

The Placentation of Perameles.

(Contributions to the Embryology of the Marsupialia—I.)

By

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With Plates 29—33.

INTRODUCTION.

IN a preliminary note (1) communicated to the Linnean Society of New South Wales I recorded the occurrence of an allantoic placenta in *Perameles obesula*, and gave a short account of its structure based on an examination of a single stage, at that time the only one in my possession. Since then, the acquisition of certain important earlier and later stages has enabled me to study the placentation of *Perameles* in some detail, and the results of this investigation are presented in the following pages. I am now able not only to amplify the short statement of the preliminary note, but to give a fairly connected account of what I believe are the most important phenomena in the evolution of the *Perameles* placenta. I am also now able to state that an allantoic placenta in all respects similar to that of *P. obesula* occurs in the closely related *P. nasuta*. The stages described consecutively in the following pages have been derived from these two species indifferently, just as pregnant individuals chanced to come to hand; but so far as I have been able to make out, there are no recognisable differences in the details

of the development in the two forms. Even now, after nearly two years' collecting, the material at my disposal is by no means large. It comprises altogether six stages, of which two are post-partum. I take this opportunity of acknowledging my great indebtedness to the following gentlemen for most generous aid in the by no means easy task of securing the material on which this paper is based:—Messrs. J. B. Cooper, A. G. Hamilton, A. M. Lea, Thomas Steel, and Dr. A. E. Mills. To all these gentlemen I tender my sincere thanks.

To my friend Professor J. T. Wilson I am under a very deep debt of gratitude for invaluable help in the way of suggestion, criticism, and advice during the whole course of my work. I am also indebted to my friend Professor C. J. Martin for much kind advice.

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Lastly, I desire to thank my honoured chief, Professor W. A. Haswell, F.R.S., for his uniform kindness and consideration, and for much kindly interest in my work.

Methods.—As fixing fluids picro-sulphuric and picro-nitric acids were used. Most satisfactory staining results were got by staining sections fixed on the slide by Mann's albumen method, first with a weak watery solution of Renaut's hæmatoxylic glycerine for eighteen to twenty-four hours, followed by an alcoholic solution of eosin. Even better results were obtained by the substitution of hæmatëin for hæmatoxylin in Renaut's formula. By this method of double staining the foetal and maternal vessels can be beautifully differentiated.

GENERAL SUMMARY OF RESULTS.

BEFORE entering upon the detailed description of the various stages, it may conduce to clearness if a brief résumé of the main facts of placental development be here presented.

I. CHANGES IN THE UTERINE WALL.

The mucosa undergoes marked hypertrophy over its whole extent; the uterine glands increase both in transverse diameter and in length; the interglandular connective tissue forms a loose open network of anastomosing cells, and becomes permeated by abundant lymph; the vessels of the mucosa increase greatly in size and in number. These changes in the corium are accompanied by the transformation of the whole of the uterine epithelium into a vascular syncytium. This is ushered in by the disappearance of the cell outlines between the cells and the active proliferation of the nuclei. The uniform nucleated syncytial layer thus produced increases in thickness by the growth of the protoplasm; the nuclei also increase in number, and eventually become, in greater part, grouped together in nests, situated in lobular projections of the deeper surface of the syncytium. At the same time maternal capillaries pass up between the syncytial lobules, penetrate the syncytial protoplasm, and form a network on and just beneath its surface.

The uterine wall is now prepared for the attachment of the embryo.

II. EMBRYONIC CHANGES.

(A) Fixation of the Embryo.—(1) The embryo becomes attached to the maternal syncytium by means of the enlarged ectoderm cells over the discoidal area of true chorion with which the allantois fuses. The ectoderm, when the attachment is complete, consists of a single layer of greatly enlarged cells, roughly cubical or columnar in shape. Their irregular outer ends accurately fit into the irregularities of the surface

of the syncytium, and are firmly adherent thereto. In correlation with this close adherence of the chorionic ectoderm, this area of the uterine syncytium is markedly thicker than the remainder, and forms the allantoic placental area. In the allanto-chorionic mesenchyme, and in close relation to the inner surface of the chorionic ectoderm, run the allantoic capillaries. (2) Outside the discoidal allanto-chorionic area a somewhat annular zone of the yolk-sac wall is also brought into intimate relation with the maternal syncytium around the above-mentioned allantoic placental area, by means of a close approximation of its exceedingly thin ectodermal cells. This annular zone of yolk-sac wall corresponds to the embryonic vascular area, and at this stage the portion of the syncytium in relation to it is more highly vascular than the allantoic placental syncytium itself. This structural arrangement can hardly be considered other than a yolk-sac placental formation, functional at a time when the allantoic placenta is yet only being formed.

(B) Formation of the Functional Allantoic Placenta.

—This is brought to pass through the gradual degeneration and resorption of the enlarged chorionic ectoderm cells over the placental area proper. These cells thus take no further part in placental formation. The allantoic capillaries can now directly reach the vascular surface of the allantoic placental syncytium, to which they become intimately attached, dipping down into the depressions in its surface, and forming in places a regular interlocking system. The foetal and maternal blood-streams are now only separated by their thin endothelial walls, and perhaps a thin layer of syncytial protoplasm.

III. PARTURITION.

At birth not only is there no loss of maternal tissue (i.e. no decidua is formed), but the vesicular portion of the allantois remains persistently attached to the placental syncytium, and is gradually absorbed in situ along with the latter through the agency of maternal leucocytes.

The foetus, whilst still connected with the placental area by

the lengthened allantoic stalk, passes to the exterior, not by way of the lateral vaginal canals, but by breaking through along a median track leading backwards from a posterior common portion of the two uteri.

DESCRIPTION OF STAGES.

Structure of the Non-pregnant Uterus.

The uterine wall is shown in transverse section in fig. 1. Externally is the fairly thick serosa (*s.*) continued on from the ligamentum latum. Internal to the serosa is the muscularis, composed of circularly running non-striate fibres (*c. m.*). The mucosa (*m.*) follows immediately on the muscularis, and is on the whole sharply marked off from the latter; occasionally, however, the terminal ends of the uterine glands may penetrate into the muscularis.

The mucosa varies considerably in thickness in different uteri, averaging about .75 mm. Its free surface is thrown into irregular longitudinal folds. The matrix of the mucosa consists of fairly compact retiform connective tissue (*c. t.*), in which are embedded the uterine glands and blood-vessels.

The uterine glands (*gl.*) are very numerous, straight or greatly convoluted tubules, averaging .045 mm. in diameter. They are lined by a low columnar epithelium, outside of which is a thin tunica propria derived from the surrounding connective tissue. They open freely into the uterine lumen.

The blood-vessels enter the mucosa from the circular muscularis. The majority of the superficial vessels of the mucosa are of the nature of capillaries, with only an adventitious layer of connective tissue surrounding the endothelium; in the deeper portions of the mucosa, however, vessels with distinct muscular walls also occur.

The lining epithelium of the uterus (*ep.*) consists of a layer of low columnar cells with a thickness of about .015 mm., and continuous with the lining epithelium of the glands at the gland openings.

STAGE A.—P. NASUTA.

Both uteri were somewhat enlarged, and presented a congested appearance. In the right uterus an early blastocyst was found.

The wall of the blastocyst was separated on one side from the enclosing membrane (Selenka's "granulosa membran" [2], Caldwell's shell membrane [3]) by a space, and had a transverse diameter of .525 mm.; while, including the investing membrane, the whole blastocyst had a diameter of .675 mm. This blastocyst has not yet been examined in sections, but it probably nearly corresponds to a ten hours' blastocyst of *Didelphys*, which, according to Selenka (2), has a transverse diameter of about .5 mm.

Microscopical examination of the right uterine wall shows that as a whole it has increased considerably in thickness as compared with the non-pregnant uterus. This increase is mainly due to the enlargement of the mucosa, which now averages 1.5 mm. in thickness.

The uterine glands are closely packed together, causing the interglandular connective tissue to appear greatly reduced. They have increased both in length and in transverse diameter, the latter now averaging .075 mm., and their epithelial lining has undergone marked proliferation. It now consists of a high cylindrical epithelium with numerous small deeply staining nuclei basally situated. The meshes of the connective-tissue network are occupied by lymph coagulum, and numbers of somewhat enlarged capillaries are also present, but as yet in no great abundance.

The most important change in this uterus, however, concerns the lining uterine epithelium. Through the disappearance of the cell outlines between the cells, it has become transformed into a continuous protoplasmic layer or syncytium all over the surface of the mucosa (fig. 2, *syn.*), and at the same time it has increased somewhat in thickness, now measuring .025 mm.

Along with this fusion of the cell bodies, the nuclei have

undergone active proliferation. They now form an irregular band occupying the mid region of the syncytium, and are so numerous as to frequently overlap even in very thin sections (fig. 2). They vary considerably in shape, mostly ovalish or elongated, and are evidently in a most active phase. Though I have not been able to make out undoubted mitotic figures in my preparations, there can be no doubt that marked proliferation of the syncytial nuclei has taken place.

Minot's description (4) of the early changes taking place in the uterine epithelium of the rabbit prior to its complete degeneration is equally applicable to *Perameles*. He says "the thickening [of the uterine epithelium] is due to the enlargement and fusion of the epithelial cells, and this enlargement of the cells is due to the proliferation of the nuclei, and to the growth of the protoplasm which begins later, and continues longer (as later stages show) than the multiplication of the nuclei." It may be pointed out, however, that the agreement in the two cases goes no further than the earliest stages. As we know from the researches of Minot (4), Duval (5), and others in the rabbit, this nucleated protoplasmic layer formed from the uterine epithelium soon degenerates and disappears; in *Perameles*, on the other hand, as will be abundantly evident further on in this paper, the syncytial layer derived from the uterine epithelium not only does not degenerate, but, increasing in size and becoming vascularised by maternal vessels, persists throughout the whole period of pregnancy, and takes a most essential part in placental formation.

STAGE B.—*P. OBESULA*.

The left uterus was somewhat larger than the right, measuring 17 mm. in length by 11 mm. in breadth. It contained two blastodermic vesicles, with the "granulosa membran" of Selenka still in greater part persistent round them. The embryo measures about 7 mm. in length, and possesses at least fifteen mesodermal somites. It is characterised as follows:—Anterior end strongly flexed and enclosed in the large pro-amnion; medullary plate in anterior cerebral region still

unclosed, but just closed in trunk region; distinct sinus rhomboidalis enclosing primitive streak; fore-limb buds; median heart anlage; blood circulating; distinct auditory grooves.

Both uteri were examined microscopically, and were found to have undergone exactly the same changes. It may here be noted that such changes as have occurred are not limited to any special region of the mucosa, but occur uniformly all over it.

The general appearance of the uterine wall under a low power is shown in fig. 3. Owing to the enlargement of the uterus as a whole, the serosa and muscularis appear to be somewhat thinner than in the preceding stage. The mucosa is approximately of the same thickness as in that stage, but has altered considerably in appearance. The uterine glands (fig. 3, *gl.*) are now for the most part widely separated from each other, and the interglandular connective tissue appears greatly attenuated. It consists of a very delicate retiform tissue, and is permeated by abundance of lymph coagulum, while numerous leucocytes are also distributed through it.

The glands appear the same as in the preceding stage. The mucosa is now much more vascular than in Stage A. The syncytial lining of the uterus has undergone further enlargement and differentiation. The layer has an average thickness of .035 mm., i. e. it is somewhat thicker than in Stage A. Further, its inner surface is now found divided up into a series of numerous close-set lobular projections of somewhat irregular size (fig. 4, *syn. l.*). The greater number of the syncytial nuclei are disposed in relation to these lobules, in many cases filling them completely, in other cases forming an irregular layer in the marginal protoplasm of the lobule. Scattered nuclei also occur in the superficial portion of the syncytium, but not abundantly. Like the syncytial protoplasm, the ovalish or rounded nuclei stain deeply. They now present the appearance of typical resting nuclei, a fact which suggests that the further enlargement of the syncytium is not to any great extent at least accompanied by active division of the nuclei.

Another highly significant fact in connection with the syncytium is that it is already vascularised. Both between the lobules and enclosed in the protoplasm of the syncytium itself small capillary vessels, with distinct nucleated endothelial walls and containing maternal blood-corpuscles, can be readily made out (fig. 4, *syn. c.*). These syncytial capillaries are derived from the capillaries of the mucosa, which are seen to pass up between the syncytial lobules, and from there to ramify out in the syncytium itself. That the capillaries actually penetrate into the syncytium by their own growth seems beyond question, but no doubt the subsequent gradual enlargement of the syncytium as a whole, and especially of its lobules, also aids in bringing about the enclosure of the capillaries.

We can only regard the formation of the syncytial lobules as the result of the enlargement and growth of the protoplasm, and it seems probable that the direct invasion of the syncytium by ingrowing capillaries may have been the inciting cause of this mode of growth.

This transformation of the uterine epithelium into a vascular syncytium is a highly distinctive and peculiar feature in the developmental history of the placentation of Perameles. Such a condition has hitherto never been met with in any other mammalian form, and is especially interesting in view of the wide-spread occurrence of degeneration of the uterine epithelium prior to placental formation in so many diverse Eutherian orders. The only form known to me which in the behaviour of its uterine epithelium offers any points of analogy with the above-described transformation of the epithelium in Perameles is Sorex. Hubrecht has shown that, in this Insectivore, modification of the uterine epithelium over the placental area, by way of proliferation, is the first and most important change "that takes place in the maternal tissues preparatory to the reception, fixation, and nutrition of the blastocyst" (7, p. 491). But when one compares the details of the proliferation in the two cases they are seen to be essentially different in character, though offering interesting analogies. In Sorex, following

Hubrecht's account, we have to do with a proliferation of cells from the under surface of the uterine epithelium. These proliferated cells eventually form crypts, between which vessels penetrate. The crypts, however, play only a temporary rôle in the formation of the placenta, and take no ultimate part in its development.

In *Perameles*, on the other hand, we have to do not with a proliferation of cells, but of nuclei in a continuous syncytial layer; and what is more important is the fact that here this transformed epithelium persists to form the maternal portion of the functional placenta.

STAGES C AND D.

General Account of the Fœtal Membranes.

Before proceeding to the detailed consideration of Stages C and D, it is advisable here to give a general account of the fœtal membranes, so far as they can be made out from these two stages.

In *Perameles* the fœtal membranes have the same general arrangement as in *Phascolarctus*, my two stages exhibiting characters corresponding to the stages described and figured by Caldwell (12) and Semon (8).

