Placental Development in the Mongolian Gerbil (*Meriones unguiculatus*)

II. FROM THE ESTABLISHMENT OF THE LABYRINTH TO TERM [1]

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ABSTRACT   Placental development was studied in 24 gerbils from day 13 to term. Allantoic mesoderm contacts and vascularizes the chorionic–trager plate of germinal cytotrophoblast on day 13. Soon villous extensions penetrate the plate, carrying with them a covering of three layers of trophoblast derived from it. As the villi elongate, clumps of germinal cytotrophoblast are carried periph- erally by them. Further development of each villus results in a cylindrical mes- enchymal core with a central arteriole, and radially arranged branching lamellar extensions carrying capillaries derived from the villus arteriole. Germinal cyto- trophoblast clusters disappear near term, but some indication always remains of the trilaminar covering of the villus and its lamellae. A typical countercurrent blood flow pattern occurs. The trophospongium is derived from the ectoplacental cone and the mesometrial surface of the germinal cytotrophoblastic plate. Al- though a few clusters of small cells occur, it is essentially a giant cell tropho- spongium and never contains cells resembling the clear cells of the rat. Late in pregnancy it becomes much reduced in thickness. The unique subplacental gland begins to degenerate soon after placental establishment and is gone by the last half of pregnancy. The metrial gland begins development at midterm and be- comes a solid mass of cells filling the perivascular space of the mesometrial tri- angle at term.

In his classic studies on rodent placenta- tion, Duval (1891) described the placenta of a single specimen of *Meriones shawi* of unknown gestational age. This specimen was at the stage of incipient chorioallantoic placentation. Another study (Salzmann, '63), which is a small part of a general account of gerbil reproductive biology, deals in brief tabular form with placental development, and considers the uterine tissues in somewhat more detail. These two papers, both on *M. shawi*, a recent abstract on uterine structures during preg- nancy in *M. unguiculatus* (Fischer and Floyd, '71), and a companion study (Fischer and Floyd, '72) comprise the en- tire literature on gerbil placentation.

This study was undertaken, then, to give a more complete account of placental de- velopment in the Mongolian gerbil (*M. un- guiculatus*), and to compare and contrast these developmental events with those of its well-known relatives, the rat, mouse and hamster.

MATERIALS AND METHODS

Twenty-four pregnant gerbils from day 13 to term were autopsied. Their gestation sacs or placentae were prepared and stained for light microscopy as described elsewhere (Fischer and Floyd, '72).

OBSERVATIONS

Establishment of the chorioallantoic placenta

During the thirteenth and fourteenth days of gestation, when the embryo is

passing through the stage of fusion of the heart tubes, the allantois crosses the exocoelom, makes contact with and vascularizes the chorion, and establishes an interchange circulatory pattern with maternal blood channels.

Labyrinth. When the allantois first contacts the chorion, the latter collapses upon the base of the ectoplacental cone and fuses intimately with it, obliterating the epamniotic cavity (Fischer and Floyd, '72). The combined trophoblast of the chorion and base of the ectoplacental cone, being a very mitotically active zone, has been named the germinal cytotrophoblast (Davies and Glasser, '68). This germinal cytotrophoblast is originally a round disc of 5 to 15 cells in thickness, which lies just deep to the spreading allantoic mesenchyme and is attached to the circumference of the vascular yolk sac (fig. 1). It is an obviously cellular layer, made up of small, round basophilic cells (fig. 4). Nucleoli are prominent in the somewhat irregular nuclei. All cells of the disc are similar, there being little indication as to which cells were originally derived from chorion or ectoplacental cone. Loose stellate cells differentiate from the mesometrial surface of the plate of germinal cytotrophoblast (fig. 5). These cells will in part give rise to the trophospongium (basal zone) which is never invaded by fetal mesenchyme.

Almost as soon as the allantoic contact with the chorion is made, tongues of vascular chorio-allantoic mesoderm begin to penetrate the germinal cytotrophoblast disc (figs. 1, 2). As these tongues, or villi, penetrate, they are accompanied by germinal cytotrophoblast cells which immediately differentiate into two distinct coverings (fig. 2). The layer next to the vascular mesenchyme stains lightly with hematoxylin and eosin. Its cytoplasm is extensively vacuolated and cell boundaries, if any, are extremely vague (fig. 6). The nuclei of this layer are prominent, but not numerous. They are pale, slightly flattened cylinders and contain one or two very distinct, large nucleoli. This clear layer undoubtedly corresponds to trophoblast III of electron microscopic studies (Jollie, '64; Enders, '65) and will be referred to as such.

The germinal cytotrophoblast also appears to give rise to another layer covering trophoblast III. This layer is a dark basophilic sheet of extremely attenuated cytoplasm (fig. 6). At this stage it is at most about one-third as thick as trophoblast III. Since cell boundaries were not observed in this layer, it may also be syncytial. The nuclei of this layer are much like those of the germinal cytotrophoblast. They are round or oval, moderately condensed and contain a distinct nucleolus. Whereas the junction between germinal cytotrophoblast and trophoblast III was very sharp, this layer (which will be called trophoblast II since it position corresponds to electron microscopic descriptions) seems to gradually emerge from clumps of germinal cytotrophoblast (fig. 3).

