ELECTRON MICROSCOPIC OBSERVATIONS ON THE VILLOUS HAEMOCHORIAL PLACENTA OF THE NINE-BANDED ARMADILLO (*DASYPUS NOVEMCINCTUS*)

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INTRODUCTION

Studies of the fine structure of placentas of the haemochorial type have been made by Dempsey (1953, 1954), Boyd & Hughes (1954), Wislocki & Dempsey (1955*a*, *b*), and Sawasaki, Mori, Inoue & Shinmi (1957). Electron microscopic observations of placentas of other types have been reported by Dempsey, Wislocki & Amoroso (1955), Dempsey & Wislocki (1956), Amoroso & Matthews (1958), and Wimsatt (1958). Examination of the labyrinth of the rat placenta revealed not only that the trophoblast is present through day 21 of gestation, but also that it is cellular rather than syncytial (Wislocki & Dempsey, 1955*a*). Studies of the villous haemochorial placenta of the human by Boyd & Hughes (1954), Wislocki & Dempsey (1955*b*), and Sawasaki *et al.* (1957) have confirmed the belief that the trophoblast covering the vascular villi is syncytial and have also demonstrated that individual Langhans cells may persist until term. The nature of the syncytium was especially clearly elucidated by the studies of Wislocki & Dempsey (1955*b*) who found that the syncytium was characterized by the presence of numerous microvilli and frequent amorphous vacuoles in addition to the usual organelles.

Recent histological studies concerning placentation in the armadillo (Enders, Buchanan & Talmage, 1958; Enders, 1959) have shown that the epithelium of the vascular villi is syncytial and possesses a variable free surface. These studies also indicate that the syncytial trophoblast is derived from the cytotrophoblast and that both the cell columns and the modified fibroblasts seen in the stroma of mature vascular villi may be glandular. In the electron microscopic study reported here special attention has been paid to (1) the nature of the placental barrier, (2) the organization of the syncytium, and (3) cytological evidence of glandular activity.

MATERIALS AND METHODS

Pregnant female armadillos were killed by abrupt fracture of the vertebral column. The uterus was excised immediately and cubes of placenta of 2 mm. or less were fixed in Palade's (1952) veronal acetate buffered osmium tetroxide for $\frac{1}{2}$–1 hr., or in Dalton's (1955) chrome osmium fixative for 1 hr. Following fixation the blocks of tissue were dehydrated in several changes of ethyl alcohol and embedded in methacrylate, and sections were made on a Porter–Blum mechanical advance microtome. Initial examination of the material was made using an RCA–EMT electron microscope. Electron micrographs of the better specimens were made with an RCA–EMU 3B electron miscrope. Other portions of the placentas were fixed for routine histological preparation. If the histological preparations did not

indicate that the placenta was normal for its stage of development, the methacrylate-embedded sections were rejected. In all, placentas from seven animals were used: three from the period of initial invasion, three from the period of expansion of the placenta, and one from the period of the mature placenta. Implantation was induced by bilateral ovariectomy in the three cases collected from the period of placental invasion. The other placentas came from animals from the feral population. In addition to the placental material, five blastocysts from animals in the period of delay of implantation were prepared by the procedures described above.

DESCRIPTION

Syncytium

The placental barrier in the villous haemochorial placenta of the armadillo consists of the trophoblastic epithelium, an underlying basement membrane, and the endothelium of the foetal capillaries. Study of the electron micrographs of vascular villi reveals that the trophoblast covering these structures is truly syncytial (Pl. 1, fig. 1). Its free surface is characterized by the presence of numerous, branched, lamelliform microvilli (Pl. 2, figs. 4–6). The number, nature, and complexity of the microvilli vary within a single placenta, as might be expected from observations with the light microscope. The microvilli appear to be folds in the surface membrane of the syncytium. In areas of greater complexity they are not simple extensions but rather are projections from protruding masses of cytoplasm which extend into the intervillous space. At its base each fold is long and usually curved, becoming narrower at its distal apex, which is rounded. Secondary folds are continuous with the initial fold. Although the length from the surface and extent along the surface vary, the thickness of the folds is relatively constant. The result of this arrangement of the microvilli is an uneven surface composed of folds of the cytoplasmic membrane which terminate distally at simple rounded projections, with cup-like spaces between the bases of the folds. The complexity of these microvilli is clearly revealed in Pl. 1, figs. 2 and 3 and Pl. 2, fig. 6. The microvilli are somewhat shorter and more numerous in the mature placenta.

