THE HISTOLOGICAL DIFFERENTIATION OF THE PLACENTA FROM IMPLANTATION TO TERM IN THE GOLDEN HAMSTER (CRICETUS AURATUS WATERHOUSE)

by

FRANK WILLIAM ADAMS

A THESIS

submitted to

OREGON STATE COLLEGE

in partial fulfillment of
the requirements for the
degree of

MASTER OF SCIENCE

June 1951

APPROVED:

Redacted for Privacy

Assistant Professor of Zoology

In Charge of Major

Redacted for Privacy

Head of Department of Zoology

Redacted for Privacy

Chairman of School Graduate Committee

Redacted for Privacy

Dean of Graduate School

Date thesis is presented May 25, 1950

Typed by Mary Adams

ACKNOWLEDGEMENT

I wish to express my appreciation to Dr. Howard H. Hillemann for suggesting this problem and for the generous amount of time and valuable guidance which he has given during the period of this study.

TABLE OF CONTENTS

THE HISTOLOGICAL DIFFERENTIATION OF THE PLACENTA FROM IMPLANTATION TO TERM IN THE GOLDEN HAMSTER (CRICETUS AURATUS WATERHOUSE)

INTRODUCTION

Of the many papers treating on the subject of the development of rodent placentae, the only ones touching on the morphogenesis of the hamster placenta are those of Graves (1945), Venable (1946) and Ward (1948). Venable was interested in the preimplantation stages while Graves was concerned with both embryo and membranes through the first nine days prepartum. Ward considered implantation and associated endometrial changes into the fifth prenatal day.

This paper relates with special emphasis to the morphogenesis of the hamster placentae (vitelline and allantoic) from day 6 prepartum to term (day 16).

A study of the several fetal extraembryonic membranes and their relations to the endometrium is regarded as preliminary to any investigation of special cell types and of various problems in the placental physiology of this animal including the question of placental transmission.

MATERIALS AND METHODS

The placentae (vitelline and allantoic) from a total of 21 pregnant hamsters representing days 6 through 16 of gestation were prepared and studied.

Fetal age was determined by the time lapse from observed coitus to sacrifice. All loculi were placed in Bouin's fixative. To accelerate fixation, the larger loculi were also injected.

The paraffin-embedded loculi were serially sectioned at 6-10 microns and stained with hematoxylin and eosin. For proper paraffin-infiltration of the larger loculi, three days at low temperature (56° C.) were required. At least five paraffin changes were made during this period.

OBSERVATIONS

DAY 6

Embryo. At the level of maximum development the blastocyst is composed of a single layer of trophoblast cells and an inner cell mass which almost fills the blastocyst cavity. The trophoblast is somewhat flattened on the antimesometrial (omphaloidean trophoblast) side (fig. 1). A large number of mitotic figures are present in the developing embryo.

Uterus. The blastocyst is enclosed in an implantation chamber (cup) of the uterus. Points of contact between the blastocyst and uterus are characterized by complete erosion of the uterine epithelium except for a few disintegrating epithelial cells adjacent to the mesometrial (allantoidean trophoblast) surface of the blastocyst. Elsewhere the uterine epithelium shows no degeneration at this time, and the lumen is clear.

The implantation reaction is definite and manifests itself

in the endometrium. The decidua is thickened, with the portion adjacent to the embryo (primary decidua) more dense than that adjacent to the muscularis (secondary decidua). In the centripetal portion of the dense decidua near the embryonic area are maternal blood sinusoids lined with an intact endothelium. These are filled with red blood cells along with many leucocytes (fig. 1). In observing the distribution of blood vessels, more were found in the mesometrial half of the endometrium than in the antimesometrial portion.

The less dense appearing peripheral portion of the endometrium consists of many vacuolated cells. The contents of these cells have been dissolved out during the processes of fixation and dehydration.

Uterine glands in the antimesometrial half are pushed toward the muscularis. In the mesometrial half of the endometrium they are found near the lumen, and more commonly in the periphery.

DAY 7 (EARLY)

Embryo. At this age the embryonic trophectoderm approaches from either side to form an amniochorionic canal connecting two flares, one being the true amniotic cavity antimesometrially, and the other the false amniotic cavity (chorionic cyst, ectoplacental cavity, epamniotic cavity) mesometrially. A layer of entoderm is reflected over the outside and extends in a U shape around the embryo. A double layer of mesoderm lies between the ectoderm and the entoderm. This mesoderm has a slit which is the incipient

extra-embryonic coelom.

The trophoblast has transformed into giant cells. These giant cells have invaded the stroma and left a thin vestige known as Reichert's membrane.

A dome shaped ecto-placental cone (Träger) consisting of a dense mass of deeply staining cells has been established.

Uterus. The epithelium of the implantation chamber is entirely eroded away leaving a residue of cellular debris. The closure between the implantation chamber and the lumen proper is represented by a thin bridge of stroma.

The epithelium lining the uterine lumen shows extensive erosion. A few degenerating mucosal cells remain along the mesometrial surface only.

Near the muscularis, the antimesometrial stroma appears to be fairly dense. This dense appearance is noticeable also in the mesometrial half of the uterus and adjacent to the embryo mesometrially. In the latter area, the cells appear to be arranged in cords. Elsewhere the endometrium consists of highly vacuolated cells.

The blood sinusoids have increased in number, the most of which are located in the mesometrial half of the endometrium. These blood sinusoids are still lined with an endothelium.

In comparison with their location of the previous day, the glands in the antimesometrial portion of the endometrium have been pushed farther toward the muscularis.

DAY 7 (LATE)

Embryo. The true and false amniotic cavities are now separate. The entoderm and ectoderm of the embryo are well differentiated. Mesoderm is visible between the ectoderm of the false amniotic cavity and the entoderm of this region.

The placental cone has thickened. Lacunae of maternal blood bounded by placental cone cells only (have no endothelium) are located within the folds of the placental cone.

The giant cells have migrated ahead of the placental cone to invade the stroma.

Reichert's membrane is sharply outlined and an increasing number of giant cells have invaded a short distance into the stroma. Between Reichert's membrane and the stroma are many accumulations of maternal red blood cells.

Uterus. The few remaining glands are now crowded almost against the muscularis. The original uterine lumen has been reduced to a small irregular opening appearing in cross section as a deflected slit. This clear lumen lacks an epithelium and is lined by stroma.

DAY 8

Embryo. The embryo has a well developed neural groove and somites.