Still a third layer covering the villi occurs. This layer is continuous with the underlying trophospongium, those cells which have just differentiated from the mesometrial surface of the plate of germinal cytotrophoblast. Such trophospongial cells are stellate, bathed in maternal blood (figs. 2, 5). Those adjacent to the protruding villi seem to flatten out against them, but processes still remain which contact other such cells or bridge from villus to villus (figs. 2, 3). The nuclei of this layer (trophoblast I, according to the nomenclature of Jollie ['64]) are very large and prominent. The perinuclear cytoplasm is abundant, but becomes very attenuated as it covers the villus. This cytoplasm, though basophilic, does not stain as intensely as that of trophoblast II. In some sections, all three trophoblastic layers can be distinguished (fig. 6), but usually layers I and II are difficult to discriminate.

As the newly established villi (composed of the vascular mesenchymal core plus the three trophoblastic coverings) continue to grow in length, clumps of germinal cytotrophoblast separate from the original plate and are carried peripherally (fig. 8). These clumps occur in various positions relative to the villus. Some are located between the villus mesenchyme and trophoblast II syncytium (fig. 7). Here they are in a position to contribute to trophoblast III and II as the villus enlarges. It has been suggested that some angiogenic mesenchyme is derived from trophoblast

(Davies and Glasser, '68). If true, these clusters of cells would be opportunely placed for that purpose.

Other clumps of germinal trophoblast, apparently derived from near the mesometrial surface of the plate, migrate to the villus apices (fig. 7). It is possible that they could serve as a common origin for cells of trophoblast I as well as trophospongium.

Embryonic blood now circulates in the placenta. Blood is distributed to all villi and descends to the villus tips within large capillary loops (figs. 3, 7). Venous blood is collected from these loops at the placental surface.

Heretofore there has been little apparent organization of maternal blood circulation. Now, however, a single placental artery enters the decidua basalis by piercing the myometrium. Its wall then changes from the typically muscular artery to become a compact sheath of decidual cells (figs. 1, 11). The "sheathed artery" follows a tortuous, coiled path to the lateral edge of the subplacental gland. As it turns around the edge of the gland, its walls are invaded and replaced by giant cells from the trophospongium. This trophoblastic arterial channel conducts the blood to a large blood space just below the plate of germinal cytotrophoblast (fig. 1). From here, it flows within large trophoblastic spaces between the villi of the labyrinth (figs. 2, 3, 7) percolates through the underlying trophospongium, and drains into venules of the decidua basalis.

Trophospongium. The massive trophospongium occupies more than half of the thickness of the placental disc (figs. 1, 8). Its more central cells, recently derived from germinal cytotrophoblast, are small and stellate, with large, vesicular nuclei and prominent nucleoli. Peripherally, there is a gradual metamorphosis to secondary giant cells. These giant cells are variously shaped; some remain stellate while others become polygonal or round (fig. 9). They are typical uninucleate giant cells with a cytoplasmic volume hundreds of times greater than that of their precursors, and contain highly polyploid nuclei. They have never been observed in mitotis. These giant cells have an affinity for maternal blood cells, which they apparently phagocytose in large numbers. The significance of this phenomenon, which commonly occurs in many species, is under investigation.

Other cell types are also present within the trophospongium. Near the tips of villi of the labyrinth, clusters of germinal cytotrophoblast cells have invaded the trophospongium to a limited extent. These clusters are composed by mitotically active, basophilic cells. They are always surrounded by a complete layer of trophospongial stellate cells. Also present are some clusters of small, round, clear cells and multinucleate basophilic cells, also surrounded by the typical stellate cells. These cells are presumably derived from germinal cytotrophoblast clusters, but their significance is unknown.

Decidua. Because of the rapid expansion of the 13–14 day conceptus, the decidua capsularis and decidua parietalis are being stretched and thinned. The decidua capsularis between the conceptus and the subplacental gland is being rapidly encroached upon and destroyed by advancing giant cells. Little healthy decidua remains here. However, basal to the subplacental gland the decidua basalis remains quite thick. Eosinophilic granular cells are extremely numerous now in this decidua.

Subplacental gland. At this time the subplacental gland (Fischer and Floyd, '72) has become a slightly thinned concave disc (concavity toward the embryo) because of the expansion of the conceptus (fig. 1). The central half, which, because of decidual degeneration, is becoming exposed to the giant cells, now begins to regress. There are several areas of pyknotic nuclei, and most of the cords nearest the conceptus have formed multinucleate, degenerate masses of cytoplasm (fig. 9).

The basal half, however, is still well developed. Many mitotic figures are present and glandular cords continue to invade the decidua basalis (fig. 10).

Hereafter, the blood supply to the subplacental gland is exclusively derived from sinusoids draining the trophospongium. These large sinusoids almost completely surround every cord of the gland and then collect into venules of the decidua basalis.

Development and expansion of the labyrinth

The period of the fifteenth through the eighteenth day of gestation is concerned with modifications of the various fetal membranes to bring them to their definitive states. On the other hand, this is the time of rapid regression of most of the maternal tissue.

Yolk sac. The bilaminar omphalopleure remains intact throughout this period, and changes little. However, villi are forming and elongating on the vascular splanchnopleure. At the junction of vascular yolk sac and bilaminar omphalopleure (at the mesenchymal circumference of the placental disc) a rapid proliferation of parietal endoderm cells and Reichert's membrane occurs. This new, spreading sheet of endoderm invaginates into the neighboring chorio-allantoic mesenchyme and separates this mesenchyme from the trophoblast of the placental surface. The endoderm also closely invests all vessels communicating with the placental surface. Thus, the mesenchyme is displaced centrally, and is separated from the placenta by an endoderm-lined sinus, originally noted in the rat by Duval (1891) (fig. 17).