The total thickness of the syncytium is increased at the locations of the nuclei. Although there is ordinarily only a thin layer of cytoplasm which is relatively free of microvilli covering the distal aspect of the nuclei, there is always an appreciable thickness of cytoplasm separating the nuclei from the basement membrane. The nuclei are characterized by the presence of a single, large nucleolus.

Within the cytoplasm of the syncytium are numerous rod-like mitochondria with well-defined cristae. The cristae are not in a highly ordered parallel arrangement but are more commonly villiform. Mitochondria are more numerous near the free surface of the syncytium, and are frequently oriented parallel to it. A few are also associated with the basal cytoplasm. The mitochondria do not appear to alter greatly in structure or number from the period of placental expansion to the period of the mature placenta.

The endoplasmic reticulum is largely confined to the distal cytoplasm. During the period of placental expansion double strands of reticulum are commonly found in concentric circles within protoplasmic projections into the intervillous space (Pl. 1, fig. 1). In the juxtanuclear cytoplasm and other areas beneath the general

level of the surface of the syncytium, occasional double strands of reticulum are seen in addition to numerous endoplasmic vesicles or branched cisternae. The form of the reticulum varies considerably; strands in the promontories and cisternae in the distal cytoplasm are most commonly encountered. The electron-dense particles of the particulate component (Palade's particles, presumably ribonucleoprotein) are found free in the cytoplasm as well as associated with the reticulum. In the mature placenta protoplasmic projections into the intervillous space are less frequently encountered, and the endoplasmic reticulum is characteristically in the form of dilated cisternae which contain an amorphous material of moderate electron density.

The membranes and vesicles of the Golgi complex are located at the basal margin of the region of the syncytium in which endoplasmic cisternae are found. In other words, they are directly distal to the morphologically distinct basal cytoplasm of the syncytium. Although the individual regions of Golgi membranes lie at the same level within the syncytium, there is no evidence that they are continuous. The form and extent of these regions are comparable to those of non-syncytial glandular cells. The increase in cytoplasmic density and in number of ribonucleoprotein granules found in the cytoplasm of the syncytium of the mature placenta makes the Golgi complex difficult to discern at this stage, but its relative position remains the same.

Beneath the Golgi membranes is an area of cytoplasm containing canaliculi formed by the invagination of the basal membrane of the syncytium (Pl. 1, fig. 2). The appearance of the canaliculi in sections indicates that they are tortuous and probably branched. In later pregnancy the canaliculi are more extensive and may be in partially dilated or non-dilated form (Pl. 2, fig. 5). Filamentous structures are frequently found within this area of the cytoplasm, giving it a fibrillar appearance.

Stroma

The basement membrane which underlies the syncytium is composed of a felt-work of an amorphous material of moderate electron density and a few collagen fibres (Pl. 1, fig. 2). The stroma of vascular villi contains a few collagen fibres in the period of placental expansion. In the mature placenta, however, collagen fibres are a conspicuous component of the basement membrane and the connective tissue in general.

The endothelial cells forming the foetal capillaries are relatively unspecialized except for the occasional microvilli and the frequent presence of lipid droplets. At no time in pregnancy are discontinuities or areas of especial thinness found in the endothelial cells (Pl. 2, fig. 1).