The amnion is now a large attenuated sac of ectoderm covered by somatic mesoderm. Progressing toward the embryo, the cells of

the somatic mesoderm of the amnion and the splanchnic mesoderm of the yolk sac become increasingly larger. These two germ layers contain the cavity of the intra-embryonic coelom in continuity with the large exocoelom.

Somatic mesoderm beginning at the embryo continues outward and completely lines the peripheral wall of the large exocoel. Somatic mesoderm is forced as a thin membrane against the medial ectoderm of the false amniotic cavity.

In the area of the embryo, the entoderm appears as an attenuated strand, but in the area of the exocoelom these cells are cuboidal and surround newly formed blood islands. The entoderm continues around the peripheral ectodermal wall of the false amniotic cavity, to the junction of the ectoderm of the false amnion and the stroma of the endometrium. At this junction, the entoderm becomes thin, deflects sharply in a reverse direction, forms an acute angle, and then continues as a very thin line against Reichert's membrane (fig. 3). In moniliform, the small nuclei of the parietal (outer, non-persistent, ephemeral) entoderm extend to circumscribe the yolk sac cavity (vitelline cavity). Antimesometrially from the embryo, the spheroid nuclei of the parietal entoderm appear larger and project in endothelial fashion into the yolk sac cavity.

Beyond the parietal yolk sac is found Reichert's membrane along whose course lies an occasional nucleus like those of typical giant cells. Although in general Reichert's membrane is apposed to

the outer yolk sac layer, there are occasional spaces separating these two. The spaces contain red blood cells in various stages of disintegration.

Allantois. At this stage the allantois has progressed across the extraembryonic coelom approximately to the half way mark. It is composed of a loose network of splanchnic mesodermal cells taking origin from the posterior end of the embryo.

In the allantoic area the center region of the medial ectodermal wall of the false amniotic cavity, with its closely apposed somatic mesoderm, is found pressed against the mesometrial wall (ectoderm) of the false amniotic cavity. This leaves the false amniotic cavity proper in the form of a circular canal (fig. 3).

Uterus. There is no evidence of a uterine epithelium. As previously mentioned, the border of the uterine lumen is formed by maternal blood lucunae together with the alignment of parietal yolk sac cells.

Giant cells are present in the stroma, having penetrated beyond the limits of the chorio-allantois proper, and are more numerous on the mesometrial side of the lumen.

The uterine glands have vanished.

The placental cone encloses many irregular spaces filled with maternal blood cells. No endothelium lines these blood lucunae. The blood is in direct contact with the placental cone tissue. Much of the maternal blood appears in the process of hemolysis.

DAY 9

Membranes. The amnion is highly attenuated with the nuclei of the ectoderm alternating with the nuclei of the somatic mesoderm which lies on the outer surface of the amnion.

The visceral (inner, permanent) yolk sac consists of a simple cuboidal epithelium overlying the splanchnic mesoderm. Fetal blood vessels containing nucleated red blood cells develop from the splanchnic mesoderm of the inner surface of the yolk sac (fig. 5).

As observed on day 8, at the point of junction between the yolk sac and the placental cone area, the entoderm is sharply deflected to follow a reverse direction and form an attenuated parietal yolk sac entoderm with small widely separated nuclei. This parietal entoderm is nonvascular and lies in apposition to Reichert's membrane. Reichert's membrane contains only a few giant cell nuclei, the others having migrated into the stratum compactum. The area of the stratum compactum invaded by the giant cells appears to have lost its cellular organization and is composed of an amorphous material with clear vacuoles. Maternal blood empties into the area between Reichert's membrane and the parietal yolk sac. Previously the giant cells had been observed to migrate freely in all directions away from the implantation chamber, but at this stage the more advanced migration is restricted to the mesometrial side of the embryo (fig. 4).

Until this time, the placental cone has had the shape of a dome, but now it assumes a definite cone shape, the margins of the apex forming an acute angle (fig. 2). The placental cone is still composed of dense cells, has a wavy outline, and encloses in the interstices, maternal red blood cells which are for the most part in various stages of dissolution. Trophoblastic endovascular plasmodial cells (Bridgeman 1948) are present within the maternal lucunae of the placental cone. The migrating giant cells have isolated a section of maternal tissue adjacent to the cone (fig. 4). This decidua has a liver-like appearance. Conversion of the isolated maternal tissue to the liver-like appearance may be due to the action of the giant cells, since the liver-like tissue lies behind the advancing line of giant cells. Between the isolated maternal tissue area and the mesometrial endometrium a network structure confines scattered giant cell nuclei. This network circumscribes the entire embryonic area.

Allantois. The allantois has reached the lower lamina, having traversed the extra-embryonic coelom. The endothelium of the allantois is in contact with somatic mesoderm which in turn is pressed against the medial lamina. A smooth splanchnic mesodermal membrane extends across the allantoidean placental area and restricts the allantoic blood vessels to this region (fig. 4). Allantoic blood vessels filled with nucleated red blood cells extend by finger-like villi into the medial side of the placental cone. These villi are lined by the endothelium of the allantois.

Thus, separating the maternal red blood cells from the fetal blood are the following membranes: placental cone ectoderm, somatic mesoderm, and allantoic endothelium. This combination forms a thick villous haemo-chorial placenta (fig. 6).

Uterus. Blood vessels in the uterine stroma on the meso-metrial side have a large number of leucocytes among the red blood cells.

A cross section of a maternal blood vessel in the meso-metrium reveals a very hypertrophied endothelium with nuclei bulging into the lumen. Inside this particular blood vessel and occupying almost all of the cross sectional area is found a trophoblastic endovascular plasmodial cell. This cell is much larger than the giant cell, and has a large blue staining nucleus and a lavender mass of cytoplasm.

Antimesometrially, the epithelial lined uterine lumen is being re-established, separating the decidua capsularis from the uterine wall.

DAY 10

Membranes. The amnion remains intact, but is extremely attenuated.

The visceral yolk sac is composed of cuboidal cells with deep staining nuclei. The cytoplasm is observed to take on a bluish tint. The visceral yolk sac epithelium is thrown into convolutions or villi which project into the cavity of the yolk

sac. This yolk sac is vascularized by a well-developed layer of splanchnic mesoderm. The endothelial vessels contain nucleated red blood cells.

The parietal yolk sac transforms immediately into an attenuated layer with the small yolk sac nuclei dotting its course.