Labyrinth. The relative thickness of the labyrinth increases to about four-fifths of the placental disc by the eighteenth day, due to the increase in length of the original villi.

The villi are organized as cylinders made up of a core of mesencyhme, each carrying a single central fetal arteriole and lined by the three layers of trophoblast. This organization becomes more obvious in the later stages (figs. 18, 19). From the periphery of the cylinder, flat, branched, mesenchymal lamellae extend outward and interdigitate with similar lamellae from the same or adjacent villi (fig. 18). The lamellae are also lined by the trilaminar trophoblast, and contain tortuous fetal capillary networks. Numerous trophoblast I cells span the distance between adjacent lamellae and divide the interlamellar maternal blood space into innumerable trophoblastic tubules (fig. 19).

The germinal cytotrophoblast at the placental surface is now a layer of three to five cells in thickness. There is, however, widespread migration and scattering of germinal cytotrophoblastic cell clusters throughout the labyrinth (fig. 12). They may occur at any point along the length of the villi or their lamellae. At the tips of the villi there is a general coalescence of germinal cytotrophoblast into a thin shell separating labyrinth and trophospongium (fig. 13).

The pattern of both fetal and maternal blood circulation has now become quite clear. Fetal arteries cross the endodermal sinus and each immediately enters a single placental villus. It travels, unbranched, to the villus tip, where it divides into a spray of capillaries which meander back toward the placental surface within the lamellae of that villus. Near the surface, these capillaries coalesce into short veins at the periphery of the villus.

The maternal blood supply is essentially as described in the preceding stage, except that now trophoblast giant cells have completely usurped the arterial wall of the sheathed artery within the decidua basalis. The trophoblastic tubules of the labyrinth are of a considerably smaller caliber than heretofore, and are more definitely arranged between the adjacent lamellae (figs. 18, 19).

Trophospongium. There is little change in the trophospongium, except that it has become thinner relative to the labyrinth. This is due to the rapid expansion of the entire conceptus, not to diminished growth of the trophospongium. The shell of germinal cytotrophoblast separating it from the labyrinth continues to generate trophospongial cells as well as cells of trophoblast I for the labyrinth.

The giant cells are now becoming the dominant cell type of the trophospongium. At the circumference of the placental disc is a zone made up entirely of trophospongial giant cells (fig. 13).

Decidua. There is a marked thinning and degeneration of the decidua capsularis and parietalis. In some specimens the capsularis breaks down completely by day 18 but in others this does not occur until well into day 20 of gestation.

Likewise, the decidua basalis is thinning rapidly. Many large anastomosing venous channels draining the placenta give the area a spongy appearance (fig. 14). The

granular cells still make up a significant part of the cell population in this region.

Subplacental gland. The subplacental gland undergoes almost complete involution during this period. There are numerous areas of pyknosis, and many multinucleate degenerate clumps near its border with the decidua basalis. Giant cells from the nearby trophosphongium encroach upon the gland remnants and many masses are completely surrounded by them.

Metrial gland. In contrast to the regression of other maternal tissues, the metrial gland now gradually develops and differentiates. The gland forms definite sheaths around vessels of the mesometrial triangle. Various cell types are present in the metrial gland region. In addition to the more common spindle-shaped cells, large and small round cells occur, some of them vacuolated. Some cells contain prominent eosinophilic granules which resemble those of the endometrial granulated cells of the decidua basalis (fig. 15).

The mature placenta

During the period from about day 19 of gestation to parturition, which usually occurs from days 24 to 26, the definitive fetal membranes appear. Once established, little change except growth in size occurs during this last six- to eight-day period.

Yolk sac. At about the twenty-third day, Reichert's membrane ruptures and contracts down to a much folded and convoluted membranous mass at the circumference of the placental disc. All parietal endoderm cells and remaining primary giant cells also become included in this mass. Thus, due to prior decidual degeneration, the endoderm of the visceral yolk sac is now exposed to the uterine lumen, and inversion of the germ layers is complete.

Labyrinth. The labyrinth has now grown until it constitutes about seven/eighths or more of the total thickness of the placental disc. The basic structure of the labyrinth is as was previously described (figs. 18, 19). The clusters of germinal cytotrophoblast are fewer, and gradually decrease until near term when they are absent. The placental barrier is extremely thin at this time and its layers distinguished only with difficulty. Trophoblast III is still a clear, vacuolated layer next to fetal capillaries and mesenchyme. The nuclei are scarce and condensed, in contrast to their earlier pale appearance (fig. 21).

Trophoblast I cells are conspicuous where the perinuclear cytoplasm and nucleus bulge into the maternal blood tubule. Their nuclei are large, several times the size of trophoblast II nuclei, and are also moderately condensed (fig. 21). The cytoplasm of trophoblast I in the perinuclear regions is not as intensely basophilic as that of trophoblast II, but elsewhere is too attenuated to be visible as part of the placental barrier.

Trophospongium. The trophospongium is thin during the definitive period. Early in the period several clusters of small germinal cytotrophoblast cells are present, surrounded by giant cells. These soon disappear. Thus, in the final days, a trophospongium composed of one to three layers of giant cells is all that remains (fig. 20). Near term, many of these giant cells also degenerate, leaving only a few scattered healthy cells to represent the once considerable trophospongium.