Owing to the mode of growth and the development of an exceedingly voluminous proamnion the embryo is found, at the stage when the amnion is complete, sunk down into the cavity of the yolk-sac, and partially surrounded by the upper portion of the yolk-sac wall (text fig., *y. spl.*), which is thus invaginated into the yolk-sac cavity. Semon distinguishes this invaginated portion of the yolk-sac wall (or briefly "yolk-sac splanchnopleure") simply as "inneres Blatt."

The space in which the embryo, enclosed in its amnion, lies is, of course, the extra-embryonic splanchnocœle (text fig., *cœ.*), and is closed externally by a discoidal area of true chorion.¹ It is with this discoidal area that the allantois fuses, and over it the allantoic placental connection is eventually established.

¹ We use the term chorion here in the sense specified by Minot ('Human Embryology,' p. 286), viz. the true chorion is that part of the extra-embryonic somatopleure which remains after separation of the amnion.

The periphery of this true chorionic area thus indicates the limit of extension of the cœlom, and beyond that limit chorion and invaginated yolk splanchnopleure alike merge into the

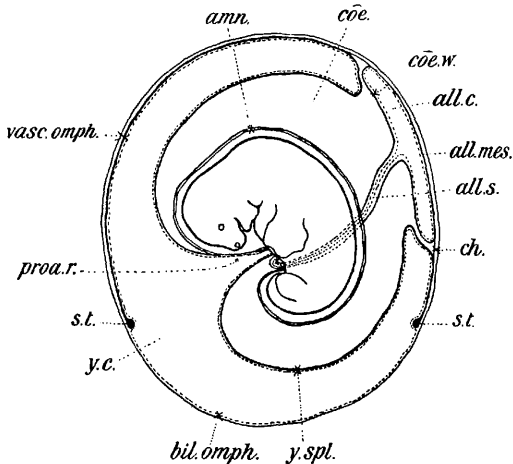


Diagram showing the arrangement of the fetal membranes in Perameles. *amn.* Amnion. *all.c.* Allantoic cavity. *all.mes.* Allanto-chorionic mesenchyme. *all.s.* Allantoic stalk. *bil.omph.* Bilaminar omphalopleure. *ch.* Marginal zone of true chorion around the allanto-chorionic area. *cœ.* Extra-embryonic splanchnocele. *cœ.w.* Inner or cœlomic wall of allantois. *proa.r.* Persistent remnant of proamnion. *s.t.* Sinus terminalis. *vasc.omph.* Vascular omphalopleure. *y.c.* Cavity of yolk-sac. *y.spl.* Invaginated yolk-sac splanchnopleure. The ectoderm is represented by a thin line, the entoderm by a dotted line, and the mesoderm by a thick line.

unsplit wall of the blastodermic vesicle or primitive yolk cavity (text fig., *vasc.omph.*). For this outer unsplit wall of the yolk-sac no very suitable name exists in the literature of embryology. Semon simply terms it "äusseres Blatt." If we restrict the use of the term chorion, as Minot has done, then such terms as "omphalo-chorion" (Fleischmann), "Dot-

tersackchorion seu pseudo-chorion" (Selenka), are open to objection. Hubrecht's term "omphaloidean diplotrophoblast" (9, p. 385) is also inadequate, since it is only properly applicable to the somatopleural constituents of the as yet unsplit yolk-sac wall. To avoid confusion it seems desirable to employ a distinctive term descriptive of this unsplit yolk-sac wall in its entire thickness and extent; and for this end I propose to adopt, at the suggestion of my friend Professor J. T. Wilson, the term "omphalopleure."

The term omphalopleure, then, signifies the whole of the wall of the blastodermic vesicle or primitive yolk-sac, beyond the region of extension of the splanchnocœle. The employment of the term omphalopleure will thus prevent the unnecessary use of the expression "blastodermic vesicle wall" in stages when the embryo is completely folded off, and one no longer wishes to speak of a blastodermic vesicle as such. According to the extension of the unsplit mesoderm the omphalopleure may be trilaminar or bilaminar in greater or lesser extent. Also a unilaminar condition may be temporarily found in a position corresponding to the lower pole of the blastodermic vesicle, prior to complete ventral extension of the yolk-sac entoderm.

In Marsupials the trilaminar portion of the omphalopleure is co-extensive with the vascular area, the sinus terminalis marking not only the margin of the vascular area, but also the peripheral limit of the unsplit mesoderm. We may thus refer to the trilaminar omphalopleure in Marsupials as the "vascular omphalopleure" (text fig., *vasc. omph.*). Beyond the sinus terminalis mesoderm is absent, and there the omphalopleure consists solely of ectoderm and entoderm (text fig., *bil. omph.*). We shall hereafter refer to this as the "bilaminar omphalopleure," which seems more expressive than Semon's term "Prokalymma" (8). We can thus distinguish in the outer wall limiting the whole spheroidal embryonic formation three areas of widely different structure: towards each pole a discoidal area,—the one limiting the extra-embryonic cœlom, and consisting of true chorion; the other limiting the yolk-sac

cavity, and consisting of bilaminar omphalopleure; between these and running round the mid region of the whole structure, a somewhat annular zone of vascular omphalopleure.

The allantois of *Perameles* consists of a long stalk (text fig., *all. s.*) and a terminal expanded and much-compressed vesicular portion. The stalk, leaving the embryo immediately behind the yolk-stalk, curves round its right side, and, extending through the extra-embryonic cœlom, expands at its distal end to form the flattened vesicular portion. In the stalk the allantoic cavity is reduced to a narrow compressed canal opening distally into the continuous cavity of the vesicular portion (*all. c.*). From the flattened form of this latter we may, for descriptive purposes, term that portion of its wall next the cœlom the inner or cœlomic wall (*cœ. w.*), and that turned towards the chorion the outer or placental wall.

In Stage C the mesoderm of the outer wall of the allantois is found fused with the somatic mesoderm of the discoidal chorionic area (*all. mes.*), the enlarged ectodermal cells of which are firmly adherent to the vascular maternal syncytium. For the chorion, after the allantois has fused with it, we shall employ the term "allanto-chorion" (Fleischmann). The allantoic vessels consist of a large vein and two smaller arteries. They extend unbranched in the stalk, and, in fact, constitute its greater bulk. At its distal end the arteries branch out on the inner wall of the vesicular portion of the allantois, while the vein is there formed by the union of two main factors which accompany the main arterial trunks. The latter branch in a dichotomous manner, each of the larger arterial branches being accompanied by a corresponding venous channel. This arrangement is, however, as Fleischmann (10) has pointed out for the cat (cf. his fig. 7, Taf. iv), confined to the larger trunks; the finer branchings do not thus correspond. These vessels ramifying on the inner wall of the allantois pass round the margin of the allantoic vesicle into the allanto-chorionic mesenchyme of the outer wall, and there form a rich capillary network corresponding to the so richly developed network described and figured by Semon (8) for *Phascolarctus* (cf. his

fig. 38, Taf. iv). Of the vitelline vessels unfortunately I can give only a very incomplete account. In opening up the uteri in both Stages C and D the vascular area was partly destroyed, so that I can only state the course of the main trunks. As in *Æpyprymnus* and *Phascolarctus*, according to Semon's account (8), the yolk-sac is supplied by a vitelline artery and a vitelline vein.

The vitelline artery on leaving the yolk-stalk runs obliquely backwards in the yolk splanchnopleure, and finally passes over into the vascular omphalopleure, where it bifurcates into a right and left trunk, which together constitute the circular sinus terminalis (text fig., *s. t.*). From the sinus smaller branches pass off into the vascular area. Whether the two trunks actually inosculate or are only connected by capillary anastomosis I am unable to state.

The vitelline vein is formed close to the base of the yolk-stalk by the union of two main factors which arise in the vascular omphalopleure by the union of tributaries coming from the capillary network of the vascular area. These two main vitelline trunks coming from opposite sides of the vascular area pass over from the vascular omphalopleure to the yolk splanchnopleure, and there run posteriorly over the left side of the head of the embryo. They gradually approximate as they approach the yolk-stalk, near the base of which they unite to form the single vitelline vein.

The last point to which we need refer in this general account concerns the existence of a persistent remnant of the proamnion somewhat similar to the "proamnion-rest" described by Semon (8) for *Phascolarctus*. As in that form, the persistent connection between the amnion and the here non-vascular yolk splanchnopleure forms a small pear-shaped area bounded laterally by the main factors of the vitelline vein, and extending from their point of union up to about the level of the eye on the left side of the embryo. A section through this proamniotic area is represented in fig. 14. It will be seen therefrom that both the ectoderm and entoderm over the area are considerably modified.

The ectoderm (fig. 14, *ect.*) is markedly thickened, and at the margins of the area forms cushions several cells in thickness. The superficial cells often project freely, and are club-like in form, with the nucleus lying in the freely projecting part of the cell. Apparently in *Phascolarctus* such a marked thickening of the ectoderm does not exist.

The entoderm presents a somewhat varied appearance in different sections. In the section drawn (fig. 14, *ent.*) it is a quite irregular layer of some thickness. Many of its cells are greatly enlarged and vesicular-looking, presenting quite a degenerate appearance. Even in places where the entoderm over the area does not differ greatly from the entoderm of the yolk splanchnopleure, one often meets with similar isolated enlarged and vesicular-looking cells. In *Phascolarctus* Semon describes the entoderm over the area as "stark verdickt und eigenthümlich gewulstet" (8, p. 31). At the edges of the area (fig. 14) the somatic mesoderm of the amnion (*amn.*) is continuous with the mesoderm of the splanchnopleure, so that the continuity of the extra-embryonic cœlom is here definitely interrupted. The mesoderm penetrates into the area for a short distance peripherally; but, contrary to what Semon describes for *Phascolarctus*, it does not form a continuous layer extending right through and separating the ectoderm of the amnion from the entoderm of the yolk-sac. In the centre of the area these layers may be either in close apposition or separated by a narrow cleft. This central portion of the area thus consists of true proamnion.

STAGE C.—P. OBESULA.

The left uterus was very much larger than the somewhat enlarged right, and formed a large globular swelling containing a single embryo (fig. 5) with a crown-rump measurement of 7 mm. For details of the internal anatomy of this embryo see table (appendix).

This is a most important stage, since it shows the mode of attachment of the embryo. Microscopic examination of the

empty right uterus shows that it has undergone changes parallel with those undergone in the pregnant left, a vascular syncytium of some thickness having been formed all over the surface of the mucosa.

In this and the following stages I propose to describe separately (1) the changes in the uterus, and (2) the structural features of the foetal membranes and their relations to the uterine wall.

I. Left Uterus.—The discoidal allantoic placental area is situated on the ant-mesometrial side of the uterus. The uterine surface is thrown into a series of irregularly longitudinal folds, this folding being especially marked in the allantoic placental area. One may emphasise this by stating that from edge to edge of the area in a straight line the breadth in its mid region is only about 4 mm., while following the folds the allantoic placental area has a breadth in sections of 13—14 mm.

The muscularis is apparently somewhat thicker than in the preceding stage.

So far as the corium is concerned no very sharp distinction can be drawn between the portion of it lying beneath the allantoic placental area and that outside the latter. Still for descriptive purposes it is convenient to speak of these two portions separately.

The corium beneath the allantoic placental area varies very greatly in thickness over its extent owing to the greatly folded nature of the surface. Measured from the bottom of a depression between two folds the corium may have a thickness of only .6 mm., while in the region of a fold the thickness may reach as much as 2.7 mm. Outside the allantoic placental area the mucosa is not so markedly folded, and is on the whole thinner. The corium here varies in thickness from .5 to 1.7 mm. This difference in thickness is mainly due to the expansion of the interglandular connective tissue below the allantoic placental area, so that here the corium has a less compact appearance, and the glands are on the whole more widely separated from each other than in the corium outside

this area. Abundance of lymph coagulum is found throughout the meshes of the delicate interglandular connective tissue.

The uterine glands have not essentially altered since Stage B. Some few of them, however, are now enormously enlarged, and lined by a low cubical epithelium.

In the allantoic placental area the gland openings are occluded by the chorionic ectoderm cells, which at this stage form an almost continuous layer firmly attached to the surface of this portion of the syncytium. In the region surrounding the allantoic placental area the gland openings are similarly occluded by the close contact of the vascular omphalopleure with the syncytial surface.

The corium is now very richly supplied with blood; the capillaries are numerous and greatly dilated.

Syncytium.—The syncytium in this stage is found to have undergone differentiation into three fairly well-defined regions corresponding to the three areas we have already distinguished in connection with the fetal membranes, viz. the allanto-chorion, the vascular omphalopleure, and the bilaminar omphalopleure. The area of the syncytium to which the enlarged ectoderm cells of the allantochorion are attached we shall term the allantoic placental syncytium, as distinguished from that portion of the syncytium in relation to the omphalopleure.

(a) **Allantoic Placental Syncytium.**—This is at once to be distinguished from the remainder of the syncytium, not only by the fact that the chorionic ectoderm is at this stage firmly adherent to it, but also by the facts of its greater thickness, and the larger size and deeper staining qualities of its nuclei (figs. 6 and 7, *pl. syn.*). It has now an average thickness of 1 mm., i.e. it is just about three times as thick as the syncytium in Stage B.

The outer surface of the layer is not smooth, but wavy and irregular, while its inner surface is distinctly lobulated. The large and deeply staining ovalish or rounded nuclei are for the most part closely aggregated together in nest-like groups in

the deeper lobular zone of the syncytium, while scattered nuclei also occur in its superficial portion just as in Stage B (figs. 7 and 8, *pl. syn.*).

The syncytium is now much more vascular than in Stage B, numbers of enlarged capillaries with distinct endothelial walls occurring throughout the protoplasm. As in Stage B, the capillaries are found to enter the syncytium between the lobules. They pass mainly into its superficial zone in order there to ramify just beneath its surface, clothed at this stage by the chorionic ectoderm.

(b) Syncytium beyond Allantoic Placental Area.—The allantoic placental syncytium at its margin becomes greatly reduced in thickness, and continues on as the syncytium in contact with the vascular omphalopleure (fig. 6, *ex. syn.*). Here it has a thickness of about .05 mm. It has essentially the same characters as the allantoic placental syncytium. The nuclei are, however, smaller, and stain somewhat less deeply. They are, as a rule, aggregated in nests in the lobules, though here and there they tend to become more irregularly distributed throughout the protoplasm.

What, however, specially characterises this portion of the syncytium in contact with the vascular area is the richness of its blood-supply. At this stage it is distinctly more vascular than the allantoic placental syncytium. The capillaries form a rich network just beneath and upon its irregular free surface (fig. 6, *syn. c.*). The significance of this fact will be pointed out later, in connection with the description of the vascular omphalopleure.