Immediately outside the parietal yolk sac are found many well-developed blood spaces formed by a network of the cytoplasmic processes of the giant cells. These spaces are filled with maternal blood. The giant cells are now larger than they have been on previous days.

Reichert's membrane is still present. Many maternal blood cells in various stages of disintegration, neutrophils and lymphocytes, as well as scattered nuclei of giant cells, are seen between Reichert's membrane and the parietal yolk sac. Blood bathing the yolk sac in this manner is suggestive of a fetal nutrition through a vitelline placenta subsidiary to that of the chorio-allantois.

Allantoidean Placenta. The endothelium of the allantois has grown through the somatic layer of the chorion (serosa) and has come into direct contact with the ectodermal cells of the placental cone. Such an arrangement may be described as "haemochorial", with the reservation that the somatic mesoderm has been thinned out, penetrated by allantoic endothelium and therefore no longer functions as a partial barrier between fetal and maternal blood.

In the region of the allantoic placenta, the splanchnic mesoderm of the allantois is stretched across the placenta in a straight line. Adherent to this mesodermal membrane on the mesometrial side are found the endothelial blood vessels of the allantois which contain nucleated red blood cells. These grow into and through the chorion and form larger vessels between the placental cone itself and the uterine stroma.

The giant cells have penetrated and limited a portion of the basalis, the cells of which appear to be reduced. This area of endometrium is broken up by numerous large spaces containing maternal red blood cells. The giant cells limiting the above-mentioned liver-like structure have caused disintegration of the stroma to the extent that a definite break occurs in this area. The space thus formed is filled with stromal cell debris.

Uterus. The uterine stroma of the basalis is highly vascularized, containing many large endothelial lined blood vessels as well as lucunae lacking an endothelium. Some of the blood vessels contain a high percent of neutrophils which adhere to the inner walls of the blood spaces.

Antimesometrially, the decidua basalis is divided, the medial half bounding the decidua capsularis and the lateral portion remaining attached to the muscularis. The space between represents the re-established uterine lumen and is lined on either side with a new epithelium (fig. 7). At each end of the lumen the epithelium on either side is in contact, obliterating the lumen. The

re-forming uterine lumen is intermittent along the entire length of the loculus.

DAY 11

At eleven days there is continued growth.

Membranes. The visceral yolk sac is increasingly vascularized. The space between the parietal yolk sac and Reichert's membrane is filled with maternal red blood cells.

Allantoidean Placenta. The chorio-allantoic placenta remains haemo-chorial, consists of cone ectoderm and allantoic endothelium and is labyrinthian in its arrangement.

The placental cone itself is greatly broken up by blood lucunae of maternal origin. This area is continuous with the previously mentioned liver-like decidua basalis which is also broken up by maternal blood lucunae. These blood lucunae are lined by the stromal cells of the endometrium. Clear vacuoles are present, which represent the position of cellular inclusions removed by fixation and clearing.

A line of demarcation is seen between the "liver" decidua basalis and the remainder of the decidua basalis. Most of the giant cells lie along this line of demarcation and are seen invading the decidua basalis toward the mesometrium.

It appears that most of the decidua basalis is becoming vacuolated and liver-like in structure.

The giant cells have grown considerably since day 10, and have attained a diameter about twenty times that of the blood cells.

Uterus. Some maternal vessels in the mesometrial decidua contain numerous leucocytes with relatively few red blood cells. In other vessels, both red blood cells and leucocytes may be present in about equal numbers. In the maternal blood lucunae lined with stroma, the leucocytes are either few in number or lacking.

Toward the mesometrium, some maternal blood vessels are completely filled with leucocytes, while in adjacent vessels red blood cells predominate.

Trophoblastic endovascular plasmodial cells are seen in some maternal arteries and veins, particularly in the mesometrial region. In one maternal artery of the mesometrium there was seen an endovascular plasmodial cell along with many laked red blood cells surrounding scattered vacuoles. It may be that the plasmodial cell is responsible for this dissolution.

Antimesometrially, the stroma has been compressed and stretched until it is no greater in thickness than the combined muscularis and serosa. The muscularis is also narrowed. Here the uterine lumen is complete and lined with epithelium.

The uterine epithelium projects around the uterine endometrium and establishes the new uterine lumen.

DAY 12

Membranes. Six structures are met in order antimesometrially from the amnion outward. The first is the convoluted and highly vascularized villous visceral yolk sac which is composed of a simple squamous splanchnic mesoderm medially and a convoluted

villous entoderm laterally. The second is the yolk sac cavity. Limiting the cavity is the parietal yolk sac membrane composed of simple epithelium with spherical nuclei bulging into the yolk sac lumen. Third, Reichert's membrane appears as a definite non-cellular layer apposed to the parietal yolk sac. Fourth, maternal blood cells lie against Reichert's membrane in irregular blood lucunae limited peripherally by the remaining thin stroma. In the stroma are areas in which the uterine lumen is being re-established. In these areas, the uterine stroma is bounded peripherally by simple cuboidal epithelium which is followed by the re-established lumen. This lumen has an outer columnar epithelium apposed against a layer of basalis, which will remain after birth. The fifth is the muscularis composed of circular and longitudinal smooth muscle. Sixth is the serosa, composed of simple squamous epithelium.

Mesometrially, the visceral and parietal yolk sacs and Reichert's membrane have not undergone any changes from the previous day.

Allantoidean Placenta. In the region of the allantoidean placenta, peripheral and adjacent to the persistent splanchnic mesodermal wall, are large allantoic blood vessels. Capillaries from these project mesometrially and have thoroughly broken up the remnants of the placental cone leaving only scattered ectodermal cells. For the most part, the allantoic capillaries seem to course in irregular lines in a mesometrial direction. These are paralleled by similarly arranged slender blood lucunae containing maternal blood.

Only the endothelium of the fetal capillaries is interspersed between fetal and maternal blood streams. Thus there is now a haemo-endothelial placenta which is labyrinthine in arrangement (fig. 8).

Immediately beyond the region of apposition of fetal and maternal circulations there are irregular islands of the original placental cone cells. These islands have been isolated by maternal blood lucunae, which also break up the basalis.

Integral Chorio-allantoic and Yolk Sac Placenta. At points of contact between the yolk sacs and allantoidean placenta, an occasional visceral yolk sac blood vessel projects through the parietal yolk sac and Reichert's membrane into the allantoidean placenta in the form of a finger. Both yolk sac epitheliums and Reichert's membrane accompany the "finger" for a short distance, but further along, the barrier between maternal and fetal blood is represented only by visceral yolk sac vascular endothelium.