Decidua. No trace of the decidua capsularis or parietalis remains, and the decidua basalis undergoes marked thinning. Many necrotic areas appear in the decidua basalis adjacent to the trophoblast giant cell layer. The network of venous channels enlarges and coalescences into a few extensive venous sinuses that occupy most of the space of the decidua basalis (fig. 22). There is no remnant of the subplacental gland.

Metrial gland. This period marks the height of development of the metrial gland. It is now a mass of compact, large cells that fills all the space around and between vessels of the mesometrial triangle (fig. 22). There are many large granular cells scattered throughout and many large palely staining cells with large nuclei. The latter seem to be especially associated with arteries (fig. 23).

DISCUSSION

Timing of developmental events. In comparison with the other commonly studied myomorph laboratory rodents, placental development in *M. unguiculatus* is remarkably slow (table 1). Even though

TABLE 1

Comparison of timing of developmental events in myomorph rodents [1]

Event	Species				
				Gerbil	
	Rat	Mouse	Hamster	M. shawi	M. unguiculatus
Implantation	6 [2]	5 [5]	6 [7]	5 [8]	8 [9]
Amniogenesis	8 [3]	7 [6]	7 [7]	7 [8]	12 [9]
Obliteration of Epamniotic cavity	9 (early) [6]	8 [6]	8 [7]	9 [8]	13
Establish. of Chorio-allantoic placenta	9 [2,4]	9–10 [6]	9 [7]	9 [8]	14
Rupture of Reichert's membrane	16 [2]	15–16 [6]	14 [7]	—	23
Parturition	21–22 [2]	19 [6]	16 [7]	20 [8]	24–26

[1] Each column lists days of gestation.
[2] Bridgman, '48a.
[3] Bridgman, '48b.
[4] Davies and Glasser, '68.
[5] Boyd and Hamilton, '52.
[6] Amoroso, '52.
[7] Orsini, '54.
[8] Salzmann, '63.
[9] Fischer and Floyd, '72.

there is a difference of several days in total gestation length, the timing of events through placental establishment is uniform in the rat, mouse, hamster, and even M. shawi. The early stages in M. unguiculatus, however, all lag behind, beginning with implantation one to two days late, and continuing slowly to placental formation five days later than the other related forms. However, Reichert's membrane remains until two to three days before parturition in all these species except the rat, where it ruptures earlier. One of the more unusual aspects is that M. unguiculatus should differ so greatly from its close relative, M. shawi, a North African gerbil. As can be seen from table 1, M. shawi corresponds closely to the other myomorph species (Salzman, '63). Not included in the table is the development of the subplacental gland. This gland begins development in M. shawi on day 7 and degenerates by day 13, while in M. unguiculatus the glandular development commences at day ten and complete degeneration doesn't occur until day 18. Thus here also is a lag in development.

Special features of gerbil placentation. In most respects the placenta of Meriones closely resembles that of other muroid rodents (table 2). A most unusual feature is the presence in the decidua basalis of a mass of epithelial cords derived from uterine epithelium, the subplacental gland. This structure was first observed by Salzmann ('63), who called it the "basophilic cell complex." He also recognized its origin from the uterine epithelium and surmised that the cells might be rich in RNA. We have previously termed this structure the "subplacental gland" on the basis of its histological structure (Fischer and Floyd, '71, '72). It is composed of an intricate system of thick and narrow epithelial cords branching from the epithelium of the original uterine lumen. These cords invade and almost completely displace the decidua basalis. Large venous sinusoids of the decidua basalis remain, however, and come to envelope the cords of the gland. This intimate association of vascular and epithelioid structures is characteristic of most endocrine glands.

The blood supply of the subplacental gland is unusual, for it does not seem to contain capillaries supplied with arterial blood. Instead, venous blood draining the placenta enters and flows through the sinusoids of the gland. The significance of this "portal" vascular arrangement is un-

TABLE 2

Synopsis of basic data on the fetal membranes of Meriones

Implantation
 Orientation of disc: mesometrial.
 Orientation of first attachment: antimesometrial.
 Depth: interstitial, but shallow.

Decidua
 Capsularis: complete.
 Parietalis: zonary.
 Basalis: contains unique subplacental gland.

Amniogenesis: by folds which divide a common proamniotic cavity (formed by
 invagination of trophoblast basal to the inner cell mass) into amniotic and
 epamniotic cavities.

Chorion: an early, temporary, membrane forming the internal limit of the epamniotic
 cavity. Fuses with the ectoplacental cone.

Yolk sac:
 Bilaminar omphalopleure: ruptures several days before parturition; forms
  endodermal sinus on placental surface.
 Choriovitelline placenta: none.
 Vascular yolk sac: complete inversion; villous overall.

Chorio allantoic placenta
 Shape: discoid.
 Type: labyrinthine.
 Fine morphology: probably hemo-trichorial.
 Location: mesometrial.

Allantoic vesicle: none.

clear, but may be important in understanding the gland's function.

A related unusual feature of gerbil placentation is the position of the main maternal arterial channel supplying the placenta. In other muroid rodents this channel ascends directly through the decidua basalis and the center of the placenta to reach the surface. In *Meriones*, because of the development of the massive subplacental gland in the decidua basalis, the placental artery must course laterally to bypass the gland before entering the placenta. Therefore, the arterial channel traverses the placenta eccentrically rather than centrally.