Beyond the sinus terminalis, where the syncytium is in contact with the bilaminar omphalopleure, it is on the whole just about half as thick as over the vascular area. Here, though the characteristic arrangement of the nuclei in nests is still to be seen, the nests are small and inconspicuous, and are often separated by fairly wide intervals, in which the nuclei are irregularly distributed in the protoplasm (fig. 6). The nuclei are similar in size and in staining properties to those of the syncytium in contact with the vascular area. The vas-

cularity of this region is considerable, but much less so than in the syncytial region in relation to the vascular omphalopleure.

II. FETAL MEMBRANES.—(a) Chorionic Ectoderm.—The ectodermal cells of the discoidal area of allanto-chorion are at this stage found firmly adherent to that portion of the syncytium we have already described under the term allantoic placental.

The chorionic ectoderm consists of a single layer of irregularly columnar or cubical cells, of large size and with large ovalish or rounded deeply staining nuclei (figs. 6, 7, and 8, *ch. ect.*). The layer is on the whole sharply marked off from the underlying syncytium by the fact that the protoplasm of the ectoderm cells stains much less deeply than the syncytial protoplasm. The outer ends of the ectoderm cells project quite irregularly, and are found to be accurately adapted to the irregular syncytial surface, dipping down into and filling up every little depression in its surface. The connection, then, between the chorionic ectoderm and the underlying syncytium is of the closest and most intimate character. Such close and accurate apposition could only have arisen through a mutual process of growth and enlargement, affecting both the ectoderm cells themselves and the underlying syncytium.

So far the above description of the chorionic ectoderm would apply to the whole of that layer in a stage slightly earlier than the one under consideration. In this latter, however, the ectoderm is not uniform in character over its whole extent, since over certain portions of it degenerative processes have already set in. Such a portion is represented in fig. 9. It will be there seen that the ectoderm no longer forms a continuous and uninterrupted layer of fairly regular cells, but is irregular and definitely interrupted on the right side of the figure, thus allowing the allantoic capillaries to come into direct contact with the vascular syncytium. A comparison of the chorionic ectoderm in fig. 8 (*ch. ect.*) with that shown in this fig. 9 will render at once apparent the marked changes which have taken place in the characters of the cells. Here they are

of a very varying size and shape, and in places, through the disappearance of the outlines between adjacent cells, large multinucleate cells have been formed. The protoplasm of these degenerating cells often stains just as deeply as that of the syncytium, rendering it difficult to determine accurately the limit between the two. In many of the ectoderm cells, shown in fig. 9, the nuclei are also seen to be in various stages of disintegration. Many of them stain only slightly; the nuclear membrane is becoming indistinct, while the chromatin is found broken up, and diffused in the form of small granules throughout the delicate nuclear reticulum. Eventually the position of the nucleus is only marked by a few straggling irregularly thickened remnants, which finally become diffused throughout the protoplasm, and lost to view.

It may be noted that degeneration does not take place in a uniform manner over any given area, but quite irregularly in patches, so that in a small portion of the allantoic placental area (as in fig. 9) various stages in the degenerative process are met with. In certain portions of the chorionic ectoderm where it still forms a continuous layer of fairly regular cells, and shows no signs of the degenerative process just described, I have found that the inner ends of the cells are greatly vacuolated, a fact which suggests that a process of vacuolation may also play a rôle in the retrogression of the chorionic ectoderm.

That the chorionic ectoderm is destined to disappear is abundantly evident from this stage alone, and I am inclined to believe that the allantoic capillaries, so closely related to its inner surface, are by no means the least active agents in effecting its removal. Of direct fusion of the degenerate ectoderm with the syncytium there can be no question. All the facts negative such a view.

The rôle of the ectoderm is apparently merely that of attaching the embryo to the previously prepared maternal syncytium. Once the allantoic capillaries have spread out on its inner surface, it degenerates and disappears in order to allow of closer proximity between the fetal and maternal

capillaries, and thus takes no part in the constitution of the functional placenta.

(b) Allantois and Mesenchyme of Allanto-chorion.—The allantoic stalk is ovalish in cross-section (fig. 10), measuring in long diameter .3 mm., and in short .18 mm. In it run the three allantoic vessels, two smaller arteries (*all. a.*), and a larger vein (*all. v.*). The vessels are lined by a delicate endothelium, round which the mesoderm is condensed to form a thin sheath. Lying in the mesenchyme between the two arteries is the small canal of the stalk (*all. cl.*) lined by a layer of somewhat flattened entoderm. The stalk is covered externally by a layer of mesothelium, internal to which and forming the matrix of the stalk are branched mesenchyme cells.

The stalk enters the body of the embryo behind and to the right of the intestinal loop to which the yolk-stalk is attached, and has the usual relations; i. e. the stalk, now consisting of the entodermal canal and the two arteries, passes back in the median line attached to the inner surface of the ventral abdominal wall, and its canal finally opens into the cloaca. In the abdomen and close to the body of the embryo, the entodermal lining of the canal consists of a low cubical epithelium. At its distal end the stalk expands into the flattened vesicular portion of the allantois, the canal of the stalk being in direct continuity with the cavity of the vesicular portion (fig. 11). This latter is an exceedingly thin-walled sac, possessing a continuous cavity of very irregular form (fig. 7, *all. c.*). The inner or cœlomic wall of the allantois (fig. 7, *cœ. w.*) is fairly smooth and unfolded, but its outer wall has grown out into great hollow folds which enter the deep depressions of the uterine surface, and thus is of far greater extent than the inner wall.

The allantoic cavity is lined by a very thin layer of entoderm with small flattened or ovalish nuclei (fig. 7, *all. ent.*). The mesoderm covering the inner wall (fig. 7, *cœ. w.*) consists only of a thin mesothelial layer, except along the vessels. The mesoderm of the outer allantoic wall is now organically con-

tinuous with the somatic mesoderm of the chorion, forming the allanto-chorionic mesenchyme. This is, at this stage, an exceedingly thin layer, which becomes somewhat thicker at the margin of the allantoic placental area and around the larger allantoic capillaries (figs. 6, 7, and 8, *all. mes.*). The mesenchyme consists of small branched cells, the delicate processes of which anastomose with each other, and with the entodermal lining of the allantoic cavity. I find that the allantois of a late uterine embryo of *Macropus dorsalis* shows essentially the same structural features as the vesicular portion of the allantois of *Perameles*, only in the *Macropus* embryo the vessels are less marked; and there is, of course, no union with the chorion. In both cases the allantoic wall is characterised by its extreme tenuity.

In the inner or cœlomic wall of the allantois, between the mesothelium and the entoderm, run the main branches and factors of the allantoic arteries and vein. Corresponding to their characteristic mode of branching, one finds in sections the larger trunks in pairs, a smaller and slightly thicker walled arterial trunk accompanied by a larger venous channel. In the inner wall the vessels have distinct thin sheaths of condensed mesenchyme. In order to reach the outer surface of the allantois these vessels, ramifying in the inner wall, turn round the periphery of the flattened vesicle. Seeing the allantoic cavity is a continuous and uninterrupted one, there are no direct passages across the cavity by means of cellular bridges, as Hubrecht describes for the allantois of *Erinaceus* (9). The vessels of the inner wall gradually decrease in size by repeated branchings as they approach the periphery of the vesicle, their mesodermal investing sheath becomes reduced to a layer a single cell thick, and they pass round into the allanto-chorionic mesenchyme. There they again branch repeatedly, forming a network of small capillaries, with only endothelial walls. The ultimate branches of this capillary system come into very close contact with the inner surface of the chorionic ectoderm, and even in places where cells of the latter have disappeared, into contact with the vascular maternal

synectium (fig. 9). The true chorion at the margin of the allantoic placental area yet remains to be mentioned (text fig., *ch.*). It will be seen from figs. 6 and 7, representing sections through the opposite margins of the allantoic placental area, that the allantois does not at this stage completely extend over the whole of the chorionic area, but leaves outside its periphery a narrow marginal zone of true chorion, which intervenes between the allanto-chorion and the vascular omphalopleure.

On the one side (fig. 6) the allantois does not even extend completely to the outer limit of attachment of the chorionic ectoderm, but leaves here a marginal attached portion of true chorion. On the other side (fig. 7) the margin of the allantois corresponds fairly accurately with the outer limit of attachment of the chorionic ectoderm, so that here only a narrow strip of free chorion remains. On both sides the ectoderm cells of this marginal chorionic zone become gradually reduced in size, and pass over into the thin ectoderm of the vascular omphalopleure. Closely adherent to the inner surface of this transitional chorionic ectoderm is the thin single layer of somatic mesoderm of the chorion (figs. 6 and 7, *som.*), continuous on the one side with the allanto-chorionic mesenchyme (*all. mes.*), and on the other with the mesoderm of the yolk splanchnopleure (*y. spl.*).

(c) Yolk Splanchnopleure.—The line along which the somatic mesoderm of the chorion is continuous with the mesoderm of the yolk splanchnopleure marks the outer limit of the splanchnoceles (figs. 6 and 7, *cæ.*), and thus also the commencement of the vascular omphalopleure (*vasc. omph.*). The mesoderm of the yolk splanchnopleure is a thin layer, carrying fairly numerous vessels, except in that portion of it included between the two main factors of the vitelline vein, which is, as Semon has pointed out (8), permanently non-vascular. Its ectoderm is similar to that of the vascular omphalopleure.

Traced round to its connection with the embryo, the yolk splanchnopleure narrows to form the yolk-stalk, or vitelline duct, which opens into the gut at the apex of the intestinal loop.

(*d*) Vascular Omphalopleure and Yolk-sac Placenta.—The vascular omphalopleure includes, as already pointed out, the area of the yolk-sac wall between the periphery of the true chorion and the sinus terminalis, and is co-extensive with the vascular area. Its entoderm (figs. 6 and 7, *vasc. omph.*) consists of a fairly thick, somewhat flattened layer of varying width, with oval or rounded nuclei staining deeply like the protoplasm. The unsplit mesoderm is a thin and delicate layer carrying the very numerous capillaries of the vascular area.

The ectoderm is especially noteworthy on account of its extreme tenuity (fig. 6, *ect.*). It consists of a delicate thin layer of mostly flattened cells with small oval or fusiform nuclei. Here and there at intervals, cells of a somewhat triangular shape are found, with their outer pointed ends projecting beyond the level of the general surface of the ectoderm.

In Didelphys, according to the descriptions both of Osborn and Selenka, the ectoderm of the vascular omphalopleure is a much thicker layer than in Perameles. Osborn describes it as consisting of "elongated cells with amœbiform processes which are closely applied to the lining epithelium of the uterus" (11, p. 378; cf. also his fig. 4, Pl. xvii); and Selenka, describing the layer in a $7\frac{3}{4}$ days' embryo, says (2, p. 137), "Bei weitem der grösste Theil dieser Ektodermzellen dehnt sich aus und nimmt blasige Form an, unter gleichzeitiger Vergrösserung der Kerne (Taf. xxviii, fig. 5, *d.*). In diesem Felde von blasigen Zellen bemerkt man gegen Ende der Incubation vereinzelte Fleckchen kleiner nahezu kubischer Ektodermzellen (*c* und *a*) und hier und da sah ich an Schnitten sogar Andeutung von Zottenbildung (*b*) mit axialen Mesodermzellen." Again, in a 5—6 days' old Hypsiprymnus he describes the ectoderm of the vascular omphalopleure in the following words (2, p. 184):—"Doch zeigten sich die Ektodermzellen des Chorion auffallend vergrössert und gegen die Uterushöhle Zapfen-oder kuppelartig vorgewölbt (Tafel xxxii, Figur 2)." Caldwell, again, referring presumably to Phasco-

larctus, says (12, p. 657), "The whole vascular area is covered by flat cells of the subzonal membrane." In a uterine embryo of *Macropus ruficollis* at a stage slightly later than the one of *Perameles* under consideration, I find that the ectoderm of the vascular omphalopleure consists of a fairly thick flattened layer, which more nearly resembles the ectoderm of the vascular omphalopleure of *Perameles* than the ectoderm of the same.

So far, then, as the forms mentioned are concerned, it appears that the extreme thinness of the ectoderm of the vascular omphalopleure in *Perameles* is an exceptional and noteworthy feature. A glance at fig. 6, which includes the whole of the extent of the vascular omphalopleure on one side, will show that, although the latter is separated in sections from the syncytium, there is an accurate and fairly close correspondence between the two, elevations in the one corresponding to depressions in the other, and vice versa. The vascular omphalopleure, in other words, appears moulded to fit the irregular surface of the maternal syncytium, and without doubt during life the two surfaces were accurately apposed the one to the other, the above-mentioned projecting ectoderm cells even serving as an actual attachment. It has already been pointed out that the portion of the syncytium in relation to the vascular omphalopleure possesses a very rich network of maternal capillaries, on and just beneath its surface, and that at this stage it is even relatively much more vascular than the allantoic placental syncytium. The foetal capillaries of the vascular area are thus only separated from the maternal by a thin and delicate ectodermal layer, plus a thin layer of syncytial protoplasm, the latter often absent indeed where the maternal capillaries actually reach the surface.

These facts point to the conclusion that, prior to the period of functional activity of the allantoic placenta, the placental function is subserved by the close contact of the vascular omphalopleure with the vascular maternal syncytium, an arrangement which we are therefore justified in designating as an actual yolk-sac placenta.

That the yolk-sac placenta is of high functional importance in the nutrition of the embryo at this stage is borne out not only by the fact that the vitelline vein is nearly three times as large as the allantoic, but also by the further fact that the larger proportion of the purified and food-laden blood coming from the vascular area passes directly to the heart. So far as one can judge from structure alone, this veritable yolk-sac placenta of *Perameles* appears to be more efficiently adapted for respiratory and nutritive functions than the arrangement found in other described Marsupials; e. g. in Macropods the ectoderm of the vascular omphalopleure is a comparatively thick layer, the uterine epithelium persists, though in a somewhat modified form, and the maternal capillaries existing below it are not very numerous, and nowhere directly project on the free surface.

(e) Bilaminar Omphalopleure.—Beyond the sinus terminalis (fig. 6, *s. t.*) mesoderm is absent, the wall consisting here solely of ectoderm and endoderm, for the most part in close contact with each other.

The endoderm is, on the whole, slightly thicker than that of the vascular omphalopleure. It consists of a layer of cells of varying size and shape, so that its inner contour is somewhat irregular (fig. 6, *bil. omph.*, and fig. 12, *ent.*). In places the endoderm cells present a vacuolated appearance.