The fibroblasts have irregular outlines with numerous processes which may abut on adjoining fibroblasts. There is no indication that the cytoplasm of these cells is ever continuous. The cytoplasm of the fibroblasts contains a few mitochondria and strands of endoplasmic reticulum with frequent vesiculations. The ground substance of the cytoplasm is not very electron-dense in the early stages. The Golgi membranes are inconspicuous. The mature placenta, however, contains numerous highly modified fibroblasts. These are rounded cells containing a vast array of dilated endoplasmic cisternae. The extent of dilation is somewhat variable. Within the cisternae is a finely granular and moderately electron-dense substance. Ribonucleoprotein granules are abundant and are clearly associated with the membranes

of the reticulum which completely fills the cytoplasm except in the region of the Golgi complex and in small areas where a specific granulation is observed (Pl. 5, fig. 12). The Golgi complex of these cells occupies an area nearly as large as that of the nucleus and is primarily composed of numerous concentric strands of Golgi membranes (Pl. 5, fig. 11). Contained within this region are a few vesicles derived from the reticulum, Golgi vesicles, mitochondria, and unidentified background substance.

Cell columns

Cell columns form the proliferating tips of the vascular villi from which they are separated by a layer of syncytium (Pl. 3, fig. 7). The syncytium overlying the free surface of the cell columns is exceedingly thin, but in all instances observed it forms a complete covering. Between the cells of the cell columns are numerous spaces (Pl. 3 fig. 8). Within the individual cells lipid droplets are common and mitochondria are present but are not especially numerous. A scant reticulum is generally present in addition to the numerous ribonucleoprotein granules that are seen free or in clusters in the cytoplasm. Occasional lipid droplets are surrounded by concentric rings of reticulum. The Golgi complex is poorly developed in these cells. Within the intercellular spaces large accumulations of a granular substance of moderate electron density are seen. In the regions abutting on the intercellular masses the cell membranes are occasionally indistinct, and a granulation similar in density to that of the intercellular granules is discernible in the adjacent cytoplasm. In no instances was a basement membrane observed underlying the syncytium covering the cell columns. However, where the cells of the cell columns are in close association with the syncytium, desmosomes (terminal bars, adhesion zones) are present, and associated filaments (tonofibrils) can be seen in the cytoplasm (Pl. 3, fig. 7; Pl. 4, figs. 9, 10). The thin syncytium overlying the cell columns frequently contains vacuoles, in some of which granular material of identical appearance to that of the intercellular substance is seen. This overlying syncytium displays great irregularity in thickness. Although microvilli are common in some areas, they are sparse in others and never show the complexity seen in other portions of the placenta. The desmosomes vary in area from small points of contact to complete sheaths surrounding a projection into the syncytium. Frequently the paired adhesion plates of the individual desmosomes are readily apparent (Pl. 4, fig. 10).

Preliminary observations on early implantation

Blastocysts and early implantation stages proved to be more difficult to fix than did the placenta of the expansion period and the mature placenta. Nevertheless, preliminary observations of these stages are of considerable interest. The abembryonic trophoderm of the blastocyst is composed of a single layer of epithelial cells without any indication of internal or external supporting membranes (Pl. 6, fig. 16). The adjacent cell surfaces interdigitate only toward the basal end of the cells. These interdigitations are not the peg or tongue-in-groove type commonly present in epithelia (Fawcett, 1958) but are plaque-like extensions of the cytoplasm. The basal plasma membrane (fronting on the blastocoel) of the cells is relatively smooth, but microvilli are present on the convex distal surface. The mitochondria are most

numerous near the surfaces of the cells, but a few are also found near the basal membranes. Our observations are insufficient to permit description of the other organelles.

The invasive trophoblast is characterized by the presence of numerous small vesicles of undetermined origin, and fat droplets. The cytoplasm is not very electron-dense, and ordinarily only scattered mitochondria are discernible. The surfaces of the tongues of invasive syncytium frequently display numerous simple microvilli. These microvilli are confined to areas where the trophoblast is free from contact with epithelial cells. The tongues of syncytium are most frequently seen in the connective tissue between endothelial cells and the glandular epithelium of the endometrium (Pl. 6, fig. 17).