A further difference in *Meriones* placenta occurs in the trophospongium. In the rat, the clear, vacuolated "glycogen cells" form a conspicuous part of the trophospongium. Their origin has been a source of past debate (Davies and Glasser, '65). No such cells occur in the gerbil trophospongium. There are many nests and clusters of cells in the early stages of chorio-allantoic placentation, but these are all of the germinal cytotrophoblast type. Some of these clusters evidently coalesce into multinucleate giant cells which seem to be transient and soon degenerate.

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PLATE 1

EXPLANATION OF FIGURES

All figures are oriented with the mesometrial side down.

1   Placenta, day 14. The allantoic mesenchyme (M) has spread over the germinal cytotrophoblast plate (arrowheads), and villi (encircled) penetrate it at irregular intervals. Below the extent of the villi is the trophospongium (Tr). Large blood sinusoids (B) intervene between the trophospongium and the subplacental gland (SG). Within the decidua basalis (D) is found the tortuous, sheathed placental artery (arrows). × 21.

2   Labyrinth of the day 14 placenta. The germinal cytotrophoblast plate (GC) is penetrated by vascular villi (V) covered by thin trophoblastic layers derived from the plate. Extensions of germinal cytotrophoblast are being carried with the villi. Maternal blood (MB) circulates in coarse trophoblastic tubules between stellate cells of trophoblast I. × 85.

3   Detail of villus from figure 2. The fetal capillary loop (FC) is covered by a clear trophoblastic layer (arrowheads) derived from the adjacent germinal cytotrophoblast cells (GC). A dark trophoblastic layer covers the clear one. Cells of the outermost layer (arrow) bridge across the maternal blood tubule (MT) to neighboring villi. × 214.

4   Detail of germinal cytotrophoblast plate, day 14. The plate is homogeneous except for the lower layer which is differentiating into cells of trophoblast I (Tr I) and trophospongium. Maternal blood (MB). × 343.

5   Trophospongial cells, day 14. Differentiating from deeper clusters of germinal cytotrophoblast, the large, stellate trophospongial cells (arrow) are bathed in maternal blood. × 343.

6   Detail of a villus tip, day 14. Occasionally nuclei of all four layers separating fetal (F) and maternal (M) blood can be compared. They are: trophoblast layers I, II, and III, and fetal endothelium (FE). × 853.