The ectoderm differs markedly from that of the vascular omphalopleure. It is a very much thicker layer, the cells are large, rich in protoplasm, and vary greatly in form and size. Their outer ends project more or less freely in a quite irregular manner, so that the free surface of the layer presents a roughened irregular appearance (fig. 6, *bil. omph.*, and fig. 12, *ect.*).

Like Semon, I see no evidence in sections of the existence at this stage of "pseudopodia-like" processes of these ectoderm cells, such as Caldwell (12) describes as serving to attach the blastodermic vesicle to the uterus.

The significance of the persistence of this bilaminar portion of the omphalopleure for a longer or shorter period in dif-

ferent mammals has been already discussed by Semon (8). He has come to the conclusion that it has an important physiological meaning; in his own words (p. 55), "hier erfolgt eben der Durchtritt der von der Mutter gelieferten Nahrungstoffe in das Innere des Dottersacks, von wo aus weiterhin die Aufnahme und Uebergabe an das Blut durch die Entodermzellen der gefässhaltigen Zone ausgeführt wird." We may, however, point out that in *Perameles* only a small proportion of the uterine secretion need take this indirect way of reaching the vessels of the vascular area. By far the greater proportion of the secretion, no doubt, passes directly through the thin ectoderm of the vascular omphalopleure into the yolk-sac vessels.

STAGE D.—P. OBESULA.

Upon the examination of this stage was based the preliminary account already published (1). It is specially important since it shows the allantoic placenta well developed. Both uteri were greatly enlarged; the left contained two embryos, measuring respectively 8 and 8.25 mm., while the right contained a single embryo measuring 8.75 mm. from crown to rump. For the structural characteristics of this latter embryo see table (appendix).

These three embryos all present substantially the same features of placental connection. Fig. 13 represents the larger of the three embryos attached to the placental area of the uterine wall, and still partially enclosed in its membranes. The dissection from which this figure was made was prepared by opening up the uterus by a ventral longitudinal incision, which also involved the closely adherent omphalopleural wall. In the figure, then, we see the inner surface of the yolk-sac wall lying on the inner surface of the uterus, which has been spread out flat.

In the middle of the figure lies the embryo seen through the amnion and the yolk-sac splanchnopleure (*y. spl.*). At the back of the embryo and partly concealed by the body of the latter is the allantoic placental area (*pl. a.*), also seen through

the yolk splanchnopleure. The allantoic stalk with its three vessels (*all. a.* and *all. v.*) is seen to emerge from under the embryo's right side, and at its distal end the vessels spread out on what is the inner wall of the vesicular portion of the allantois. The distribution and mode of branching of the allantoic vessels is clearly shown. As already described, the vein (*all. v.*) is formed by the union of two factors which accompany the corresponding arteries (*all. a.*).

The placental area is discoid in shape and, from the presence of a prominent rim on the side visible, appears somewhat depressed below the general surface of the uterus. In sections it is found to commence a little behind the anterior margin of the flexed head end of the embryo, and to terminate some distance behind the level of its curved posterior end. Its length, in the direction of the long axis of the embryo, is thus about 9 mm., while in its middle region, following the folds, it has a breadth of about 12 mm. transversely to the long axis of the embryo.

The flattened allantoic stalk has an approximate length of 8 mm.

The course of the vitelline vessels is also shown in the figure. Leaving the yolk-stalk, the artery (*vit. a.*) passes obliquely backwards, traversing the yolk splanchnopleure (*y. spl.*) to reach the vascular omphalopleure (*vasc. omph.*), and there it almost immediately divides into two right and left branches, which form the sinus terminalis (*s. t.*), a portion of which is visible. The area outside the sinus (below) in the figure is part of the bilaminar omphalopleure (*bil. omph.*). From the yolk-stalk the two factors (*vit. v.*) of the vitelline vein pass anteriorly in the yolk splanchnopleure, and gradually diverging from each other, they pass over into the vascular omphalopleure, where they are formed by the union of lesser factors coming from the capillary system of the vascular area.

I. UTERUS.—The serosa, muscularis, and corium are essentially the same as in Stage C.

(a) Allantoic Placental Syncytium.—This presents the same general features as the corresponding area in Stage C.

but is somewhat thicker (averaging .12 mm.) than in that stage. It is also much more highly vascular (cf., e. g., fig. 15 with fig. 7). The capillaries entering between the syncytial lobules ramify in great abundance at and just beneath the surface, where they form a rich network. These superficial capillaries are large, and vary considerably in diameter, averaging about .01 mm., some attaining a width of .028 mm. The surface of the syncytium is here by no means smooth, but owing to the bulging of the capillaries on the surface it presents an irregularly ridged structure (figs. 16 and 17, *pl. syn.*).

(b) Syncytium beyond Allantoic Placental Area.—That portion of it in contact with the vascular omphalopleure forms a fairly uniform layer, averaging .09 mm. in diameter. It is thus nearly double as thick as the corresponding portion of the syncytium in Stage C, and is also rather more vascular. These facts are significant in view of what has been said above on the high functional importance of the yolk-sac placenta prior to the complete formation of the allantoic.

The superficial capillaries of this portion of the syncytium are markedly developed; many of them lie at the surface (fig. 24, *syn. c.*), which here presents a wavy contour, but is not ridged, as is the allantoic placental syncytium.

That area of the syncytium in relation with the bilaminar omphalopleure presents the same features as were described for the corresponding region in Stage C. It is, however, somewhat thicker than in that stage.

II. FETAL MEMBRANES.—(a) Chorionic Ectoderm.—The chorionic ectoderm has now almost completely disappeared. It is still, indeed, recognisable as a continuous layer of cells at the margin of the allantoic placental area (fig. 15, *ch. ect.*), but over the remainder of the latter it is represented only by more or less isolated degenerating cells (figs. 19—21, *ch. ect'*).

The persistent marginal zone of ectoderm (fig. 15, *ch. ect.*) is narrow but of very variable width. Its most peripheral cells, adjoining the ectoderm of the vascular omphalopleure, are the least altered, but the remainder are irregular, and

vary both in size and shape. A comparison of fig. 15 with fig. 7 shows at a glance the marked change in the character of the marginal chorionic ectoderm in this stage; for the process of degeneration and absorption which had set in, in the central part of the placental area in Stage C, has now extended nearly to the margin.

In connection with the disappearance of the chorionic ectoderm at this stage it may be noted that the straggling isolated cells of it which yet persist have become greatly hypertrophied. In some cases they are multinucleated (figs. 20 and 21, *ch. ect.*), or the single nucleus is also hypertrophied and vesicular (figs. 15 and 19, *ch. ect.*). Fig. 20 is worthy of remark as showing how such isolated and hypertrophied cells may be gradually undermined by the ingrowth below them of an allantoic capillary; the area of contact of the larger cell shown in the figure with the syncytium is in this way greatly reduced, while the smaller cell is entirely separated from the syncytium, and awaits its resorption in isolation in the allanto-chorionic mesenchyme.

(*b*) Allantois and Allantoic Placenta.—In its general features the allantois is essentially similar to that of Stage C. The allantoic stalk with its vessels now, however, is just about half as thick again as that of the preceding stage (cf. fig. 23 with fig. 10), thus showing that the allantoic circulation has increased considerably in volume. In correlation with this increase in the blood-supply, the capillary network (fig. 22, *all. cap.*) in the allanto-chorionic mesenchyme is now much more richly developed than in Stage C.

Now that the chorionic ectoderm has almost wholly disappeared, the capillaries are able to attach themselves closely to the syncytial surface. We have already laid emphasis on the characters of the allantoic placental portion of the maternal syncytium, and have pointed out that its surface is both highly irregular and very vascular, and in certain patches exhibits an irregular system of interlacing vascular ridges separated by depressions. With this irregularly ridged and highly vascular surface the allantoic capillaries are in most intimate contact;

so close, indeed, is the attachment that the walls of the capillaries appear as if united with the syncytial protoplasm. The capillaries dip down into and accurately fill up the depressions between the vascular ridges, so that there is here and there formed an actually interlocking system of vascular projections of the syncytial and allantoic surfaces respectively (figs. 16 and 17). As already indicated, this interlocking does not occur uniformly all over the placental area, but varies in its degree of perfection in different places (cf., e. g., figs. 15, 18, and 19 with fig. 17). The interlocking here referred to represents the highest state of placental differentiation realised in *Perameles*.

It is thus evident that in this placental differentiation foetal and maternal elements take an approximately equal share. In the functional organ so produced, it will be noted that the foetal and maternal blood-streams are separated from each other only by the thickness of two endothelial walls, with at most the addition of a thin layer of syncytial protoplasm. We may here point out that in *Perameles*, contrary to what obtains in most other mammals,¹ the uterine glands of the placental area do not degenerate, but persist throughout the whole period of pregnancy. In this stage some of the gland openings in the placental area are still occluded by persistent portions of the chorionic ectoderm in a more or less degenerate condition; others of the openings, however, are obstructed by allantoic capillaries extending right over them (fig. 18, *gl.*). It may be that nutritive substances derived from the uterine secretion of such glands are directly absorbed by the allantoic capillaries occluding their openings.

(c) *Yolk Splanchnopleure*.—This is essentially as in Stage C. We may mention, however, that the yolk-sac cavity no longer stands in open communication with the gut, as was the case in that stage.

(d) *Vascular Omphalopleure and Yolk-sac Placenta*.

¹ Strahl (15) and Vernhout (14) describe a similar persistence of the uterine glands in the mole. According to Vernhout they are invaded by the "plasmidotrophoblast" shortly before parturition.

—The vascular omphalopleure is on the whole similar to that of Stage C. Here and there, however, the flattened cells of the entoderm give place to larger somewhat cubical cells with rounded free ends. In the protoplasm of some of these larger cells there occur vacuoles. Over the sinus terminalis and the larger vessels of the vascular area the entoderm cells are also markedly enlarged, and much more so than in Stage C. The entoderm cells in these positions are now somewhat club-shaped in form, with their enlarged ends projecting freely and containing the ovalish or rounded nuclei (fig. 24, *ent.* over *s. t.*). Selenka has already described a similar condition of the entoderm cells of this region in Didelphys. He says (2, p. 138), “Die Entodermzellen des Chorion verändern gleichfalls vielfach ihre Gestalt während der letzten zwei Tage des Foetallebens. Sie werden cylindrisch oder birnförmig, zumal in der Nähe der grösseren Blutgefässe. Streckenweise behalten sie aber ihre frühere abgeplattete Form bei oder nehmen mehr oder wenig an Volumen zu.”

The unsplit mesoderm of the vascular omphalopleure is exactly as in Stage C.

The ectoderm is, as in that stage, an exceedingly delicate layer of greatly attenuated cells (fig. 24, *ect.*). In my preparations of this stage, not only is the vascular omphalopleure very evidently stamped with the contour of the highly vascular syncytial surface, but in places the two are in most intimate attachment, thus affording support for the belief already expressed that we have here an actual yolk-sac placental connection.

In this stage, then, we regard the yolk-sac placenta as being in functional activity along with the allantoic, though now it has diminished considerably in importance, as the examination of the foetal circulation shows. The vitelline vein in this stage is both absolutely and relatively smaller than in Stage C, and now most of its blood has to pass through the capillary system of the liver before reaching the inferior vena cava. These facts, taken in conjunction with the already mentioned greater size of the allantoic trunks in this stage as compared with the

preceding, show conclusively that with the advent of the allantoic placenta the yolk-sac circulation is giving place to the allantoic. The latter, indeed, is now the predominant one; and we may add that just as, in the preceding stage, most of the blood coming from the yolk-sac placenta passed directly to the heart, so now most of the blood coming from the allantoic placenta passes by way of the left allantoic vein and the ductus venosus Arantii directly into the inferior vena cava.

The question whether the yolk-sac placenta remains functional, though in a diminished degree, throughout the whole period of intra-uterine life of the embryo; or whether, as seems likely from comparison with other placental mammalian forms, it soon after this stage gives entire place to the later appearing allantoic placenta, can only be definitely decided when further material is available. As tending to support the latter alternative, it may be pointed out here that in the next (post-partum) stage, while the allantois was still found adherent to the syncytium of the placental area, no portion of the omphalopleure was to be found in the uterine cavity. Further, the syncytium outside the allantoic placental area no longer showed a richly vascular surface, but was rapidly retrogressing, and indeed was already partly covered by the regenerating uterine epithelium. The syncytium of the allantoic placental area, on the other hand, though in process of absorption, had not altered to such a marked degree.

These facts render it probable that the omphalopleure breaks up and disappears some time before the end of intra-uterine life (cf. also next section).

Unfortunately I am unable to give any details as to the relative dimensions of the vascular area in this and the preceding stage. It may, however, be mentioned that the vessels of the vascular area in this stage are apparently not nearly so richly developed as in a Macropod embryo of about the same developmental stage.

(e) Bilaminar Omphalopleure.—This presents features tending to suggest that it is even now in process of degeneration. The ectoderm has on the whole become greatly flattened

and attenuated. This is especially noticeable close to the sinus terminalis (fig. 24, *bil. omph.*). Further out one meets with scattered projecting cells of large size and of irregular form, the protoplasm and nuclei of which stain deeply.

The entoderm has also become considerably thinner in places. Where it has not undergone attenuation the cell protoplasm is often found to be greatly vacuolated, with irregular deeply staining nuclei. Here and there, also, unaltered entoderm cells are met with either singly or in groups.

STAGE E.—*P. NASUTA* (post-partum).

The material available for this most important stage consisted of the genital organs (less the cloaca) of a female *P. nasuta*, together with two newly born young from the pouch.

The new-born young (fig. 36) had a crown-rump measurement of 14 mm., and a head length of 6 mm. For the details of their external characters and internal anatomy see table (appendix).

Both uteri were considerably enlarged: the left, the larger of the two, measured 17 mm. in length by 9 mm. in breadth; the right had a length of 16.5 mm. and a breadth of 8.25 mm.

When the uteri were opened up it was found that parturition had been recently accomplished, and that in each uterus the flattened vesicular allantois with its stalk attached was still adherent over the placental area (fig. 25, *pl. a.*). This latter formed a fairly sharply circumscribed ovalish area, bounded by an almost continuous ridge, and differed from the rest of the irregularly ridged uterine surface by its closer texture. It was situated on the dorso-mesial inner surface of the uterus, i. e. ant-mesometrially. The area measured 9 mm. in length by about 5 mm. in breadth (i. e. without following the folds). The allantoic vessels ramifying in the inner wall of the allantois could not, in surface view, be very definitely made out. Apart from the adherent allantois no other portions of the fetal membranes were encountered in the uterus.