Uterus. Observation of small and large arteries in the mesometrium reveals a number of trophoblastic endovascular plasmodial cells adherent to the endothelial lining.

DAY 12½

Membranes. The only change noticed is in the convoluted visceral yolk sac membrane which mesometrially is becoming progressively more villous with secondary fingers. It is highly vascular in the area of the allantoidean placenta.

Allantoidean Placenta. The allantoidean placenta remains haemo-endothelial. The maternal blood lucunae and fetal allantoic capillaries form a fine and complex interlacing network. The placental cone is thoroughly broken up with its ectodermal cells spread along a line, the junctional zone.

Integral Chorio-allantoic and Yolk Sac Placenta. There is no change from day 12 when the penetration of visceral yolk sac blood vessels into the allantoidean placenta was first observed.

DAY 13

Membranes. Reichert's membrane is present antimesometrially as are previously mentioned membranes.

Allantoidean Placenta. The allantoidean placenta has extended its boundary centrifugally in such a manner that its outer circular margin overlaps the yolk sac. Thus, arranged from the embryo toward the mesometrium are: the amnion; the highly folded and vascular visceral yolk sac and yolk sac cavity; the parietal yolk sac; Reichert's membrane; and the allantoidean placenta proper comprising maternal blood spaces, isolated cone cells and allantoic endothelium containing fetal red blood cells.

Large maternal blood lucunae exist between the allantoidean placenta and Reichert's membrane in its association with the parietal yolk sac (fig. 9). In addition, there are maternal red blood cells in great profusion. Visceral yolk sac blood vessels penetrate the allantoidean placenta as previously described on day 12.

Day 14½

Membranes. Antimesometrially the membranes other than the amnion are closely pressed to the wall of the uterus. The amnion, which is still intact and consists of two layers, is followed peripherally by the visceral yolk sac composed of an inner layer of a simple squamous splanchnic mesoderm and an outer layer of cuboidal entoderm. The parietal yolk sac has disappeared here. Thus the vitelline cavity also has disappeared from the antimesometrial side.

Reichert's membrane has disappeared from this area, although it is still present in the mesometrial half of the uterus. Maternal blood lucunae lie between the visceral yolk sac and the re-established uterine lumen. It should be noted that the medial uterine epithelium which was present on the 13th day has now disappeared. Thus, the maternal blood lies between the visceral yolk sac layer and the outer epithelium of the new lumen (complete inversion of germ layers).

Outside the re-established uterine epithelium is a thin layer of basilar stroma. Maternal blood vessels lie both directly against the epithelium and within the stroma.

Outside the basilar stroma are the circular and longitudinal smooth muscles covered by the serosa.

Proceeding toward the mesometrial portion of the uterus, the visceral yolk sac is thrown into progressively more complicated and longer villi, all of which are vascularized. The parietal yolk

sac persists as an attenuated layer with nuclei bulging into the yolk sac lumen. This yolk sac extends only as far as the hypertrophied basalis adjacent to the allantoidean placenta.

Here Reichert's membrane is present. It lies against the parietal yolk sac and extends from the allantoidean placenta, disappearing before it reaches the previously described antimesometrial pole.

Allantoidean Placenta. The allantoidean placenta which is more extensive than before, remains haemo-endothelial in structure. Some placental cone ectoderm cells are isolated and others form a definite boundary or junctional zone (Bridgeman 1948) between the allantoidean placenta and the decidua basalis. Immediately mesometrial to the junctional zone, the basalis is composed of stromal cells heavily permeated by maternal blood lucunae having no endothelial lining. Numerous giant cells are present, both in the basalis and among the cells of the junctional zone.

Near the junctional zone, but within the allantoidean placenta, are found a series of allantoic blood vessels which pass from the allantois through the allantoidean placenta to the junctional zone. These vessels have an endothelial lining. There is a loose scattered cell network between the allantoidean placenta proper and this endothelium (fig. 10).

Very few giant cells are found within the allantoidean placenta. There are, however, a number of dark staining, closely packed circular islands of cells among which occasional giant

cells may be found. No explanation is offered for these "islands" other than that suggested by their resemblance to the original placental cone cells.

The allantoidean placenta at this stage, as on the previous days, is penetrated by blood vessels from the yolk sac.

Uterus. In the mesometrial region, the uterine epithelium of the re-established lumen is folded into numerous villi which project into the lumen itself. This epithelium is not present on the medial (toward the embryo) side of the lumen. The enclosed lumen is filled with maternal blood cells.

DAY 15

Membranes. Mesometrially and antimesometrially the amnion, yolk sac and Reichert's membrane are the same as on day 14½ (fig.11).

Allantoidean Placenta. The allantoidean placenta presents its maximum development (fig. 12). The area of exchange is more vascular than previously and gives the appearance of a lacy network separating maternal and fetal blood supplies. This network is composed of a thin allàntoic endothelium. A few scattered placental cone cells remain, and islands of what are thought to be placental cone cells are still found. Bounding the allantoidean placenta is the junctional zone of compressed and alined placental cone cells.

Just beyond the junctional zone is the vacuolated decidua basalis containing many giant cells and numerous large irregular maternal blood lucunae. Mesometrially the decidua basalis is

more compact and uniform, except for interruptions by maternal blood vessels. This area is bordered by a dense decidua basalis lying against the circular and the longitudinal smooth muscle coats.

There is no change observed in the integral chorio-allantoic and yolk sac placenta.

Uterus. Trophoblastic endovascular plasmodial cells occur frequently in the maternal arteries and veins of the mesometrium.

As viewed in cross section, the uterine epithelium with its cavity has progressed around the greater portion of the uterus. The main mesometrial area supplying blood to the placenta remains intact.

The total area occupied by maternal blood appears to be greater than that occupied by fetal blood in the region of exchange. Approximately ten per cent of the fetal red blood cells are nucleated.

DAY 16

Membranes. Antimesometrially, the membranes are as in day 15. Peripheral to the intact amnion is the visceral yolk sac, composed of a vascularized inner splanchnic mesodermal layer and an outer cuboidal entodermal layer. The parietal yolk sac and Reichert's membrane are absent. Thus the visceral yolk sac forms the inner wall of the new uterine lumen which contains disintegrated cellular material. The outer wall of the new uterine lumen is lined with an irregular cuboidal to columnar epithelium apposed peripherally

by a moiety of vascular basilar stroma. The circular and longitudinal smooth muscle layers, and the serosa form the outer wall.