PLATE 2
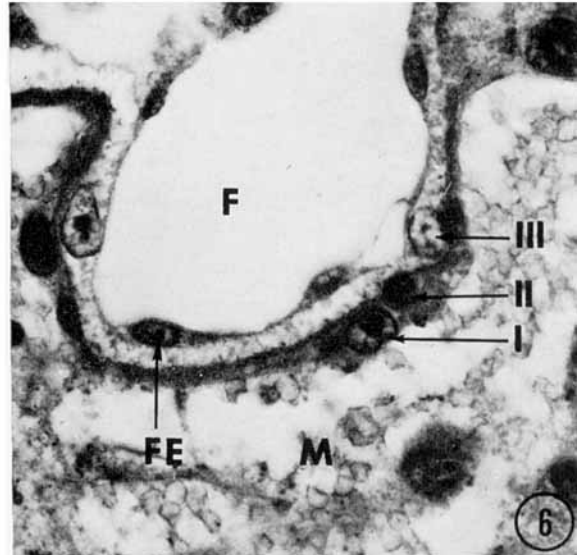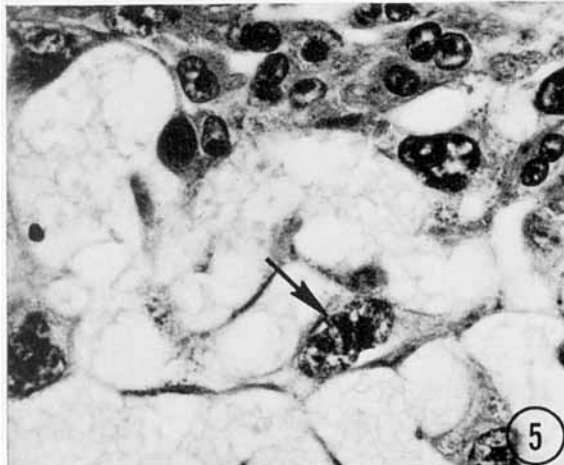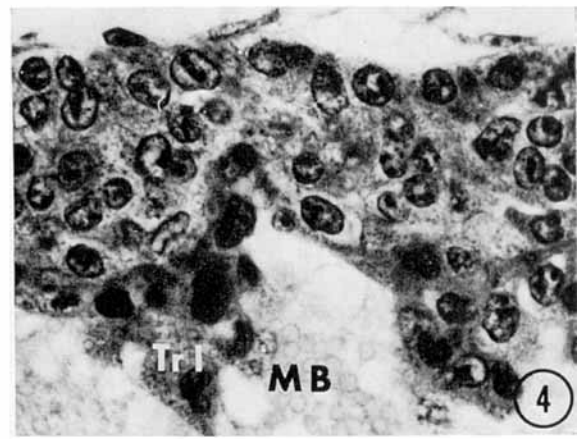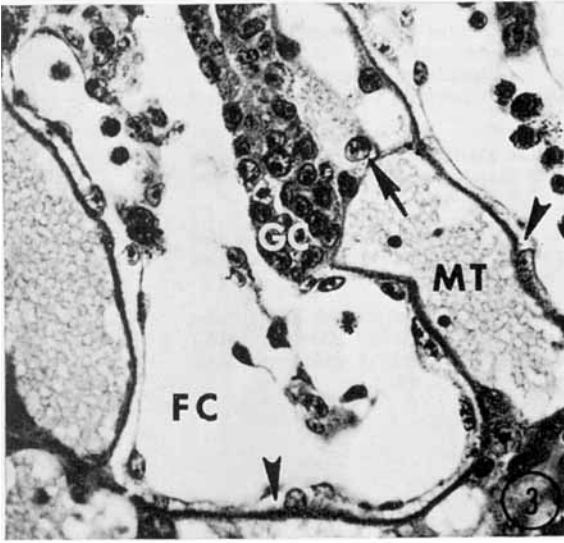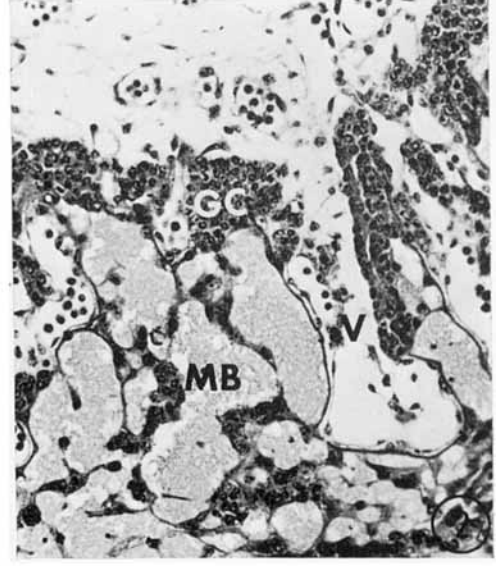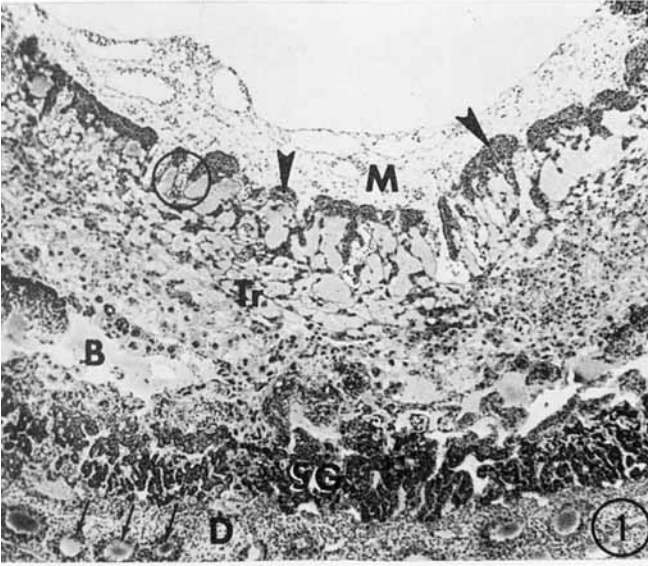
7 Villus tip, day 14. A fetal capillary loop (FC) descends between two clusters of germinal cytotrophoblast. Other clusters are more externally situated (arrow). × 343.

8 Placenta late in day 14. Villi have elongated (compare with fig. 1), and there is extensive migration of germinal cytotrophoblast cell clusters along them (arrow). Degenerate multinucleate masses of the subplacental gland (SG) occur in the trophospongium. × 21.

9 Junction of trophospongium and subplacental gland, day 14. Uninucleate trophoblast giant cells (arrows) are associated with numerous maternal leucocytes, and surround multinucleate masses of degenerate subplacental gland (DSG), although normal subplacental gland (SG) cells are present below. × 85.

10 Cells of basal aspects of subplacental gland, day 14. Two-cell thick cords of very basophilic subplacental gland cells penetrate the lighter decidua basalis. × 853.

11 Sheathed placental artery, day 14. The tortuous artery (A) has lost its typical muscular coat and appears to have a wall of modified decidual cells. Decidua (D). × 85.

12 Placental surface and labyrinth, day 16. A fetal vessel (FV) runs in the surface mesenchyme and a maternal arterial channel (MA) near the surface. Note the scattering of germinal cytotrophoblast (arrows) clusters throughout the labyrinth. × 85.