The left uterus alone was submitted to microscopic examination.

I. UTERUS.—The serosa and muscularis are of about the same thickness as in the non-gravid uterus. The muscularis is penetrated by numerous large vessels.

As in previous stages, the whole mucosa is folded, the folds being especially marked in the placental area.

Corium beneath Allantoic Placental Area.—This portion of the corium now differs markedly in appearance and character from the remainder, being as a whole much denser and more compact-looking; and its component parts—interglandular connective tissue, uterine glands, and blood-vessels—have all undergone important modifications.

In the preceding stages we have seen that the connective tissue of the whole corium consisted of a very delicate retiform tissue. Now, however, in this region the connective-tissue cells have not only increased in number, but also very greatly in size. From the large, usually rounded, deeply staining cell bodies less deeply staining processes pass off, which anastomose with similar processes of adjacent cells to form a much coarser and closer network than that seen in preceding stages, or even in the corium outside this region in the present stage (fig. 26, *c. l'*).

There can be no doubt that we have here to do with a process of proliferation of the connective-tissue cells beneath the placental area, accompanied by their subsequent hypertrophy.

This proliferation and overgrowth of the connective tissue in *Perameles* offers interesting points of comparison with the formation of the decidual cells in the pregnant human uterus, which arise, as Minot has rendered certain, by the direct proliferation and enlargement of the anastomosing connective-tissue cells of the mucosa (4, p. 419).

Numbers of polynuclear leucocytes occur throughout the proliferated connective tissue, especially in its superficial portions immediately beneath the syncytium.

Many of the uterine glands of the placental area, and especially their peripheral portions, are now in process of marked degenerative change. Various stages in the degenera-

tive process are met with, from the first signs of alteration of the gland epithelium to the almost complete obliteration of the gland lumen, by an accumulation of cellular débris, derived from the completely disintegrated epithelial lining of the gland (fig. 26, *d. gl.*).

The deeper portions of the glands adjacent to the muscularis are on the whole less altered. The gland epithelium here still forms a distinct deeply staining layer, but it is somewhat thinner, and not quite so regular as the gland epithelium of former stages. The gland secretion not being able to pass away, owing to the degeneration and occlusion of the peripheral ends of the glands, is here often found in the lumen as a deeply staining coagulum. The mouths of the glands still open freely on the placental area. The glands would thus appear to retain their function throughout the whole period of intra-uterine development of the fœtus.

The blood-vessels also show considerable alteration. The vessel walls appear greatly thickened, and the endothelial cells have increased in size (fig. 26, *m. v.*) and proliferated, thus markedly diminishing the lumen, and in some cases occluding it completely (fig. 26, *m. v'*). In other more advanced cases the whole vessel is found to have undergone fibrous degeneration, and appears quite solid in section (fig. 26, *m. v''*). In the coagulated blood in certain of the vessels, polynuclear leucocytes are found to occur.

Corium beyond Allantoic Placental Area.—Here the corium has not undergone such marked change as that of the placental area proper.

Though in parts the connective-tissue cells have undergone a considerable amount of proliferation, yet the tissue as a whole presents the same open and loose appearance as in the preceding stages.

The glands, too, present a more normal appearance, and even where degeneration of their epithelium occurs it has not advanced to such an extent as beneath the placental area.

The blood-vessels of this region show the same essential

alterations as in the placental region. Here, however, the vessels are not nearly so numerous as in the latter.

Allantoic Placental Syncytium.—Following the folds of the mucosa in section, this portion of the syncytium has a breadth of about 9 mm. in the mid region of the placental area; it varies in thickness from .15 to .28 mm., and is thus slightly thicker on the average than in Stage D.

The syncytium here is now in active process of absorption and retrogressive metamorphosis.

The syncytial protoplasm is coarsely granular, and numerous irregular spaces and clefts occur throughout its extent (figs. 27 and 28, *sp.*). Its nuclei are much less numerous, and no longer form such distinct nest-like groups in the syncytial lobules (fig. 29). They vary very greatly in size and in shape, being often quite irregular, and occur in all stages of retrogressive change. Many of them are vacuolated and greatly hypertrophied (fig. 27).

Throughout the protoplasm great numbers of leucocytes occur. The majority of these are of the polynuclear variety, possessing oval or rounded slightly staining cell bodies, in which numbers of small deeply staining nuclei lie (fig. 27, *p. leuc.*).

It seems certain that these polynuclear leucocytes are the active agents in the absorption and removal of the degenerating syncytium, and accordingly it may be observed that the leucocytes greatly predominate in the more degenerate areas.

The placental syncytium is still vascular (figs. 28 and 29), though the superficial capillaries are now not nearly so prominent as in Stage D.

The persistence even in this advanced stage, of comparatively unaltered portions of the syncytium, shows that no essential alteration takes place in the latter from Stage D up to the time of birth, and that the features peculiar to the present stage are solely characteristic of post-partum metamorphosis.

Syncytium beyond Allantoic Placental Area.—This portion of the syncytium has undergone more marked alteration in character than the placental portion. On its deeper

surface in many places it is no longer sharply marked off from the underlying connective tissue, but there is a gradual transition from the one to the other (fig. 30, *ex. syn'*).

The small and often deeply-staining nuclei are irregularly distributed throughout the altered protoplasm, which stains deeply, and is often vacuolated. The maternal capillaries are now very greatly reduced both in size and in number. They occur quite irregularly in the protoplasm, and no longer form a superficial network (fig. 30, *syn. c.*).

Polynuclear leucocytes occur in numbers in the connective tissue immediately below the syncytium, but only sparingly in the syncytium itself.

In regions where disintegration of the syncytium is well marked, i. e. where its remains are practically incorporated with the underlying connective tissue, regeneration of the uterine epithelium has already commenced. Here, as in the human uterus, the uterine epithelium is regenerated by the growth of the gland epithelium at the openings of the uterine glands. In fig. 30 the opening of such a gland is shown, with its lining epithelium spreading out over the degenerate syncytial surface (*ex. cyn'*) to form the thin and somewhat irregular uterine epithelium (*r. ep.*), better seen in fig. 31. The regenerative process does not take place uniformly all over the surface of the syncytium in this region, but in patches, and is apparently conditioned by the stage of degeneration of the syncytium.

As we have already pointed out in connection with Stage D, it seems probable that the much more degenerate condition of this region of the syncytium, as compared with the placental, is to be correlated with the presumed early retrogression of the entire omphalopleure.

II. FŒTAL MEMBRANES.—Allantois.—The allantois is the only portion of the fœtal membranes which is found intact and persistent in the uterus. In its general relations it is essentially as in the preceding stage. Its outer wall closely follows the folds of the mucosa, and is about three times as extensive as the inner. In parts the outer wall is still closely

adherent to the irregular surface of the syncytium, while in others it has become separated from the latter (figs. 28 and 29).

The allantoic cavity (fig. 28, *all. c.*) is distinct and continuous, but its entodermal lining is no longer distinguishable. It contains here and there an irregular cellular detritus. The walls of the allantois have altered considerably in character. The inner (cœlomic) wall (fig. 28, *cœ. w.*) is somewhat thicker than the outer (*all. mes'*), and is now composed of a dense mesodermal layer, carrying embedded in it in pairs the branches and factors of the allantoic arteries and vein.

The allanto-chorionic mesenchyme of the outer (placental) wall (*all. mes'*) has also become quite compact in appearance. On its outer surface the allantoic capillaries project (figs. 28 and 29, *all. cap.*). They now contain enucleated fetal blood-cells, and can still in places be seen to fit in and adhere to corresponding depressions in the syncytial surface (fig. 29).

It will be apparent from figs. 28 and 29 that no essential change has taken place in the constitution of the placenta in the period intervening between Stage D and the time of birth.

The question whether or not the allantois is resorbed in situ is at once settled positively by the occurrence in the outer allantoic wall, and to a lesser degree in the inner as well, of numbers of polynuclear leucocytes similar to those already described as existing so abundantly in the placental syncytium (figs. 32—34, *p. leuc.*).

There is not the least doubt but that these leucocytes migrate from the syncytium into the allantoic walls. In sections the leucocytes are found not only at the surface of the syncytium, but actually in the spaces which exist here and there between the syncytium and the outer allantoic wall, and they are even to be seen just in process of entering the latter.

Absorption of the allantois has, however, not yet actively begun, still it is breaking up in portions of its extent (cf. fig. 28), and the cellular detritus in the allantoic cavity can only have arisen through disintegration of its walls.

And if, as we have seen, the fœtal portion of the placenta is

not expelled at birth, but absorbed in situ, it is obvious from the nature of the case there cannot be any shedding of maternal tissue, i. e. no decidua is formed.

The case of *Perameles* is thus in most striking agreement with the condition in the mole, where, according to the observations of Hubrecht¹ (9 and 13), "no afterbirth is shed, although the animal has a discoid placenta;" and he has further pointed out that "not only is the mole not deciduate, but that even embryonic tissue is left behind against the uterine surface, and is gradually resorbed in situ" (13, p. 117).

It is thus obvious, as Professor Hubrecht has pointed out to me (in litt.) that the term non-deciduate as long ago used by Huxley is altogether inadequate and misleading as applied to the post-partum conditions obtaining in *Talpa* and *Perameles*. In these two forms there is not only no complete separation of maternal and embryonic structures at birth (*Adeciduata*), but no maternal tissue is lost (*Deciduata*); on the contrary, foetal tissue is actually resorbed by the mother. For such a condition Professor Hubrecht suggests the term *Contra-deciduata*.

The discovery of the contra-deciduate character of the placenta of *Perameles* thus affords welcome testimony to the rightness of Hubrecht's opinion, based on a consideration of *Talpa* alone, that this contra-deciduate condition is "not a secondary modification which has arisen among mammals that were already frankly deciduate, but [is], on the contrary, a more primitive developmental phase" (13, p. 118), a view with which I am in complete agreement.

Possible Vestiges of other Foetal Membranes.—In connection with the margin of the allantois there are, in some sections, appearances which I can only interpret as greatly altered remnants of the walls of the yolk-sac. These remnants vary very greatly in their detailed relations and in their extent,

¹ Later confirmed by Vernhout (14).

and are often entirely absent in the sections. It is unnecessary to enter into details.

I would simply refer to figs. 32 and 33, and point out that from the knob-like projection (*a*) attached to the margin of the allantois (*all. m.*) there arise two cell layers, one from each side. The one (*c*) may possibly be a vestige of the yolk-sac *splanchnopleure*, while the other (*b*) may similarly be a vestige of the vascular *omphalopleure*.

Whether this be so or not the fact remains, that besides these structures no other traces of the yolk-sac were found in the uterus, and this fact, taken in conjunction with the already described greater degeneration of the syncytium outside the placental area as compared with that of the latter, renders it almost certain that the *omphalopleure* breaks up and disappears some time previous to parturition.

Finally I may direct attention to the cells marked *ch. ect*" in figs. 32 and 34, as they may possibly represent persistent marginal chorionic ectoderm cells.

Parturition.

In fig. 25 the genital organs of this stage are shown partially dissected. The left uterus (*L. ut.*) has been opened by a ventral longitudinal incision, so as to expose the placental area (*pl. a.*). The vaginal cæca (*v. cæc.*) and the bladder (*bl.*) are pushed over to the left side, and the allantoic stalk (*all. s.*) arising from near the centre of the inner wall of the adherent allantois has been traced posteriorly. It was found to pass backwards through a posterior common portion of the two uteri (common uterine canal) into what sections show to be a median cleft-like passage in the connective tissue lying between the two lateral vaginal canals. Through this median passage, or median pseudo-vaginal passage, as we may term it, it is obvious that delivery must have taken place.

At the time of making this dissection I was unaware of the existence of any median passage in *Perameles*. Owen (16, p. 683), in his short description of the female genital organs of *P. obesula*, makes no mention of such; and, indeed, in

my own dissections of non-gravid genital organs I had discovered no such median passage. I was therefore considerably surprised to find the allantoic stalk extending straight back into the connective tissue between the lateral vaginal canals, and not into one of the latter, which I had believed must serve for the passage of the young at birth in spite of the narrowness of their communications with the uterine cavities. The novel features revealed in the dissection were, however, further elucidated by series of transverse sections across the urino-genital strand¹ (fig. 25, *u. s.*), which demonstrated the existence of a slit-like passage enclosing the allantoic stalks, one from each uterus.

On investigation the stalks could be traced down the median pseudo-vaginal passage from the centre of the inner wall of the allantois for a distance of about 3 cm. They did not extend quite to the extreme posterior end of the urino-genital strand shown in fig. 25, but this is no doubt to be accounted for by tearing of the stalks in the process of removal of the genital organs. In part of their course they were found to be looped upon themselves.

In Stage D the allantoic stalk of the larger embryo measured only about 8 mm. in length, so that shortly prior to or during parturition a very considerable lengthening of the stalks must take place. The stalk no doubt becomes severed from the embryo only at the moment of birth, leaving merely an insignificant portion (in length about .5 mm.) attached at the navel of the latter (fig. 36). Similarly, in *Erinaceus*, Hubrecht (9, p. 347) has shown that "by far the longer portion" of the strand formed by the lengthened-out allantoic vessels at parturition remains attached to the afterbirth, which, though eventually shed, is found in the uterus shortly after delivery.

A section of the mid region of the urino-genital strand of

¹ This name is applied to the elongated mass of connective tissue in which are embedded the lateral vaginal canals and urethra. It is united to its surroundings by more areolar connective tissue, and is of very considerable length.

this stage is shown in fig. 35. It will be there seen that the median pseudo-vaginal passage (*med. p.*) is simply a cleft-like space in the central connective tissue of the strand, lying dorsally to the urethra (*ur.*) and between the lateral vaginal canals (*vag. l.*). Its walls are entirely formed by the connective-tissue core of the strand, and they exhibit no histological differentiation into coats, muscular or other. The passage is of somewhat varying outline, with a greatest long diameter of about 1.2 mm., and a short diameter of .6 mm. In this cleft together with the allantoic stalks there occur masses of coagulated blood (*c. bl.*), especially abundant along the dorsal portion of the passage, where indeed the clot in certain sections forms a definite ovalish mass almost as large as the allantoic stalks, and partially separated from the rest of the passage by an imperfect fibrous septum. This clot, however, is continuous anteriorly and posteriorly with that present in the main subdivision of the channel, and also with the extravasated blood so abundantly present in the surrounding connective tissue (fig. 35, *c. bl.*). The allantoic stalks (fig. 35, *all. s.*) are somewhat oval in outline, and measure .3 mm. by .2 mm. in diameter. They are now in process of histological degeneration. In the centre of each the cells appear clear and vesicular, and the nuclei are for the most part quite degenerate; marginally they stain very deeply. The allantoic vessels are either empty or are partly occupied by degenerating, mainly enucleated, foetal blood-cells, together with a granular deeply staining detritus. Their endothelial lining has disappeared, and their mesodermal wall is enucleated and fibrous-looking. In some sections the allantoic canal can be indistinctly made out, but no longer with an entodermal lining.