Normal glandular epithelial cells of the endometrium have large oval nuclei, with an uninterrupted, convex outline (Pl. 6, fig. 13). The basal membrane of these cells is relatively unmodified. The membranes forming the walls of the individual columnar epithelial cell form peg-like interdigitations with adjacent cell membranes, especially at the angles where three cells are in contact. Terminal bars are characteristically present at the luminal surface which has numerous simple microvilli. A few epithelial cells are ciliated. Unmodified epithelial cells contain small lipid droplets, numerous mitochondria, a few strands of reticulum, and a distal juxtanuclear Golgi region. The modification of the epithelial cells that occurs at implantation is characterized by hypertrophy of the individual cells and the accumulation within these cells of numerous large vesicles, some of which appear to be derived from the reticulum (Pl. 6, fig. 14). A fine precipitate can be discerned within many of the larger vesicles (Pl. 6, fig. 15). The only cytoplasmic inclusion sufficiently abundant to account for the amount of material suggested by these larger vesicles is glycogen (Enders *et al* 1958). No enhancement of the Golgi membranes has been observed and there is no apparent increase in the number of mitochondria. With increase in cell size the microvilli at the free surface become stubby or disappear. Degenerating epithelial cells in the area of invasion apparently become highly vesiculate and lose much of their electron density.

DISCUSSION

The placental barrier, as determined by a study of electron micrographs, consists of the syncytial trophoblast, the basement membrane, and the foetal endothelial cells. It is doubtful that the connective tissue between the basement membrane and the endothelial cells constitutes a significant part of this barrier. The basement membrane is clearly a product of the stroma, since there is no basement membrane underlying the syncytium covering the cell columns.

The syncytium itself exhibits considerable variation both in the extent of microvilli and in the amount and form of derivatives of the endoplasmic reticulum. It might be argued that the variation exhibited is a result of unequal quality of fixation. This does not seem to be the case, however, for adjacent villi show variations in structure within the zone of better fixation. Furthermore, variation in structure of the syncytium is also common in ordinary histological preparations preserved with fixatives that act more uniformly than does osmium tetroxide. It has not been possible, however, to determine whether these variations in syncytial structure are randomly localized or are characteristic of different portions of the villous tree.

A comparison of the syncytium of the armadillo with that of the human, as reported by Wislocki & Dempsey (1955*b*), reveals that there are many features in common. Both animals exhibit thinning of the syncytium in older placentas. Microvilli which may arise from protoplasmic protrusions are common to both, as are endoplasmic vesicles. However, neither the complexity of microvilli nor the polarity of intracellular organelles observed in the armadillo syncytium has been reported in the human. Furthermore, there is very little lipid in the syncytium of the armadillo except in the invading trophoblast while lipid droplets are a common feature of the syncytium of the human placenta (Wislocki & Dempsey,'1955*b*). The infolding of the basal cytoplasmic membrane to form canaliculi, which is particularly characteristic of later placentas in the armadillo, has not been reported for the human placenta. The presence of numerous vacuoles and the extent of variation of the free surface of the syncytium were considered by Boyd & Hughes (1954) and Wislocki & Dempsey (1955*b*) to be evidence of pinocytosis. The relative uniformity and complexity of microvilli and the lack of vacuoles in the syncytium of the armadillo placenta suggest a relatively stable surface with a greatly increased area as opposed to a labile surface characterized by pinocytotic activity.

The association of the mitochondria with the region of the cytoplasm in which the microvilli arise is reminiscent of the more intimate association of mitochondria with the folding of the basal plasma membrane in the convoluted tubule of the kidney and ependymal cells (Pease, 1956). It is interesting to note that the Golgi membranes are disposed towards the basal region of the syncytium. The Golgi complex in glandular cells is generally situated in a distal juxtanuclear position, i.e. between the nucleus and the secretion surface. The implication, therefore, is that as a secretory organ the syncytium should be viewed as being based on the intervillous space with its apex on the basement membrane, an orientation compatible with its function. The tortuous canaliculi formed by the basal plasma membrane serve to increase the surface available for exchange of materials between the syncytium and the stroma of the villi just as the microvilli increase the surface available for exchange between the syncytium and the intervillous space. Why the canaliculi should take the particular form which they do is not immediately apparent.