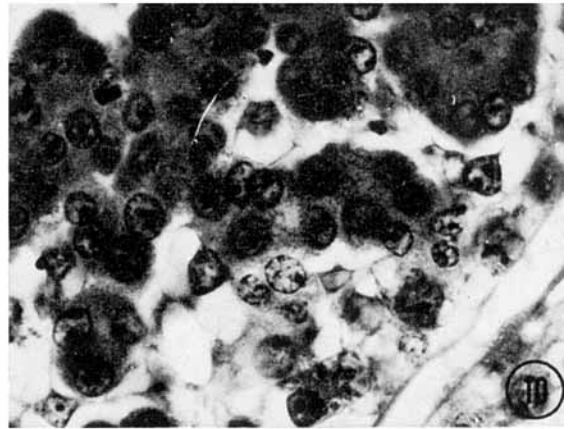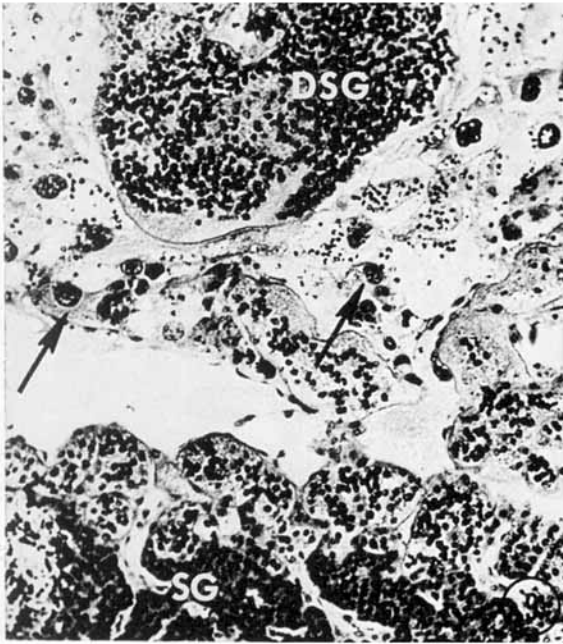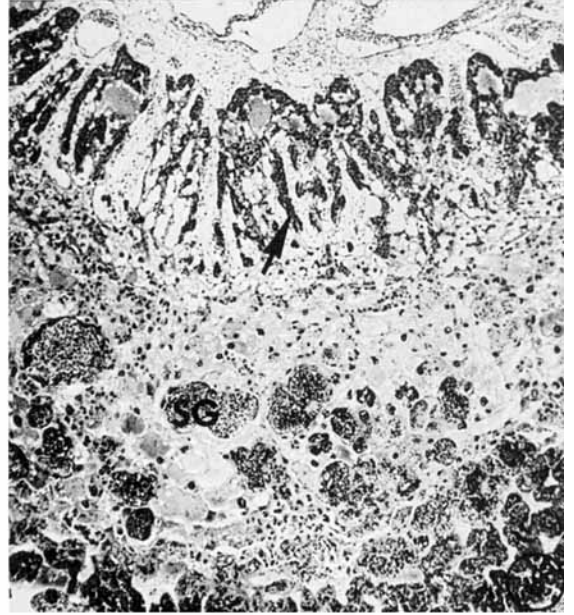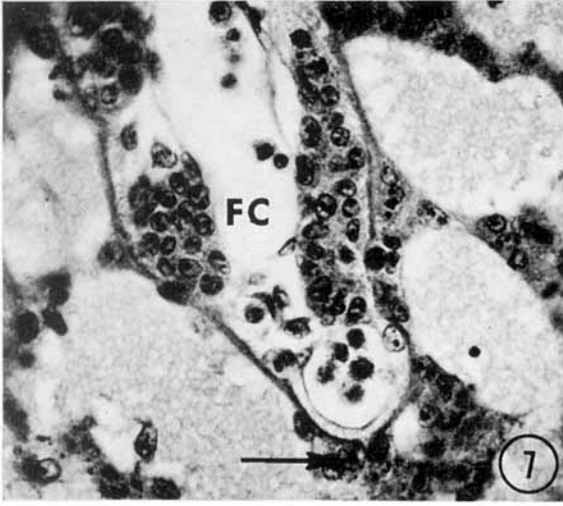13 Labyrinth–trophospongium junction, day 17. An almost complete layer of germinal cytotrophoblast cells (arrow), continuous with the clusters in the labyrinth, intervenes between the labyrinth (brackets) and the giant cell trophospongium (Tr). × 85.

14 Decidua basalis and deep aspect of placenta, day 18. The decidua is riddled with large venous channels (V) and a placental artery (A). The trophospongium is thinning now to a layer of only several giant cells (arrows) in thickness. × 21.

15 Mesometrial veins and metrial gland cells, day 18. Two veins (V) of the mesometrial triangle are shown, surrounded by a sheath of spindle-shaped metrial gland cells. Some of these are developing granules (arrow). × 214.

16 Placenta, day 20. × 21.

17 Placental surface, day 20. Endoderm (arrows) from the bilaminar omphalopleure has invaded across the placental surface to separate placental trophoblast from the surface mesenchyme. Endodermal sinus (ES). × 85.