Mesometrially also, the membranes are as on day 15. Immediately beyond the circumference of the allantoidean placenta, the following structures are found in sequence from the embryo outward: the amnion; the visceral yolk sac with villi reduced from the extensive development of day 15; the parietal yolk sac; Reichert's membrane; decidua, circular and longitudinal smooth muscle layers; and the serosa.

Allantoidean Placenta. The maximum development of the allantoidean placenta noted on day 15 is retained. Maternal blood lucunae flare in the hilus of the allantoidean placenta. Mesometrially from these blood lucunae is the highly developed area of exchange of the chorio-allantois. At the peripheral edge of the chorio-allantois is a row of large allantoic blood vessels which parallel the junctional zone.

In cross section the mesometrial basalis is flattened, vacuolated, and contains dispersed giant cells.

Integral Chorio-allantoic and Yolk Sac Placenta. Where the allantoidean placenta and yolk sac overlap there are maternal blood lucunae in direct contact with Reichert's membrane and the parietal yolk sac. Some of these maternal blood spaces are lined in part by trophoblastic endovascular plasmodial cells.

Elsewhere the parietal yolk sac is thrown into folds, forming a cavity bounded by parietal yolk sac which lies in

apposition to maternal blood spaces. The following sequence occurs: maternal blood lucunae; Reichert's membrane and parietal yolk sac layer; yolk sac cavity; and parietal yolk sac again.

The previously described condition of allantoidean placenta penetration by the combined layers of visceral yolk sac, parietal yolk sac and Reichert's membrane is also present.

Uterus. The uterine lumen in penetrating the sides of the mesometrium has excavated under some of the allantoidean placenta, causing it to protrude into the uterus as a flattened knob. The peripheral wall or the uterine wall of the re-established uterine lumen is lined with renewed columnar epithelium, but the medial or decidual wall is faced with a smooth-surfaced connective tissue selvage and lacks an epithelium. Mesometrial penetration by the uterine lumen forecasts the line of cleavage at parturition.

SUMMARY

1. Placental development from implantation to parturition has been described in the golden hamster. Like other rodents, the hamster has an inverted yolk sac (inversion or entypy of germ layers).

2. At six days post coitus the blastocyst in the implantation chamber has eroded the uterine epithelium.

3. After seven days the placental cone is established and Reichert's membrane is present. Peripheral to these are giant cells invading the stroma.

4. At eight days, the entoderm forms visceral and parietal yolk sac layers. Maternal blood in lucunae bathes the ectodermal placental cone cells.

5. The visceral yolk sac is vascularized by the end of the ninth day. The allantoic endothelium contacts the somatic mesoderm layer which in turn presses against the laminae at the base of the placental cone ectoderm. Allantoic blood vessel villi extend into the placental cone forming a haemo-chorial placenta. When the chorio-allantoic placenta is established it is immediately haemo-chorial and then transforms into a haemo-endothelial type.

6. On the tenth day of gestation, the vascular visceral yolk sac convolutes so that villi project into the yolk sac cavity. The uterine lumen is being re-established antimesometrially, giving rise to a decidua capsularis.

7. During the twelfth day, the allantoidean placenta becomes haemo-endothelial which persists to birth.

8. Reichert's membrane and the parietal yolk sac have disappeared from the antimesometrial region at 14½ days.

9. At the end of the fifteenth day, the allantoidean placenta is at its maximum development, and the yolk sac is more villous mesometrially than at any other time.

10. At sixteen days post coitus, the allantoidean placenta has become slightly flattened and is separating from the basalis where the new uterine lumen is being re-established. All membranes are present in the mesometrial region, but the parietal yolk sac

and Reichert's membrane are absent antimesometrially.

11. The formation of a fibrous layer separating the decidua from the unchanged stroma and muscularis as described in the rat (Bridgeman 1948) was never observed.

12. The changes occurring from day to day in both the vitelline and allantoic placentae are presented in concise form in Table 1.

Table 1.

MORPHOGENESIS OF THE VITELLINE AND ALLANTOIC PLACENTAE OF THE GOLDEN HAMSTER (CRICETUS AURATUS)

KEY · O=NOT FORMED P=PRESENT L=LOST PL=LOST IN SOME AREAS ONLY

VITELLINE PLACENTA											DAY	ALLANTOIC PLACENTA						
MATERNAL			FETAL							REMARKS		MATERNAL			FETAL			REMARKS
UTERINE ENDOTHELIUM	UTERINE STROMA	UTERINE EPITHELIUM	A TROPHECTODERM OR A	REICHART'S MEMBRANE	PARIETAL ENTODERM OR	ATTENUATED PAR. ENT.	VISCERAL ENTODERM	YOLK SAC SPL. MES.	ENDOTHELIUM OF YOLK SAC SPL. MES.			UTERINE ENDOTHELIUM	UTERINE STROMA	UTERINE EPITHELIUM	CHORIONIC ECTODERM	CHORIONIC SOM. MES.	ENDOTHELIUM OF SPL. MES. OF ALLANTOIS	
P	P	PL	P	O	O	O	O	O	O		6							
L	L	L	L	P	P	O	P	P	O		7							
L	L	L	L	P	L	P	P	P	P	VISCERAL YOLK SAC IS VASCULAR PARIETAL YOLK SAC IS AVASCULAR	8	L	L	L	P	P	O	ALLANTOIS APPROACHING SEROSA
L	L	L	L	P	L	P	P	P	P		9	L	L	L	P	P	P	THICK HEMOCHORIAL
L	L	L	L	P	L	P	P	P	P		10	L	L	L	P	L	P	THINNER HEMOCHORIAL
L	L	L	L	P	L	P	P	P	P		11	L	L	L	P	L	P	THINNEST HEMOCHORIAL
L	L	L	L	P	L	P	P	P	P		12	L	L	L	L	L	P	HEMOENDOTHELIAL
L	L	L	L	P	L	P	P	P	P		13	L	L	L	L	L	P	"
L	L	L	L	PL	L	PL	P	P	P		14	L	L	L	L	L	P	"
L	L	L	L	PL	L	PL	P	P	P		15	L	L	L	L	L	P	"
L	L	L	L	PL	L	PL	P	P	P		16	L	L	L	L	L	P	"

25a

LITERATURE CITED

1. Bridgeman, Jane 1948 A morphological study of the development of the placenta of the rat. J. Morph. 83: 61-86.

2. _____ 1948 A morphological study of the development of the placenta of the rat. II. An histological and cytological study of the development of the chorioallantoic placenta of the white rat. J. Morph. 83: 195-224.