Direct observations of the parturition phenomena in Marsupials are by no means numerous. I know of only three accounts:—(1) Owen (16, p. 721) quotes from a paper by Rennger to the effect that in *Didelphys azaræ* the young “in gestation make the circuit of the lateral canals in which they are found to be deprived of their foetal envelopes;” (2)

Osborn (11, p. 377) records finding in *Didelphys virginiana* "the foetal membranes . . . crowded into the uterine orifices of the vaginae, which indicates that they had been detached from the embryo in the uterus itself;" (3) Stirling (17) furnishes a valuable account of the parturition in *Macropus robustus* [*Osphranter erubescens*]. He has shown that in this form the young one passes out through the median vaginal canal; and that while the ventral portion of the yolk-sac remains in the uterus, interdigitating with the folds of the mucosa, its dorsal portion, remaining attached to the foetus, becomes, as the latter passes down the median vaginal canal, drawn out into a long stalk carrying the three vitelline vessels. The two forms, wallaroo and bandicoot, thus agree in giving birth to the young through a median channel; but the median canal of the one with its definite walls is by no means homologous with the median cleft-like passage of the other; for while the former is morphologically continuous with the lateral vaginal canals, and is a true epithelially lined tube, the latter has no connection whatever with the lateral canals, at no time possesses an epithelial lining, and in fact is non-existent prior to the first parturition.

It may further be pointed out that in the behaviour of their foetal membranes at parturition the two forms exhibit an interesting parallel and contrast. In the wallaroo, while the extra-embryonic allantois has disappeared at birth, the yolk-sac remains persistent in the uterus, and is drawn out into a long cord, which remains connected with the embryo in its passage outwards. In the bandicoot, on the other hand, it is the allantois which similarly remains attached to the embryo by its stalk during its course down the median passage, and which persists in the uterus, while the yolk-sac has entirely disappeared. This parallel behaviour of non-homologous structures, by means of which nutriment is conveyed to the foetus, tends to suggest that the passage of the young outwards is a quite gradual one.

The discovery of this unique mode of parturition in Pera-

meles led to a re-investigation, by means of serial sections of the structure of the female genital organs, especially with reference to the question of the existence or otherwise of such a median pseudo-vaginal passage in virginal and non-gravid genital organs. The results of this investigation will be set forth in detail elsewhere. Suffice it here to state that in the virginal genital organs the two uteri do not open into each other posteriorly, and there is no trace of a median vaginal passage or of any epithelial or other track, which might indicate the site of a future passage of any kind whatever.

In the non-gravid organs of animals with large pouch-young, on the other hand, the median pseudo-vaginal cleft is found to exist, but it neither stands in open communication with the common uterine canal nor does it open into the cloaca. As in the post-partum stage, the passage is wholly destitute of any epithelial lining or any other specialised wall.

As to the mode of formation of this median passage in the first instance I am unable to come to any definite conclusion. It has just been stated that in the virgin the uteri do not communicate with each other posteriorly, and no median passage exists. The latter is, then, evidently formed either just before or at the first act of parturition. That the embryo should in its passage out literally bore its way through the connective tissue seems to me improbable, but at least it would seem as if the hindrance to the exit of the fœtus offered by the narrow opening of the uterus into the lateral vaginal canals was actually greater than the resistant power of the tissue between the posterior ends of the uteri, and that rupture of the latter must occur. That some such rupture does occur is evidenced not only by the appearance of the false passage, but also by the pretty extensive extravasations of blood found both in and surrounding the track followed by the fœtus during its egress, i. e. the median pseudo-vaginal passage.

It is evident that the detailed character of the phenomena of parturition, and above all the nature of the causes producing the extraordinary condition above described, can only be definitely ascertained by the examination of the genital organs

of a female immediately prior to the commencement of the first parturition. But whatever may be the precise mode of formation of the passage, this most remarkable method of getting rid of the young would seem to be without parallel in the whole mammalian class.

New-born Young.—Here¹ I need only point out that, so far as my observations (cf. appendix) go, the new-born *Perameles* does not appear to differ to any very great extent, in its degree of development, from the new-born young of undoubted non-placental Marsupials, e. g. *Didelphys*.

STAGE F.—*P. OBESULA* (POST-PARTUM).

The material for this stage consisted of the genital organs (less the cloaca) of a female with two pouch-young measuring from crown to rump 22 mm. The left uterus, the larger of the two, measured 15 mm. in length by 6 mm. in breadth.

Microscopical examination shows that the uterus has now almost completely regained the resting condition.

The mucosa, however, is just about half as thick as that of the resting uterus. The epithelium of the uterine glands has been laid down anew, and now consists of a low cubical epithelium with fairly large ovalish nuclei. The gland lumen is nearly always occupied by a finely granular coagulum, which may contain cellular constituents. The interglandular connective tissue is in parts fairly open in appearance, consisting of a network of anastomosing cells; in other parts it is quite dense and compact owing to the presence of great numbers of young connective-tissue cells.

The syncytium and allantois have completely disappeared, and the uterine epithelium now forms a continuous layer all over the surface of the mucosa. It consists of a low layer of cubical cells with rounded closely packed nuclei in a single row.

Over the greater portion of its extent the uterine surface is

¹ I hope later to return to this question, and also to consider therewith the question of the "critical period" in *Perameles* (J. Beard, 'On Certain Problems of Vertebrate Embryology,' Jena, 1896).

comparatively smooth and flat; but in a certain section on the ant-mesometrial side of the uterus it is markedly folded and very irregular in contour, owing to the presence of irregular projections of the uterine epithelium. This folded area no doubt represents the former allantoic placental area. The projecting portions of the uterine epithelium just mentioned are apparently eventually shed off into the uterine lumen, for the lumen at this stage contains a detritus consisting of maternal red blood-corpuscles, together with cellular elements evidently derived from these irregular projections. The presence of these projections is readily intelligible when one remembers how irregular was the surface of the allantoic placental syncytium.

Genital Organs.—In this stage the lumen of the common uterine canal is still continuous with the median pseudo-vaginal passage. This latter, about its mid region, measures .7 mm. in long and .12 mm. in short diameter. It now appears lined by a very delicate layer of connective-tissue endothelium, outside which the tissue is very compact and vascular, but the extravasated blood present in it in the preceding stage has now disappeared. In its middle portion the passage contains an irregular detritus consisting of red blood-corpuscles and cellular elements.

Anteriorly, just behind the point of opening of the common uterine canal into the passage, portions of allantoic stalks are found still persistent in a degenerate condition, but with the positions of the allantoic vascular trunks still recognisable. The stalks are three in number,¹—a larger one measuring in diameter .4 mm. by 3 mm., and two smaller ones with a diameter of .2 mm. each. In the region where the remains of the allantoic stalks are found, the lumen of the passage is almost completely obliterated, since the stalks are not only closely surrounded externally by a loose layer derived from the surrounding connective tissue, but are separated from

¹ The genital organs reached me with only two young. It may be that the larger and more degenerate stalk here described has persisted from a previous parturition.

each other by delicate partitions derived from the latter. The stalks now present quite a reticular appearance; the larger one stains less deeply than the other two, and has undergone marked fibrous degeneration. The nuclei are few in number, and stain deeply and homogeneously. The lumina of the allantoic vessels are occupied more or less completely by loose branching cells.

In two other sets of genital organs, one from a *P. obesula* with pouch-young measuring 4 cm., I have found similar persistent remains of allantoic stalks in the upper portion of the pseudo-vaginal passage in various stages of degeneration and absorption. It is not necessary here to describe the appearances in detail. Suffice it to say that the enucleated stalks, closely invested by a connective-tissue sheath, undergo marked fibroid degeneration, and eventually become invaded and broken up by the ingrowth of the surrounding connective tissue.

I may point out here that the existence of these remains of the allantoic stalks, blocking up the pseudo-vaginal passage, shows conclusively that the vesicular portion of the allantois must be absorbed in utero, a view already maintained on account of the presence of maternal leucocytes in it.

Concluding Remarks.

Before concluding this paper we may briefly inquire what conclusions may legitimately be drawn from the fact of the occurrence of an allantoic placenta among the Metatheria.

Has the allantoic placenta of *Perameles* been independently evolved within the limits of the Marsupial order or is it directly and genetically related to that of *Eutheria* through the common ancestry of the Meta- and *Eutheria* from an earlier diphodont protoplacental stock? In a previous paper (18) in this Journal, on the tooth development of *Perameles*, by Professor J. T. Wilson and myself, we incidentally touched upon this question, and expressed our preference for the latter of these two views; and I may here at once say that a much fuller knowledge of the details of the placentation process in

Perameles has in no whit served to weaken our previously expressed opinion.

In view of the present very incomplete state of our knowledge regarding the condition of the foetal membranes in other Australian polyprotodont Marsupials, especially in *Dasyurus* and *Myrmecobius*, and even of the precise uterine changes in *Phascolarctus* and other Diprotodonts whose foetal membranes have been examined, it is impossible to decide finally between these two views, which alone seem to us worthy of consideration. In the concluding section of the paper just referred to we presented in brief form a case in favour of the second alternative. And in this summing up we dealt with the bearings upon the case of facts relating to the dentition, the placentation, and the mammary function. Here it is proposed rather to treat shortly of those facts and considerations which, in the opinion of the writer, tend to negative the first alternative.

From the preceding account of the placentation phenomena in *Perameles* I think we may justly conclude that the processes of utero-gestation in that form are fundamentally the same as those occurring in the more generalised Eutherians. Such differences in detail as exist are, in my opinion, to be regarded either as evidences of primitiveness of type on the part of the *Perameles* placenta, or as physiological adaptations such as Hubrecht has pointed out we may expect to find in different types of placentation, in view of "the great youth of the placenta as compared with the other chief components of the organisation of a mammal" (9, p. 388).

I wish here more especially to lay emphasis on my conviction that it is just as impossible to draw a hard and fast line between the placentation phenomena as they occur in *Perameles* and in the lower Eutherians, as it is to arbitrarily mark off from each other the various types of placental formation occurring among the Eutheria themselves.

Now it seems on a priori grounds exceedingly improbable that an allantoic placenta should have been twice independently acquired, and in such a fundamentally similar manner

within the limits of the mammalian class. Such would, in our opinion, be a most remarkable instance of parallelism.

It is true that in the existence of a vascular syncytium formed from the uterine epithelium, the placenta of *Perameles* exhibits a modification of structural arrangement of a kind occurring in no other mammal. But it cannot be held that the existence of even such a unique modification gives support to the view of the genetic independence of the placenta of *Perameles*, any more than the existence of manifold and even more marked structural differences in the types of placentation occurring among the *Eutheria* themselves witnesses to their essential morphological diversity. In each of these cases alike we find the real, or at least by far the most probable, explanation in a differentiation of truly homologous parts due primarily to physiological adaptation.

It is no doubt a tempting and easy solution of the problem to regard the allantoic placenta of *Perameles* as a direct and natural advance upon such a condition of foetal membranes as occurs in *Phascolarctus* (alone, so far as is yet known, among marsupials), where, as Caldwell (12) and Semon (8) have shown, the vesicular allantois reaches and fuses with the discoidal area of true chorion, develops a rich respiratory surface, but forms no union with the uterine wall. And certainly, if the placenta of *Perameles* be an independent acquisition within the marsupial order, *Phascolarctus* would seem to present the more primitive type of arrangement of foetal membranes. As Semon (8) has pointed out, "wir haben uns nur vorzustellen, dass beim *Phascolarctus*—Typus im Bereich der Athemfläche der Allantois eine innige Vereinigung der Keimblasenwand mit den mütterlichen Geweben eintrat um auf den Urtypus der Eihüllenordnung der Placentalarier zu kommen." At the same time he makes the further important qualification, "Deshalb, weil sich bei *Phascolarctus* in der Anordnung seiner Eihüllen primitivere Zustände erhalten haben als bei den meisten anderen Marsupialieren, halte ich ihn natürlich nicht überhaupt für ein besonders primitives Beutethier, oder gar für den Stammvater der übrigen." But,

indeed, the evidence on all hands goes to show that the Diprotodontia represent a comparatively recent offshoot from a primitive polyprotodont stem. And we are entirely unable to accept the derivation of the Eutheria from a Perameles type through a Phascolarctus type, as suggested by Semon (21, p. 310). For it must ever be borne in mind that on the strength of the evidence derived from a study of dentition the whole marsupial order constitutes a well-marked natural group, exhibiting like characteristics of degeneracy from the typical and original mammalian condition. And, in this group, Phascolarctus is distinguished not by less, but by an even greater degree of retrogressive dental modification than Perameles. It therefore seems unlikely that the former should have retained unmodified more primitive embryonal nutritive arrangements than the latter. So far, indeed, as the decision of this problem can be shown to depend upon the question of the primitiveness of the general structural organisation exhibited by Phascolarctus and Perameles respectively, it can hardly be denied that the evidence at our disposal is strongly in favour of the latter to be regarded as representing a more archaic marsupial type.

It is, of course, possible that in the remote past the immediate promammalian (?) ancestors of the protoplacental stock may have exhibited a condition of the foetal membranes somewhat resembling that of Phascolarctus; but we are unable to avoid the conviction that as in dentition, so in its embryonic appendages, Phascolarctus has shared largely in the general marsupial decadence. And the fact that in all non-placental marsupials, with the single exception of Phascolarctus, so far as is known, the allantois never reaches the chorion, but remains buried in the extra-embryonic splanchnocœle as a rudimentary structure, with no respiratory function, we consider as indirect evidence in favour of our view. For, as Seleuka and Semon have pointed out, this condition is certainly to be regarded as a secondary one; and if this be so, then the admitted existence of such a process of late secondary reduction renders our view of still earlier cœnogenetic sim-

plification, to say the least, not wholly improbable. Thus, in our view, it is unnecessary to trace the placental ancestry of Eutheria back into the marsupial group. The occurrence there of a true allantoic placenta, and its absence in the majority of members of the order, do no doubt, at first sight, suggest that in this group we must find the first beginnings of the organ. But we believe that the explanation is to be found in the fact that marsupials are, after all, a markedly specialised group, and that in its conditions have obtained producing placental disappearance, just as conditions (probably identical in character) have determined the degeneration of other early nutritional arrangements, i. e. the milk-teeth. We therefore fall back upon the view that the Metatheria and Eutheria are the divergent branches of a common ancestral stock, which was not only diphyodont but also placental.