18 Labyrinth, day 20. A villus (Vi) with central arteriole and numerous branching lamellae (arrows) is the functional unit of the placenta. × 85.
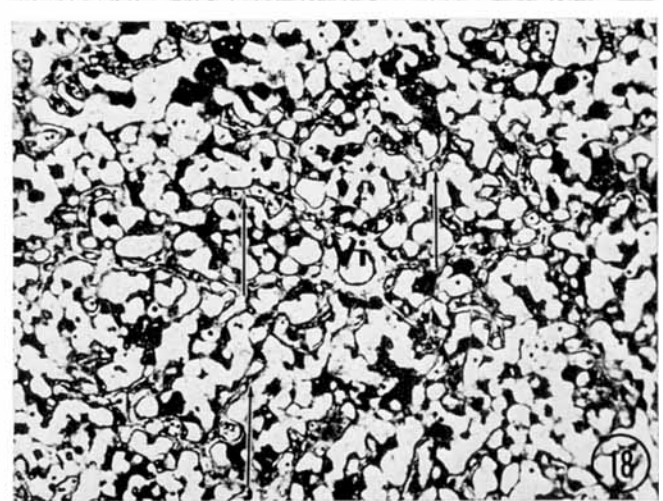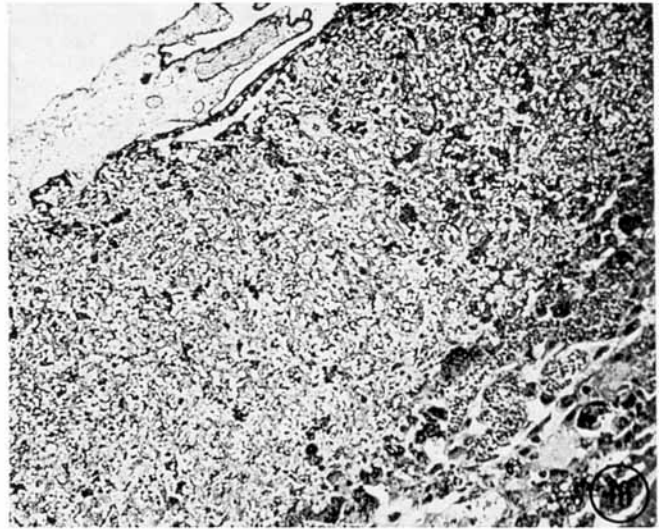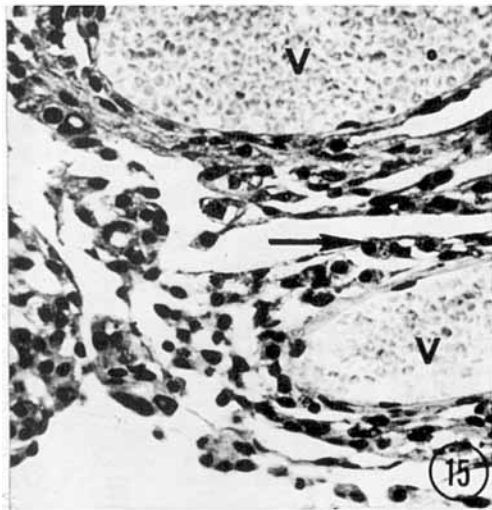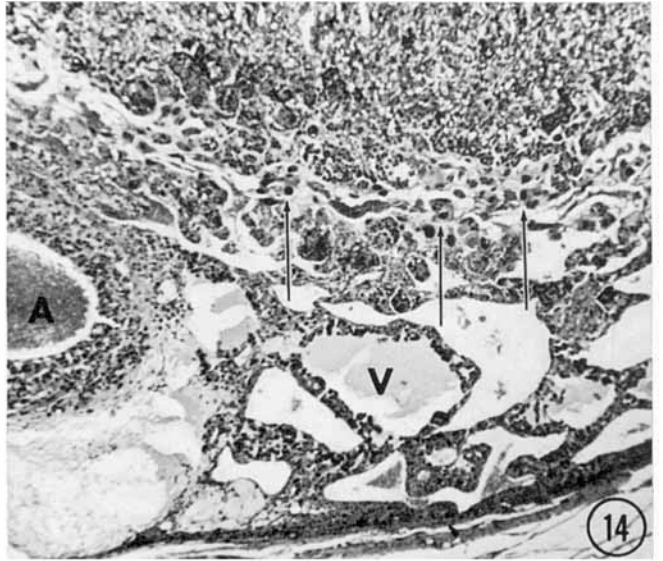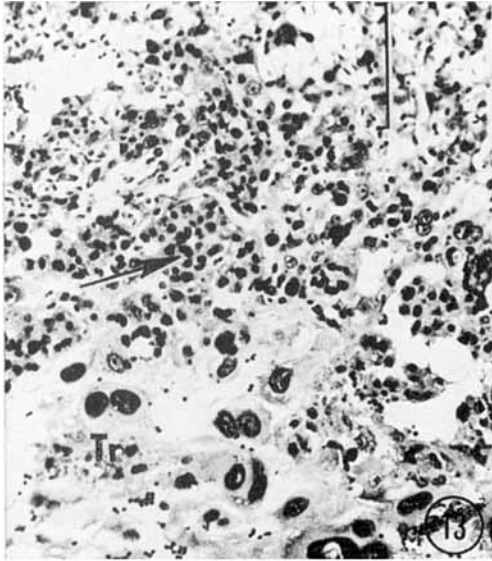
Theodore V. Fischer and Alton D. Floyd

PLATE 4

19 Detail of lamella from figure 18. Numerous capillaries (arrows) occur in the lamellar mesenchyme. Lamellae are connected by the large dark cells of trophoblast I (I), which convert the interlamellar space into tortuous maternal blood tubules (MT). × 214.

20 Placental base and zone of junction with maternal tissues, day 24. A fetal arteriole (A) within a villus is shown giving off one of its radial branches to a lamella. The trophospongium is reduced to a few cell layers covering one of the large maternal venous channels (V). × 85.

21 Placental labyrinth, day 24. The clear cytoplasm of trophoblast III (III) is still discernible, but trophoblast I and II (I&II) appear as a single dark layer. Nuclei of fetal endothelium (NE), and trophoblast I (NI), II (NII) and III (NIII) can be differentiated. Maternal blood tubule (MT). × 853.

22 Metrial gland, day 24. Between the vessels of the mesometrial triangle are packed the cells of the metrial gland (MG). A large placental vein (V) occurs in the remnants of decidua. × 21.

23 Detail of the metrial gland from figure 23. An artery (A) is surrounded by a sheath of large clear cells of the metrial gland. Smaller cells occur around veins and between vessels. × 85