It might be argued that the substance seen in the intercellular spaces of the cell columns was derived directly from the maternal blood vascular system rather than being a secretion product of the cytotrophoblast. There are two principle arguments against this possibility. In the first place, there are regions within the cytotrophoblast cells which demonstrate the same sort of granulation as the substance in the intercellular space. In addition, this substance is found in vacuoles within the syncytium overlying the cytotrophoblast. This latter observation might indicate that the secretion product was passing in either direction, except that it is found only in the vacuoles in the syncytium overlying the cell columns and never in the vacuoles in the syncytium covering the vascular villi. It does not seem probable that the syncytium would be phagocytic or pinocytotic only where it covers the cell columns. Furthermore, the syncytium is formed, in all probability, from the cells of the cell columns (Enders, 1959). Thus the substance liberated into the intercellular spaces is transported to the intervillous space during the process of formation of the syncytium from the cytotrophoblast. It is interesting to note that this material

has the histochemical characteristics of a glycoprotein (Enders, 1959). It remains to be demonstrated that the armadillo placenta produces gonadotropins.

The individuality of smooth muscle cells, mesenchymal cells, stratified squamous epithelial cells, and the units of cardiac muscle between intercalated discs has been disclosed by electron microscope studies (see Fawcett, Ito & Slautterback, 1959, for a survey of the extensive literature). A previously undescribed form of syncytium which is formed by incomplete separation of cells at telophase has been described for cnidoblasts of *Hydra* and mammalian spermatids by the above authors. The remaining examples of syncytia, with the possible exception of skeletal muscle fibres, are all of the type which develops by coalescence of previously individual cells. The fusion of individual cells to form these syncytia (multinucleate masses, giant cells, osteoclasts, syncytial trophoblast) has yet to be described.

Fawcett (1958), in his review of the nature of the cell membrane, has pointed out the frequency with which thickenings occur in the cytoplasm at areas of contact of cell membranes forming desmosomes. Intercalated discs (Fawcett & Selby, 1958), terminal bars, nodes of Bizzozero, and other specific regions of cytoplasmic contiguity have all been interpreted as modifications of the type of structure which is designated desmosome. Recently Odland (1958) has studied in greater detail the organization of these structures in human epidermis. In addition to the fibrillar element (tonofibrils) and attachment plaques (paired areas of increased density within the cytoplasm), he was able to discern intervening layers of unidentified substances occupying the space between attachment plaques. All of the studies of desmosome structure have emphasized that there is no continuity of the cytoplasm through the attachment plaques.

One of the interesting and unexpected observations concerning the armadillo placenta was that where cells of the cytotrophoblast came in close association with the syncytium, desmosomes were formed. These desmosomes are most frequently found in areas in which there are numerous vacuoles containing intercellular substance within the syncytium. Frequently the desmosomes are small areas of contact or form relatively flat regions of contiguity between the cytotrophoblast and the syncytium. The attachment plaques and fibrils are most clearly distinguished, however, in regions where there is considerable interdigitation of processes of the cells of the cell columns with the overlying syncytium. It therefore seems that the formation of the desmosomes represents an initial stage in the transformation of a cell from the cell column into a portion of the syncytium. It is reasonable that the close association of the cell membranes over a considerable surface should constitute a preliminary to fusion of the cytoplasm. However, it is rather surprising that there should be an initial increase in density of the adjacent cytoplasm prior to breakdown of the cell membrane.