We may next inquire whether the facts and conclusions detailed in the present paper have any bearing upon the question of the condition of the foetal membranes in these primitive Placentalia.

We believe that the facts of placentation in *Perameles* most strikingly confirm and support the opinion of Balfour (19), that in the primitive types of Placentalia both the allantoic and yolk-sac vessels may have been concerned in maintaining a placental circulation. We have insisted on the fundamental similarity of the placentation of *Perameles* with that of the more generalised Eutheria; and if we select *Erinaceus* as representing a fairly generalised Eutherian type, we find that here, according to Hubrecht's account (9), just as in *Perameles*, an extensive yolk-sac (omphalopleural) placental connection is developed at an early stage, only to be replaced later by the formation of the definitive allantoic placenta, through the union of a large vesicular and vascular allantois with the non-vascular chorion. Now if we leave aside the trophoblastic differentiation in the one and the formation of a maternal syncytium in the other, the type of placentation occurring in these two generalised Metatherian and Eutherian forms is an essentially similar one. This fact can in our

opinion only be regarded as conclusive in favour of the view that from such a condition of fetal membranes as is common to these two types, Perameles and Erinaceus, phylogenetic speculation on the placenta must start. We would, therefore, attach very special phylogenetic importance to the non-separation in marsupials of the vascular omphalopleure into yolk-sac splanchnopleure and somatopleural chorion. This non-separation, ensuring, as Semon (8) has pointed out, the retention of the vessels of the vascular area in a superficial position, eminently suited for the performance of nutritive and respiratory functions, we can only regard as a physiological adaptation, and as probably the first to have been adopted on the initiation of uterine development in the common ancestors of the Metatheria and Eutheria. This condition is not "probably a purely marsupial modification," as Minot would have us believe (6, p. 129), for it is undoubtedly also manifested in the occurrence in certain lowly Eutherians of a temporary yolk-sac placenta preceding the formation of the definitive allantoic one. As Hubrecht has shown in Erinaceus (9), it is only after the allantoic placenta has taken the place of the omphalopleural that the mesoderm of the vascular omphalopleure splits into splanchnic and somatic layers, and this delaying of the splitting process Hubrecht (20) attributes to the vital importance of the yolk-sac placenta.

It is not necessary to dilate on the significance of the discoid form of the allantoic placenta of Perameles. "On the Balfourian hypothesis," as Professor G. B. Howes has pointed out, the view that the discoidal type of allantoic placenta is the most primitive "is by far the most natural one warranted by the facts."¹

UNIVERSITY OF SYDNEY, N.S.W.;
April 16th, 1897.

¹ 'Nature,' vol. xl, p. 420.

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1. HILL, J. P.—“Preliminary Note on the Occurrence of a Placental Connection in *Perameles obesula*, and on the Fœtal Membranes of certain Macropods,” ‘Proc. Linn. Soc.,’ New South Wales, vol. x, (2nd ser.), part 4, 1895.
2. SELENKA, E.—“Studien über Entwicklungsgeschichte der Thiere,” IV (1 and 2), Das Opossum (*Didelphys virginiana*); V (1), Beutelfuchs und Känguruhratte (*Phalangista et Hypsiprymnus*). Wiesbaden, 1886-91.
3. CALDWELL, W. H.—“The Embryology of Monotremata and Marsupialia,” Part I, ‘Phil. Trans.,’ vol. clxxviii B., 1887.
4. MINOT, C. S.—“Uterus and Embryo: (1) Rabbit, (2) Man,” ‘Journ. of Morphology,’ vol. ii, 1889.
5. DUVAL, M.—“Le Placenta des Rongeurs,” ‘Journ. de l’Anat. et de la Physiologie,’ tome xxv, 1889.
6. MINOT, C. S.—“A Theory of the Structure of the Placenta,” ‘Anat. Anz.,’ Bd. vi, 1891.
7. HUBRECHT, A. A. W.—“Studies in Mammalian Embryology. III. The Placentation of the Shrew (*Sorex vulgaris*, L.),” ‘Quart. Journ. Micr. Sci.,’ vol. xxxv, 1894.
8. SEMON, R.—“Die Embryonalhüllen der Monotremen und Marsupialer,” ‘Zoologische Forschungsreisen in Australien und dem Malayischen Archipel.,’ Bd. ii.
9. HUBRECHT, A. A. W.—“Studies in Mammalian Embryology. I. The Placentation of *Erinaceus europæus*, with Remarks on the Phylogeny of the Placenta,” ‘Quart. Journ. Micr. Sci.,’ vol. xxx, 1890.
10. FLEISCHMANN, A.—“Embryologische Untersuchungen.” Heft 1. ‘Untersuchungen über einheimische Raubtiere,’ Wiesbaden, 1889.
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14. VERNHOUT, J. H.—‘Bijdrage tot de Kennis der Placentatie van den mol (*Talpa europæa*, L.),’ Diss., Amersfoort, 1894.
15. STRAHL, H.—“Placenta und Eihäute,” ‘Ergebn. der Anat. u. Entwicklungsgesch. von Merkel u. Bonnet,’ Bd. i, 1891.

16. OWEN, R.—'On the Anatomy of Vertebrates,' vol. iii, 1868.
17. STIRLING, E. C.—"On some Points in the Anatomy of the Female Organs of Generation of the Kangaroo, especially in Relation to the Acts of Impregnation and Parturition," 'Proc. Zool. Soc.,' London, 1889.
18. WILSON, J. T., and HILL, J. P.—"Observations upon the Development and Succession of the Teeth in Perameles; together with a Contribution to the Discussion of the Homologies of the Teeth in Marsupial Animals," 'Quart. Journ. Micr. Sci.,' vol. xxxix, 1897.
19. BALFOUR, F. M.—"On the Evolution of the Placenta, and on the Possibility of employing the Characters of the Placenta in the Classification of the Mammalia," 'Proc. Zool. Soc.,' London, 1881.
20. HUBRECHT, A. A. W.—"Die Keimblase von Tarsius," 'Festschrift für Carl Gegenbaur,' Leipzig, 1896.
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EXPLANATION OF PLATES 29—33,

Illustrating Mr. Jas. P. Hill's paper on "The Placentation of Perameles."

("Contributions to the Embryology of the Marsupialia," I.)

All sections drawn were outlined by means of Zeiss's camera lucida.

LIST OF COMMON REFERENCE LETTERS.

all. a. Allantoic artery. *all. c.* Allantoic cavity. *all. cap.* Allantoic capillary. *all. cl.* Allantoic canal. *all. ent.* Allantoic entoderm. *all. mes.* Allanto-chorionic mesenchyme. *all. v.* Allantoic vein. *bil. omph.* Bilaminar omphalopleure. *c. m.* Circular musculature. *cæ.* Extra-embryonic splanchnocœle. *cæ. w.* Inner (cœlomic) wall of allantois. *ch. ect.* Chorionic ectoderm. *ch. ect'.* Isolated chorionic ectoderm cell. *c. t.* Interglandular connective tissue. *ect.* Ectoderm. *ent.* Entoderm. *ex. syn.* Syncytium beyond allantoic placental area. *gl.* Uterine gland. *p. leuc.* Polynuclear leucocytes. *pl. a.* Allantoic placental area. *pl. syn.* Syncytium of allantoic placental area. *som.* Somatic mesoderm of chorion. *s. t.* Sinus terminalis. *syn.* Syncytium. *syn. c.* Capillary of syncytium. *syn. l.* Syncytial lobule. *vasc. omph.* Vascular

omphalopleure. *vit. a.* Vitelline artery. *vit. v.* Vitelline vein. *y. spl.* Invaginated yolk splanchnopleure.

N.B.—Unless otherwise stated, sections are transverse.

FIG. 1.—Wall of non-gravid uterus, *Perameles*. *s.* Serosa. *m.* Mucosa. *ep.* Uterine epithelium. $\times 55$.

STAGE A.

FIG. 2.—Portion of the syncytium, showing the numerous nuclei in a continuous protoplasmic layer. $\times 740$.

STAGE B.

FIG. 3.—Portion of left uterine wall (serosa not shown). *m. c.* Capillary of corium. $\times 55$.

FIG. 4.—Portion of the uterine syncytium, showing the lobular character of its deeper surface (*syn. l.*), the arrangement of the nuclei, and the presence in it of maternal capillaries (*syn. c.*). *l.* Leucocytes. *m. c.* Capillary of corium. $\times 40$.

STAGE C.

FIG. 5.—7 mm. embryo, *P. nasuta*. *all. s.* Allantoic stalk. *y. s.* Yolk-stalk. \times about 8.

FIG. 6.—Section passing through the margin of the allantoic placental area, and including the whole breadth of the vascular omphalopleure (*vasc. omph.*) on one side, and a portion of the bilaminar omphalopleure (*bil. omph.*), together with the adjacent syncytium (*ex. syn.*). *y. s.* Cavity of yolk-sac. $\times 118$.

FIG. 7.—Section of marginal portion of the allantoic placental area. $\times 140$.

FIG. 8.—Portion of allantoic placental area centrally from Fig. 7, showing the chorionic ectoderm (*ch. ect.*) as a continuous layer of enlarged cells adherent to the syncytium (*pl. syn.*), as in Fig. 7. $\times 140$.

FIG. 9.—Portion of the central region of the allantoic placental area, showing degeneration of the chorionic ectoderm (*ch. ect.*) $\times 230$.

FIG. 10.—Section of allantoic stalk. $\times 140$.

FIG. 11.—Section passing through opening of allantoic canal (*o. all. ct.*) into vesicular portion of allantois. $\times 118$.

FIG. 12.—Portion of the bilaminar omphalopleure in section. $\times 220$.

STAGE D.

FIG. 13.—Right uterus opened up, showing embryo still partially enclosed in its membranes and in relation to the allantoic placental area (*pl. a.*). For description see text (pp. 411, 412). \times about $6\frac{1}{2}$.

FIG. 14.—Section through the persistent portion of the proamniun. *amn.* amniun. $\times 140$.

FIG. 15.—Section through the marginal portion of the allantoic placental area (cf. with Fig. 7). $\times 150$.

FIG. 16.—Portion of the central region of the allantoic placental area (cf. with Fig. 8). $\times 150$.

FIG. 17.—Portion of the allantoic placental area, showing the interlocking of the allantoic capillaries (*all. cap.*) with the vascular ridges of the syncytium. $\times 325$.

FIG. 18.—Section passing through a gland opening in the allantoic placental area, occluded by an allantoic capillary (*all. cap.*). $\times 230$.

FIGS. 19 and 20.—Portions of allantoic placental area, showing isolated and greatly enlarged chorionic ectoderm cells (*ch. ect'*). $\times 230$.

FIG. 21.—Portion of allantoic placental area, showing an isolated multinuclear chorionic ectoderm cell (*ch. ect'*). $\times 230$.

FIG. 22.—Horizontal section of allantoic placental area, to show the network formed by the allantoic capillaries (*all. cap.*). $\times 225$.

FIG. 23.—Section of allantoic stalk (cf. with Fig. 10). $\times 140$.

FIG. 24.—Section passing through the sinus terminalis (*s. t.*), and including the adjacent portions of the vascular (*vasc. omph.*) and bilaminar omphalopleure (*bil. omph.*), together with the syncytium (*ex. syn.*) in contact therewith. $\times 240$.

STAGE E.

FIG. 25.—Genital organs from the ventral aspect. The left uterus (*l. ut.*) has been opened up, exposing the allantoic placental area (*pl. a.*), and the allantoic stalk (*all. s.*) has been traced back into the median pseudo-vaginal passage (*med. p.*). *bl.* Bladder. *f. t.* Fallopian tube. *r. ut.* Right uterus. *u. s.* Urino-genital strand. *v. cæc.* Vaginal cæca. $\times 2$.

FIG. 26.—Portion of the corium of the mucosa beneath the allantoic placental area, showing the alterations in the connective tissue, uterine glands, and blood-vessels. *c. t.* Hypertrophied interglandular connective tissue. *d. gl.* Gland with its lumen occupied by the disorganised epithelium. *m. v.* Vessel of corium with thickened walls. *m. v'.* Vessel with its lumen filled up by the proliferated endothelium. *m. v''.* Vessel with its lumen completely obliterated. *t. p'.* Thickened tunica propria around the uterine glands. $\times 225$.

FIG. 27.—Portion of allantoic placental syncytium in section, to show degenerative and absorptive change. *p. leuc.* Polynuclear leucocytes. *sp.* Spaces in syncytial protoplasm. $\times 550$.

FIG. 28.—Section through the marginal portion of the allantoic placental area (cf. with Figs. 7 and 15). *all. mes'.* Outer (placental) wall of allantois. *sp.* Spaces in syncytial protoplasm. *syn. o.* Lamellar outgrowth of the marginal portion of the placental syncytium. $\times 80$.

FIG. 29.—Portion of the allantoic placental area, showing the syncytium (*pl. syn.*) and the outer (placental) wall of allantois (*all. mes'*). × 230.

FIG. 30.—Portion of the greatly degenerate syncytium outside the allantoic placental area, showing the regeneration of the uterine epithelium. *d.* Detritus occupying gland lumen. *ex. syn'*. Degenerating syncytium. *gl. ep.* Gland epithelium. *gl. o.* Opening of gland into uterine lumen. *r. ep.* Regenerating uterine epithelium. × 230.

FIG. 31.—Superficial portion of the syncytium (*ex. syn'*.) and the regenerated uterine epithelium (*r. ep.*). × 520.

FIGS. 32, 33, and 34.—Sections illustrating certain appearances found at the margin of the allantoic placental area (cf. text, pp. 424, 425). *all. m.* Margin of allantois. *all. mes'*. Outer (placental) wall of allantois. *ch. ect'*. Persistent chorionic ectoderm cells (?). *syn. o.* Lamellar outgrowth from margin of allantoic placental syncytium. All × 230.

FIG. 35.—Section through the urino-genital strand of Fig. 25, showing the two allantoic stalks (*all. s.*) in the median pseudo-vaginal passage (*med. p.*). *c. bl.* Blood coagulum. *ur.* Urethra. *vag. l.* Lateral vaginal canal. × 18.

FIG. 36.—*P. nasuta*, new-born young. × nearly 8.