3. Graves, Artis Paris 1945 Development of the golden hamster, Cricetus auratus waterhouse, during the first nine days. Am. J. Anat. 77:219-251.

4. Venable, John H. 1946 Pre-implantation stages in the golden hamster (Cricetus auratus). Anat. Rec. 94: 105-120.

5. Ward, Margaret C. 1948 Early development and implantation of the golden hamster and associated endometrial changes. Am. J. Anat. 82: 231-275.

APPENDIX

KEY TO ABBREVIATIONS

al — allantois
am — amnion
bl — maternal blood lucuna
ec — extra-embryonic coelom
em — embryo
icm — inner cell mass
jz — junctional zone
mbv — maternal blood vessel
pc — placental cone
pys — parietal yolk sac
R — Reichert's membrane
st — stroma
tr — trophectoderm
ul — uterine lumen
vys — visceral yolk sac
yc — yolk sac cavity

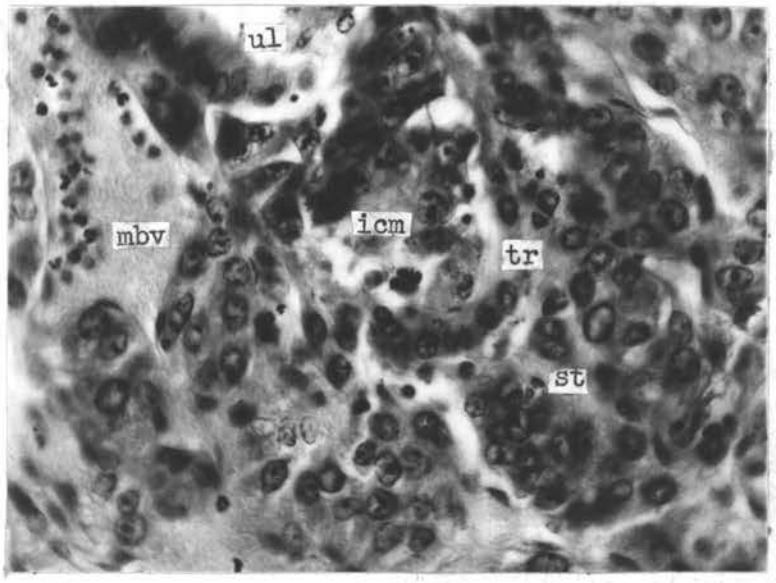

Fig. 1. Implanted blastocyst at the end of 6 days, showing erosion of the uterine epithelium in the region of the blastocyst. 516 X

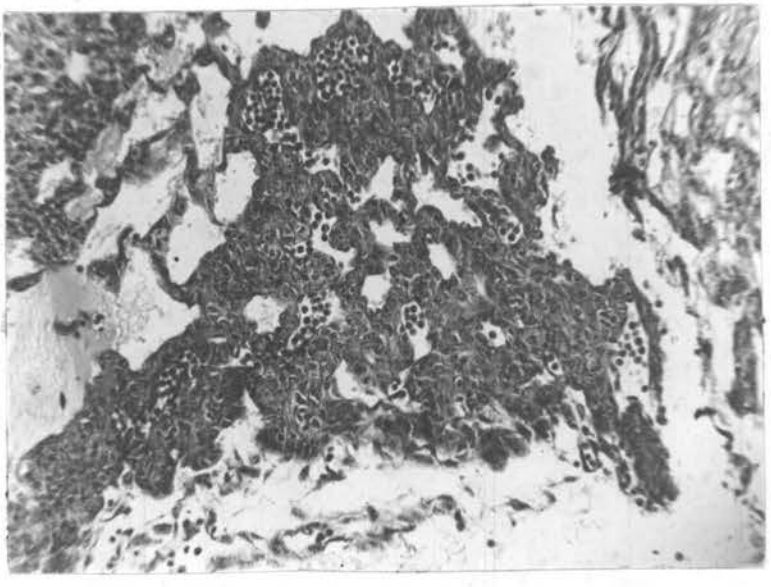

Fig. 2 Placental cone at the end of day 9. Allantoic blood vessels and maternal blood lucunae penetrate the cone. 120 X

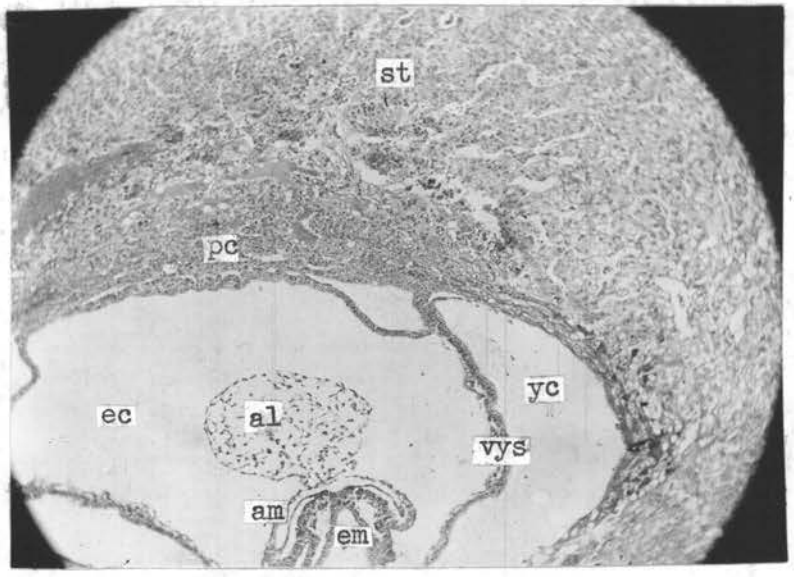

Fig. 3 Embryonic membranes and placentae at the end of day 8. The deflection (arrow) marks the transition from visceral to parietal yolk sac. 50 X