That the endoplasmic reticulum is a system of membranous components with which granules of high electron density may be associated is clearly established (see reviews of Palade, 1958, and Robertson, 1959). The particulate component has been demonstrated to contain ribonucleoprotein (Palade & Siekevitz, 1956; Palade, 1958). Additional evidence currently accumulating indicates that, while the large numbers of ribonucleoprotein particles characteristic of proliferating cells and other cells with a high rate of synthesis of cytoplasm are not associated with endoplasmic

membranes, an extensive system of endoplasmic membranes with associated ribonucleoprotein particles is characteristic of cells synthesizing specialized proteinaceous cell products (Slautterback & Fawcett, 1959). Since the cisternae represent a space which is isolated from the cytoplasm, although not necessarily from the nucleus (Watson, 1955) or the exterior (Epstein, 1957), it has been suggested by numerous authors that these spaces are areas where intermediate or final products of synthesis may be accumulated (Siekevitz & Palade, 1958; Slautterback & Fawcett, 1959). The pattern of formation of the nematocyst of *Hydra* suggests to the last-mentioned authors that the specific proteins synthesized were accumulated, probably in an intermediate form, in the cisternae of the endoplasmic reticulum. The formative material then is accumulated within vacuoles in the Golgi complex, a pattern of development which is similar to acrosome formation (Burgos & Fawcett, 1955). Hally (1958) drew somewhat similar conclusions with regard to the Golgi complex from his study of Paneth cells.

The Golgi zone is admirably positioned for the accumulation of materials resulting in the formation of an intracellular body. However, its juxtanuclear location does not seem consistent with the accumulation of the end products of synthesis in most gland cells. Palade & Siekevitz (1956) and Siekevitz & Palade (1958) have presented evidence that pancreatic secretion granules are synthesized by the ribonucleoprotein granules, segregated within the cisternae of the endoplasmic reticulum and, as zymogen granules, may retain a membranous covering derived from this structure.

The modified fibroblast cells of the mature placenta have a very extensive endoplasmic reticulum with which numerous ribonucleoprotein granules are associated. In addition, the cisternae are dilated and contain a granular substance of moderate electron density. Larger granules are present in the cytoplasm at the confluence of a number of cisternae. As in other glandular cells, the Golgi complex is highly developed. These observations and those with the light microscope are typical for a highly differentiated protein secreting cell. In addition the specific organization of the organelles of these cells suggests the following speculative interpretation: metabolites are accumulated in the Golgi complex; protein is synthesized by the ribonucleoprotein granules, the intermediate products accumulating in the cisternae; the protein granules assume final form in the cytoplasm. The arrangement of the cisternae suggests not only accumulation of intermediates, but also that they serve to transport the substance to the site of final formation.

Our investigations on the invasive trophoblast are preliminary. However, what little evidence we have garnered indicates that the trophoblast penetrates into the connective tissue of the stroma between endothelial and epithelial cells. Electron microscopy should be an excellent means of studying the initial penetration of the blastocyst into the endometrium. Studies of this nature are currently being undertaken.

SUMMARY

The placental barrier, as seen in electron micrographs, is composed of the syncytial trophoblast and the mesodermal core of the vascular villus. The syncytium has numerous elongate microvilli on its free surface. The microvilli are especially well developed in some regions of the placenta where they constitute numerous, branched, lamelliform projections into the intervillous space. A distinct zonation of inter-

cellular elements is apparent, with the endoplasmic reticulum and mitochondria being situated largely in the distal and juxtanuclear cytoplasm and the Golgi in a more proximal position. It is suggested that this orientation constitutes a reversal of the apparent polarity of the syncytium. The basal plasma membrane is invaginated forming branched canaliculi in the basal cytoplasm which often contains small fibrillar elements. The stroma of the vascular villi is composed of the basement membrane, the connective tissue elements, and the endothelial cells of the foetal capillaries. It is doubtful that the finely fibrillated intercellular space of the stroma constitutes much of a barrier. The endothelial cells of the foetal capillaries possess neither perforations nor thin areas. The fibroblasts in late pregnancy are modified and contain an extensive endoplasmic reticulum composed of dilated vesicles with numerous associated ribonucleoprotein granules. In addition, these cells have a large region of Golgi membranes and a specific granulation in their cytoplasm. It is suggested that they are protein-secreting elements.

