, capillary network; *ct*, corpusculated sub-epithelial connective tissue; *gl*, portion of one of the utricular glands. $\times 250$.

Figure 11. Vertical section through the placental area of the mucosa of the Cat, described on p. 290. *cr*, the layer of branching crypts; the epithelial lining of the crypts, *ep*, *ep*, and their highly corpusculated connective tissue walls, *ct*, *ct*, are represented; *gl*, the glandular layer; the glands are seen in section, much less numerous than the crypts, and surrounded by connective tissue; *ms*, the muscular coat. $\times$ Hartnack 3 obj. 4 Oc.; tube out.

Figure 12. Horizontal section through the crypt layer of the same uterus. *cr*, *cr*, cavities of the crypts with their epithelial lining. At *e* the epithelium covering the free surface of the walls of the crypts is seen; at *e'* the walls are in section, and the sub-epithelial connective tissue, with its corpuscles, *ct*, is exposed. $\times$ Hartnack 7 obj. 3 Oc.; tube out.

PLATE XXI.

Figure 13. Vertical section through the placenta, *Pl*, of a Cat, about half time (p. 293). *Ch*, the chorion, the vessels of which are coloured blue, so that the blue network which passes through the thickness of the placenta represents the vessels of the villi; *D*, the decidua serotina; the red-coloured vessels are the vessels of the uterine mucosa, which ascend in the walls of the crypts as far as the chorion, where they not unfrequently show considerable dilatations, *s*. *b*, bud-like terminal offshoot of a villus penetrating into the serotina; *ms*, the muscular coat. $\times$ Hartnack 3 obj. 3 Oc.

Figure 14. Horizontal section through the placenta of the same Cat. *VV*, transversely divided sinuous villi, the capillaries in which are coloured blue; *l*, *l*, laminae of uterine mucosa, forming the walls of the crypts. The red colour represents maternal vessels, as in figure 13.

Figure 15. Villi, *V*, with a portion of the chorion, *ch*, of the shed placenta of a Cat at full time; *b*, a terminal bud, such as in figure 13, *b* penetrates deeply into the serotina. $\times 40$.

Figure 16. Horizontal section through the placenta of a Fox (p. 297). *V*, the blue-coloured vessels of the foetal villi; *m*, the transversely divided colossal maternal capillaries.

Figure 17. Vertical section through the non-gravid uterine mucosa of a Bitch (p. 297). *e*, ends of columnar epithelial cells covering free surface of mucosa; *g*, tubular gland shown in its entire length; *g'*, a tubular gland cut short. At *a* the continuity of an apparently short gland, with the deeper end of a tube, is shown. *ct*, interglandular connective tissue, with its corpuscles; *b*, arteries passing into the mucosa; *ms*, muscular coat. $\times 100$.

Figure 18. Horizontal section through the non-gravid uterine mucosa of a Bitch, near the free surface. The close relation which the glands have to each other is shown; also the small proportion of interglandular tissue, in which rounded cells, not unlike lymph or white blood corpuscles may be seen. $\times 100$.

Figure 19. Surface view of the non-gravid uterine mucosa of the Crested Seal (*Cystophora cristata*). At *e* the columnar epithelium is *in situ*, elsewhere it has been removed; *g*, mouth of a tubular gland. The capillary network of the mucosa is coloured red. $\times 100$.

ADDENDUM, NOVEMBER 4.

Since the preceding pages were printed off, I have succeeded in obtaining for examination the uterus of a cat, killed five hours after giving birth to four kittens, so that I am now able to supplement my description of the placentation of this animal by stating what is the *post-partum* condition of its uterus.

The uterus was contracted, and the mucous lining thrown into well-defined rugæ. Each placental area was a narrow zonular trench, bounded at each margin of the zone by a fold of the mucosa. The surface of the non-placental part of the mucosa was unbroken and covered by epithelium. The surface of the placental zone was blood-stained, and with a number of shreds of membrane hanging from it, so that it had a torn and flocculent appearance. When thin flakes were removed from the surface of the placental zone, and examined microscopically, they were seen to consist of multitudes of free red blood corpuscles, of very delicate fibres of connective tissue, intermingled with which were fusiform and lymph-like corpuscles, and here and there a patch of cells, evidently epithelium. A series of vertical sections was then made through the placental area and adjacent non-placental part of the mucosa, and examined with low and high magnifying objectives. The free edge of the section in the non-placental area was covered by a well-defined layer of columnar epithelium, deeper than which was a thick layer of sub-epithelial connective tissue, intervening between the epithelium and the muscular coat. Lying vertically in this connective tissue were numerous utricular glands, which opened on the free surface of the mucosa, and were lined by columnar epithelium.

In the placental area itself the surface epithelium was absent, and the free edge of the section had not a smooth outline, but was irregular, and with slender filaments of connective tissue projecting from it. The thickness of the connective tissue layer on the surface of the muscular coat was appreciably less (on the average about one-third) than in the non-placental area. In this connective tissue sections through utricular glands were seen. Some of these sections were transverse to the tube of the gland, others oblique, others almost longitudinal. The epithelial lining of the glands was present, and it is not unlikely that the occasional patch of cells found on the surface of the placental area may have belonged to the glands and not to the surface epithelium. In more than one of the sections I saw in the placental area gland structures, which had not the form of cylindrical tubes, but were somewhat irregularly dilated. Numerous blood-vessels, which were the vascular trunks going to the placenta, were also seen plugged with collections of blood corpuscles.

From this description it will be seen that in the normal separation of the

placenta at the time of parturition so complete a shedding of the mucosa of the placental zone does not take place as was effected by artificially tearing off the placenta in an earlier period of gestation. The muscular coat is not exposed, but is covered by a layer of connective tissue, forming the deeper part of the sub-epithelial connective tissue of the placental area, in which portions of gland tubes and blood-vessels may be seen. This layer forms a non-deciduous serotina. The surface epithelium of this area and the more immediately subjacent tissue are, however, shed along with the placenta, and form a well-defined deciduous serotina, so that although the entire thickness of the serotina is not shed during parturition, yet a larger proportion falls off with the placenta than in the bitch, fox, and seal.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 11.

Fig. 10.

Fig. 9.

Fig. 13.

Fig. 15.

Fig. 17.

Fig. 14.

Fig. 19.

Fig. 18.

Fig. 16.