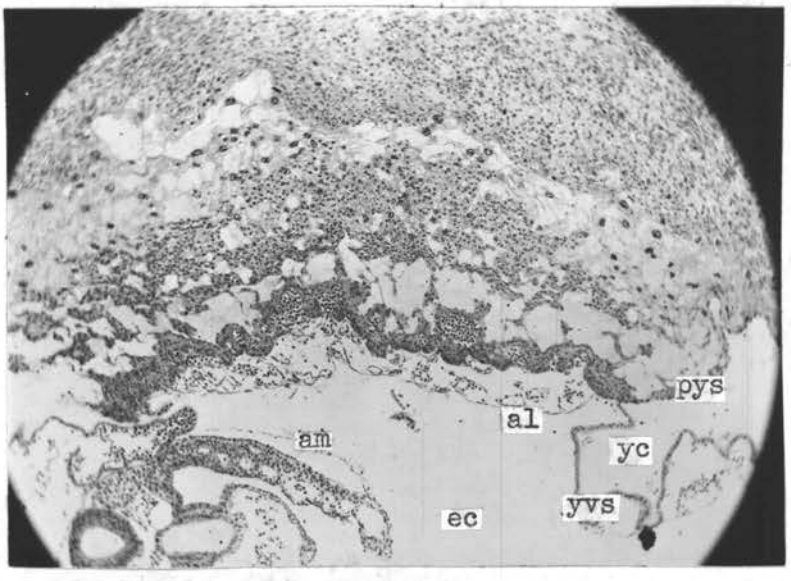

Fig. 4. The laminae at the end of the 9th day. The advancing giant cells have segregated a portion of the liver-like stroma. 50 X

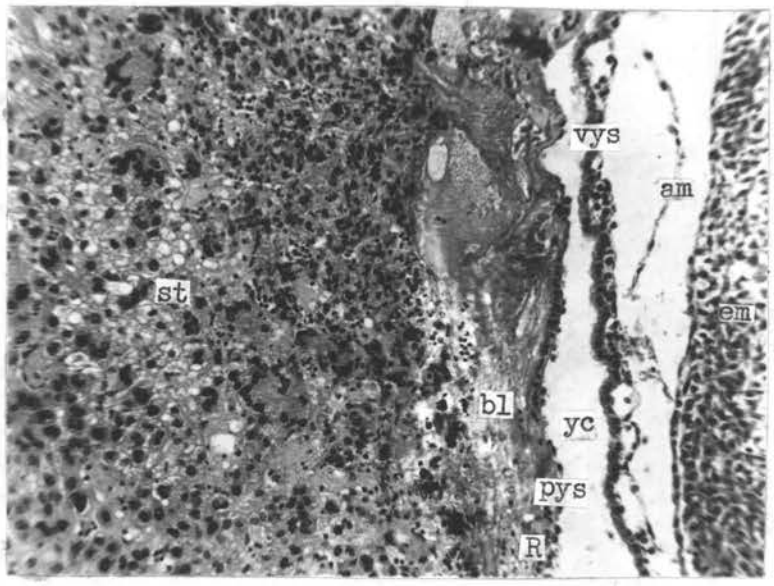

Fig. 5. Antimesometrial region at the end of day 9. Maternal blood lucunae lie in apposition to Reichert's membrane and the parietal yolk sac. 120 X

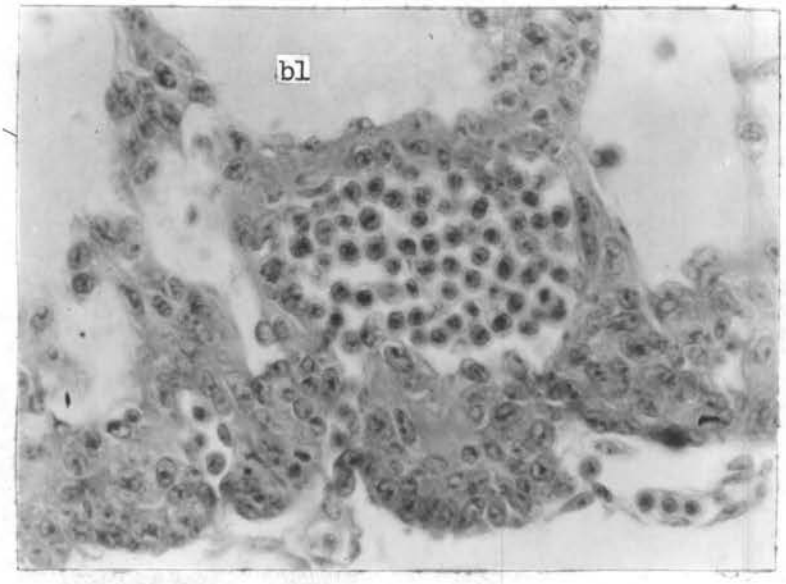

Fig. 6. A portion of the haemo-chorial placenta on day 9. 516 X.

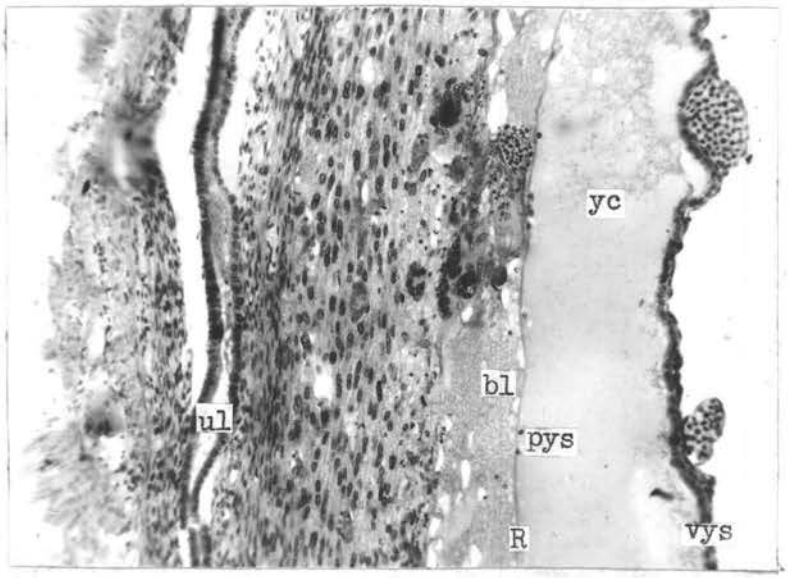

Fig. 7. Antimesometrial region at the end of day 10. The re-established lumen has divided the basalis and defined the capsularis. The clear areas outside the uterine lumen are artifacts. 120 X