Fig. 2.



Fig. 3.

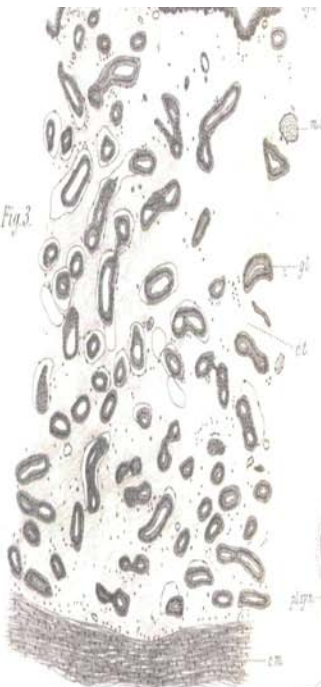


Fig. 4.

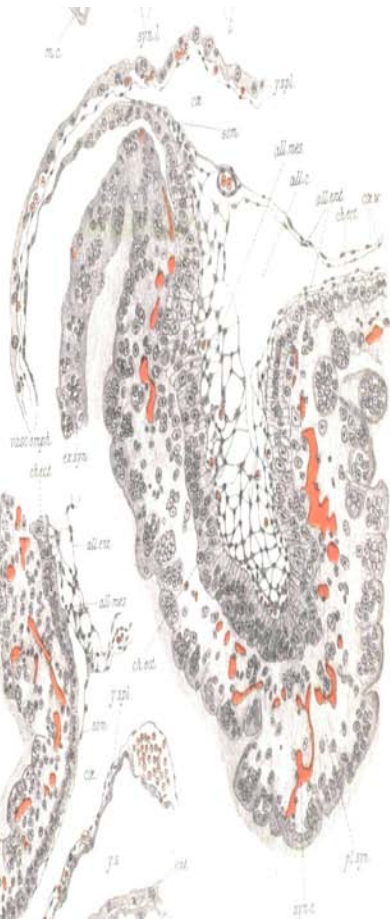


Fig. 5.

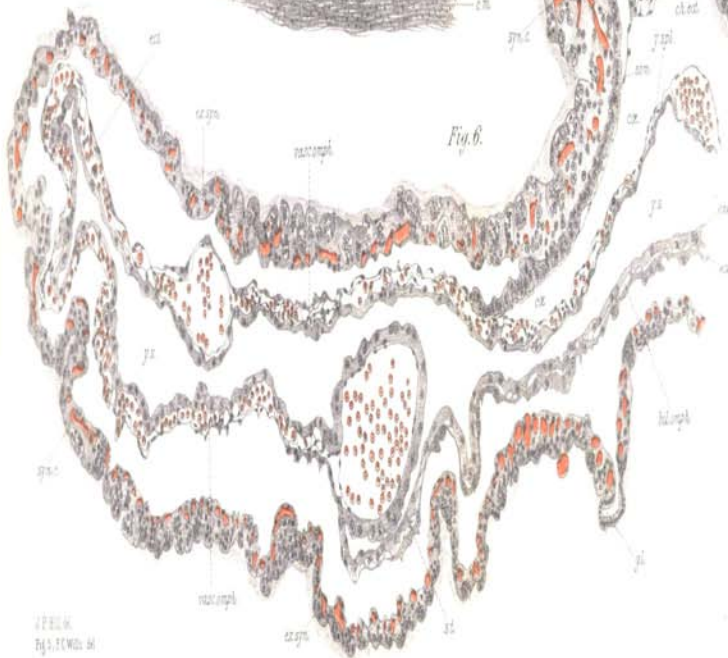


Fig. 6.

Fig. 15



Fig. 16

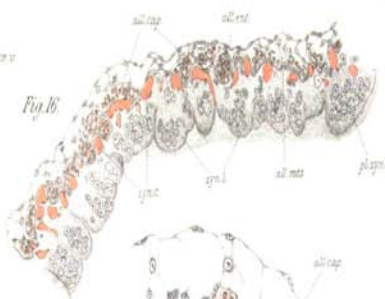


Fig. 17

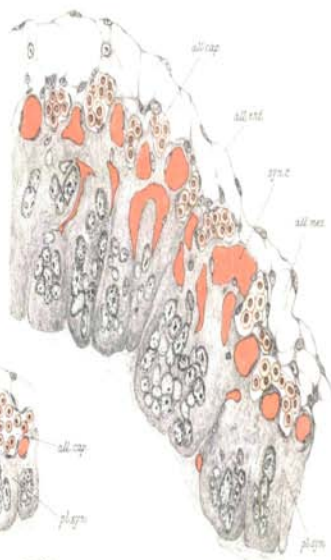


Fig. 18



Fig. 19



Fig. 20



Fig. 21



Fig. 22.



Fig. 24.

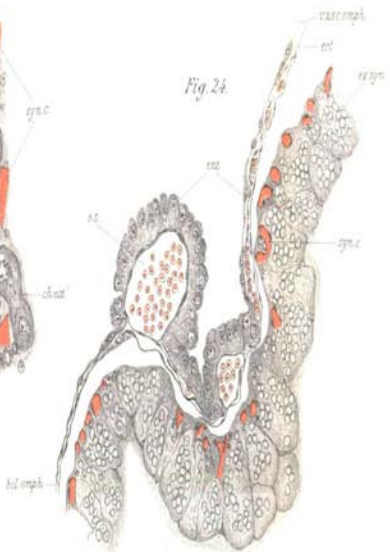


Fig. 25.

Fig. 23.

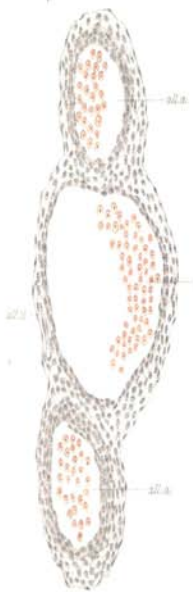


Fig. 27.



Fig. 26.



Fig. 28.

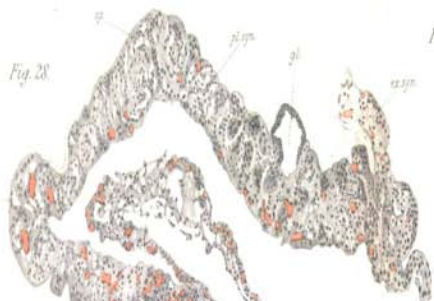


Fig. 29.

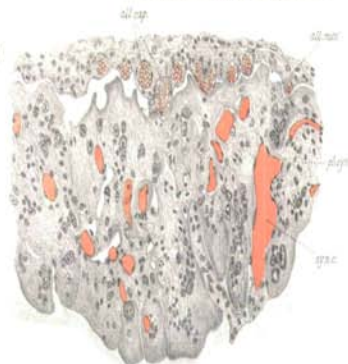


Fig. 30.

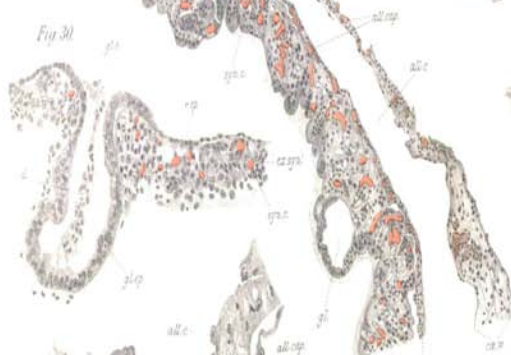


Fig. 31.



Fig. 32.



Fig. 33.

Fig. 34.

Fig. 35.



Fig. 36.



APPENDIX.

TABLE OF COMPARISON OF THE ORGANISATION OF THE EMBRYOS OF
STAGES C—E.

	<i>P. nasuta</i> , Stage C. 7 mm. from crown to rump.	<i>P. obesula</i> , Stage D. 8.75 mm. from crown to rump.	<i>P. nasuta</i> , new-born. Stage E. 14 mm. crown to rump. Head length 6 mm.
Form of body	Marked cervical flexure. Facial region definitely established. External nares formed. Distinct hyomandibular groove and precervical sinus (Fig. 6).	Head still strongly bent, neck protuberance prominent. External auditory meatus and triangular ear pinna. Snout now more marked. Precervical sinus closed.	Head raised but bent at right angles with trunk. Lips fused to form "Saugmund." Prominent snout. Positions of eyes and ear pinna just recognisable, covered by epithelium. Remains of allantoic stalk at navel (Fig. 36).
Limbs	In fore-limb, 5 digits indicated, the 3rd the largest. Hind limb still a flattened bud. In both, plantar surface still directed mesially.	In the fore-limb the 5 digits are now distinct, 1st and 5th quite small, 3rd the largest. Limb now flexed at the elbow. Plantar surface directed somewhat dorsally. Digits of hind limb still united, paddle-like, plantar surface mesially directed.	In fore-limb slender recurved claws on 2nd, 3rd, and 4th digits, the third digit the largest. In hind limb digits all indicated, but not free from each other; the 4th the largest.
Notochord and vertebral column	Notochord unconstricted, invested by a continuous mesenchymatous sheath.	Cartilaginous centra and neural arches laid down.	Marked cartilaginous centra with transverse processes and neural arches, the latter not yet united above spinal cord.

	P. nasuta, Stage C. 7 mm. from crown to rump.	P. obscura, Stage D. 8.75 mm. from crown to rump.	P. nasuta, new-born. Stage E. 14 mm. crown to rump. Head length 6 mm.
Nervous system	Distinct hemisphere anlagen. Dorsal and ventral spinal nerve-roots united. Spinal cord reaches tip of tail, but is here rudimentary. Anterior commissure of spinal cord distinct. Anterior and posterior white columns laid down. Lateral columns very thin. Hypophysis still connected with roof of mouth by a stalk with a narrow lumen.	Mesial hemisphere wall thickened in hippocampal region but still no fissura arcuata. Hypophysis no longer communicates with the oral cavity. Indications of "Sprossen."	Marked fissura arcuata along mesial hemisphere wall. Corpora striata developing. Hypophysis dorso-ventrally compressed. "Sprossen" not very marked.
Eye	Optic stalk still open. No pigment in outer wall of optic cup. Lens with cavity. Mesoderm has penetrated into optic cup.	Optic stalk still with a lumen. Outer wall of optic cup pigmented. Ovalish lens cavity. No differentiation of the retina into layers.	Retina deeply pigmented, no differentiation into layers. Eyelids united and covered by epitrachium.
Ear	Auditory vesicle surrounded by condensed mesenchyme. Long ductus endolymphaticus. Evaginations for semicircular canals.	Anterior vertical semicircular canal now formed. Utriculus and sacculus still in wide communication. Periotic capsule condensed mesenchyme.	Semicircular canals formed, but perilymphatic spaces not yet differentiated. Cartilaginous periotic.
Nose	Slit-like nasal sac in open communication with mouth.	Nasal cavities still open directly into mouth. Shallow-grooved anlagen of the organs of Jacobson. Solid anlagen of lachrymal ducts.	Adult form nearly established. Turbinal projections arising. Jacobson's organ formed, and its cartilage laid down. Lachrymal duct opens into nose.
Mouth	Palate unformed.	Palate unclosed. Lens-shaped Zalusleisten anteriorly. Taste-buds differentiating on tongue.	Palate formed, and invests larynx posteriorly. Teeth anlagen. Tongue grooved, and with distinct taste-buds.

	<i>P. nasuta</i> , Stage C. 7 mm. from crown to rump.	<i>P. obesula</i> , Stage D. 8.75 mm. from crown to rump.	<i>P. nasuta</i> , new-born. Stage E. 14 mm. crown to rump. Head length 6 mm.
Alimentary canal, &c.	Esophagus open. Separate dorsal and ventral pancreasanlagen. Cloaca not open to exterior. Lateral thymusanlagen. Yolk-sac cavity opens into gut.	Cloaca just opened to exterior, still remains of cloacal membrane. Yolk-sac no longer opens into gut. Thymusanlagen united mesially, but free posteriorly; they now reach the pericardium. Lungs now lobed, the right with a ventro-mesial lobe. Bronchi have branched out to form secondary bronchi. Diaphragm still incomplete close to the mesial line.	Pancreas completely formed. Thymusanlagen approximated in their mid-regions. Lungs with numerous simple alveoli. Cartilaginous rings round trachea. Diaphragm complete.
Heart and vessels	Distinct septum superior and septum spurium. Commencing division of the ventricular cavity indicated by an internal fold and external groove. Transversely expanded sinus venosus, opening into right auricular division. Truncus aortæ undivided. Two anterior dorsal aortæ. Yolk-sac circulation predominant.	Ventricular septum (septum inferius) almost reaches the cushions of the auriculo-ventricular ostium, likewise the septum superior, the auricles only communicating below its concave edge. Sinus venosus less extensive. Inferior vena cava established. Allantoic circulation predominant.	Adult circulation. Position of allantoic arteries still recognisable in urachus.
Urogenital system	Mesonephros of considerable size, tubules convoluted and with distinct glomeruli. Wolffian ducts open into cloaca together with allantoic canal. Distinct supra-renal Anlagen. Genital-leisten small.	Mesonephros now of large size. Peritoneal funnels of the Mullerian ducts laid down. Anlagen of ureters as short out-growths from the posterior ends of the Wolffian ducts, surrounded by condensed mesenchyme. Genital-leisten distinct, indifferent (?).	Mesonephros still of large size. Mullerian ducts laid down for part of their course. Permanent kidney definitely established and of some size, with tubuli contorti. Ureters open into cloaca mesially to Wolffian ducts. Projecting supra-renal Anlagen. Prominent genital-leisten, ♂ (?).

	P. nasuta, Stage C. 7 mm. from crown to rump.	P. obesula, Stage D. 8.75 mm. from crown to rump:	P. nasuta, new-born. Stage E. 14 mm. crown to rump. Head length 6 mm.
Skin and skeleton	Skeleton in the mesenchymatous stage.	Nucleated epitrichial layer on epidermis. No trace of hair, claw anlagen on 3rd and 4th fore digits. Skeleton cartilaginous.	Thick epitrichial layer on epidermis. Well-marked hairanagen on snout and cheeks. No ossification in cartilaginous skeleton, which is now fully formed. Upper and lower jaw ossifications.

Comparing the above three embryos with the tables and figures in Keibel's 'Normentafel zur Entwicklungsgeschichte des Schweines (*Sus scrofa domestica*),' Jena, 1897, they correspond, as nearly as one can judge, as follows:

Embryo C to No. 85, Fig. 24.

Embryo D barely to No. 91, Fig. 28.

Embryo E to No. 93.