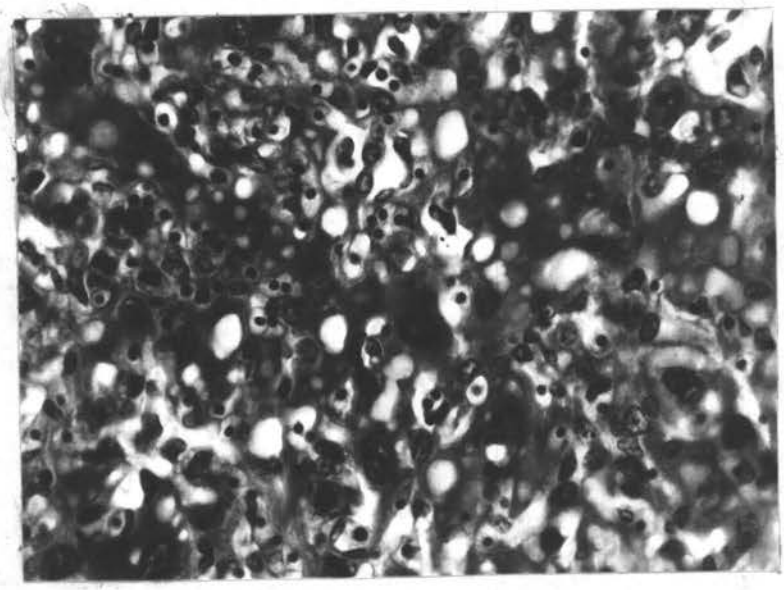

Fig. 8. Closely apposed fetal and maternal blood streams in the haemo-endothelial placenta on the 12th day. 516 X

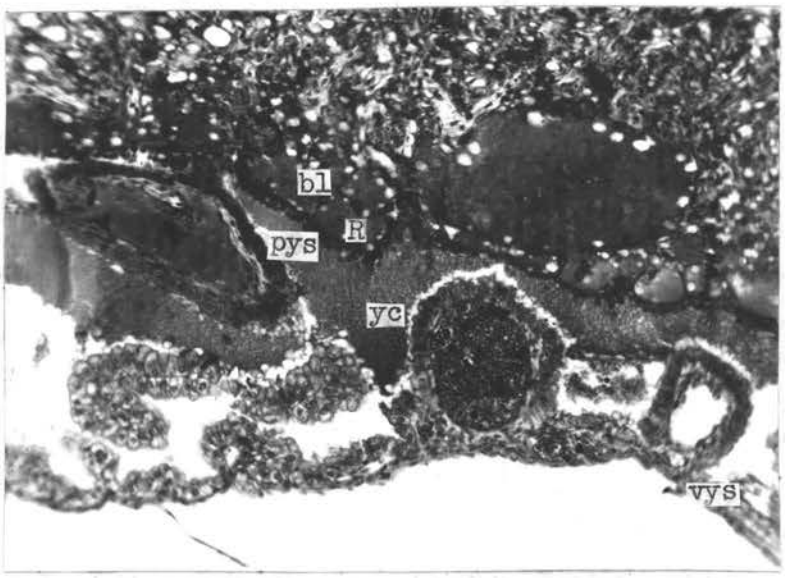

Fig. 9. Vitelline and allantoic placentae on day 13. Pools of maternal blood bathe the Reichert's membrane and the apposed parietal yolk sac. The visceral yolk sac is thrown into convolutions and villi. 120 X

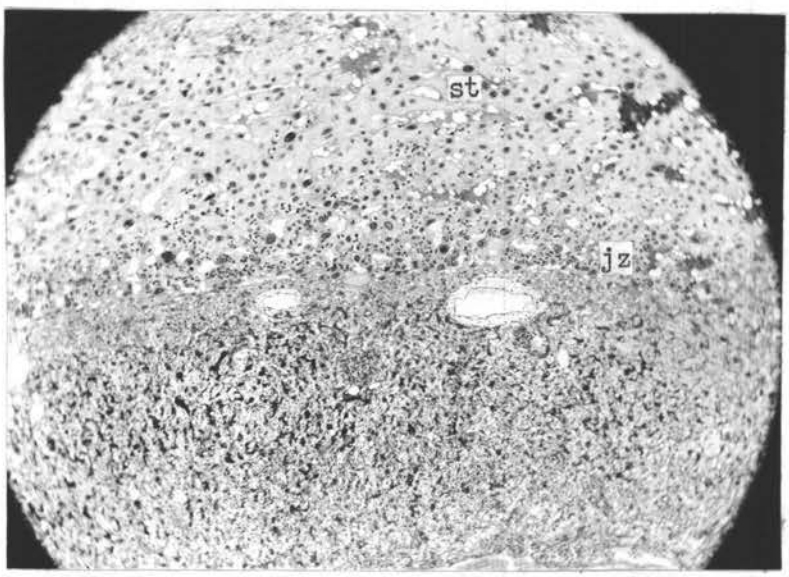

Fig. 10. Labyrinthine structure of the area of exchange in the allantoidean placenta at 14½ days. Large allantoic blood vessels lie just inside the junctional zone. Giant cells are present in the decidua. 50 X

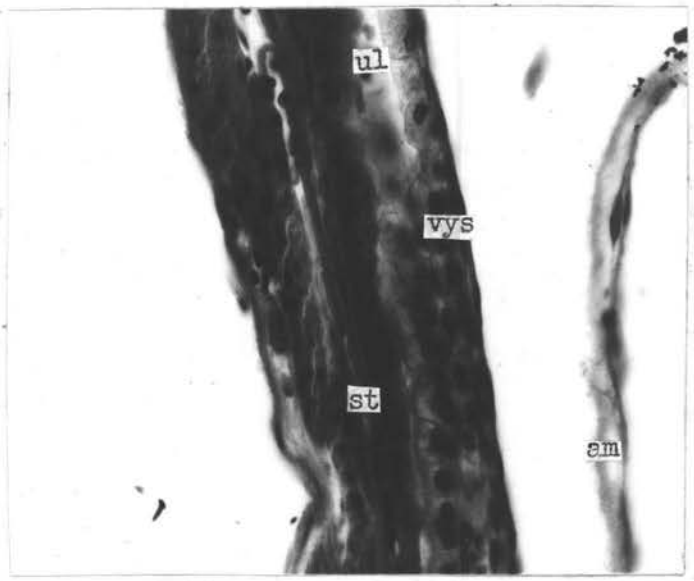

Fig. 11. Antimesometrial region at the end of the 15th day. The cuboidal epithelium of the visceral yolk sac forms the inner wall of the re-established uterine lumen (complete inversion). 516 X

Fig. 12. A topographic view of the allantoidean placenta at the end of day 15. 10 X