The syncytial trophoblast overlying the cell columns is especially thin, and no basement membrane is found in this region. Desmosomes are present, however, where the cells of the cell columns are in intimate contact with the syncytium and may constitute an initial stage in fusion of the adjacent cytoplasm. Within the intercellular spaces in the cell columns is a granular substance. It is suggested that this is a secretion product of the cytotrophoblast which is liberated into the intervillous spaces during the formation of syncytium from the cells of the cell column.

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EXPLANATION OF PLATES

These symbols are used in the following figures: *BM*, basement membrane; *D*, desmosome; *END*, endothelium; *EP*, epithelium; *ER*, endoplasmic reticulum; *ERC*, cisternae of the endoplasmic reticulum; *ERYT*, erythrocyte; *F*, fibrils; *FC*, foetal capillary; *GC*, Golgi complex; *Gr*, intercellular granulation; *L*, lipid; *N*, nucleus; *NCL*, nucleolus; *M*, mitochondria; *MC*, maternal capillary; *MBS*, maternal blood space; *S*, intercellular space; *TR*, trophoblast. All magnifications are approximate.

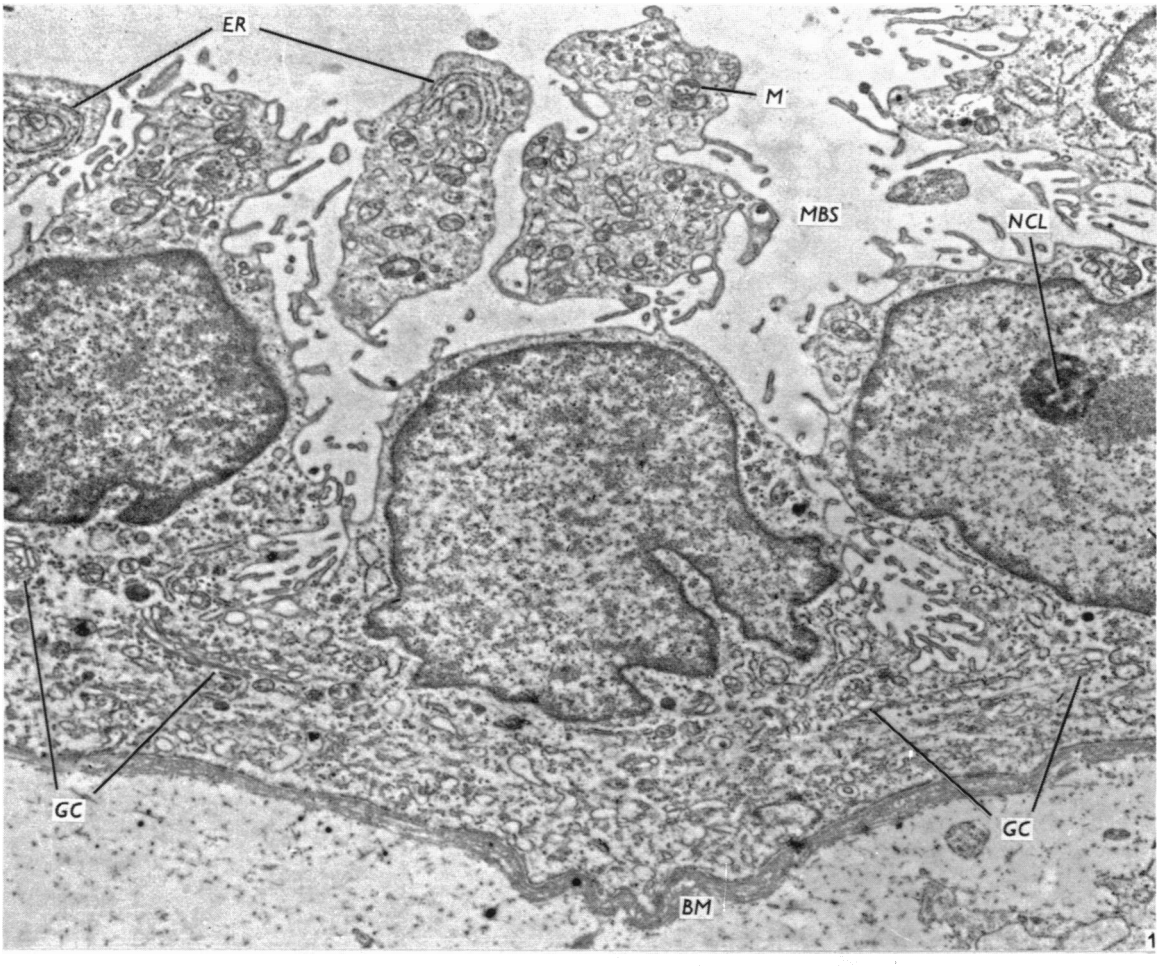
PLATE 1

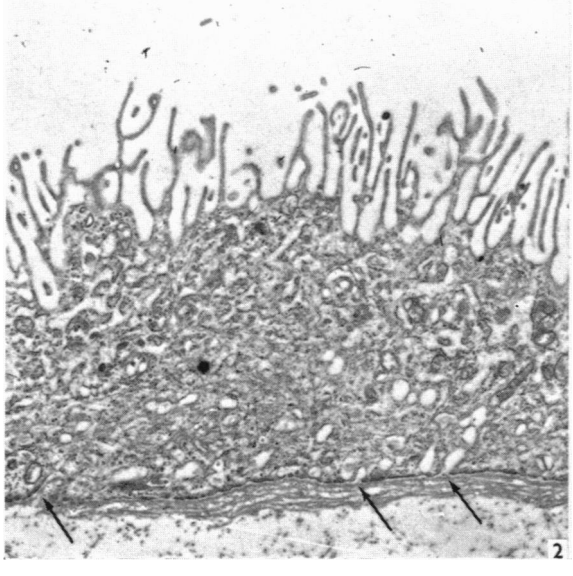
Structure of the syncytial epithelium of the vascular villi during the period of placental expansion

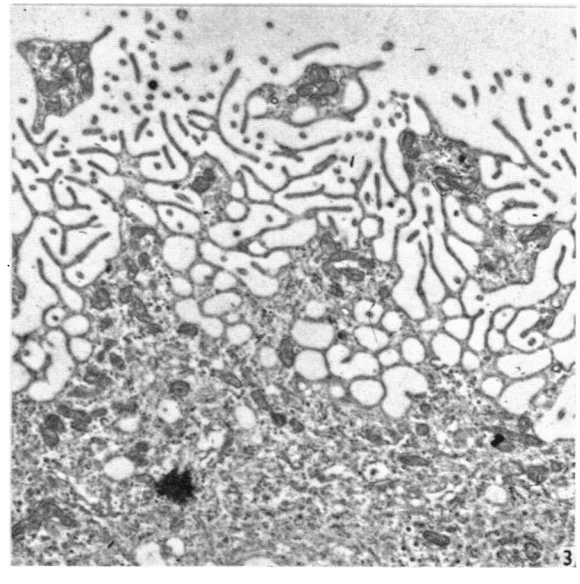
Fig. 1. Syncytial trophoblast from the period of placental expansion. Although there are parts of four nuclei visible, there are no plasma membranes between these nuclei. Both microvilli and protoplasmic projections are illustrated. A section in which the internuclear distance is much less than usual was selected. The zonation of organelles within the syncytium is readily apparent. ×5700.

Fig. 2. A portion of the syncytium from the stage of placental expansion. The infolding of the basal plasma membrane to form the canaliculi is seen at the arrows. ×7600.

Fig. 3. A tangential section of the surface of the syncytium. Note that the lamellar microvilli have a relatively uniform thickness, and that in areas of this complexity cups are formed between the microvilli. ×7600.

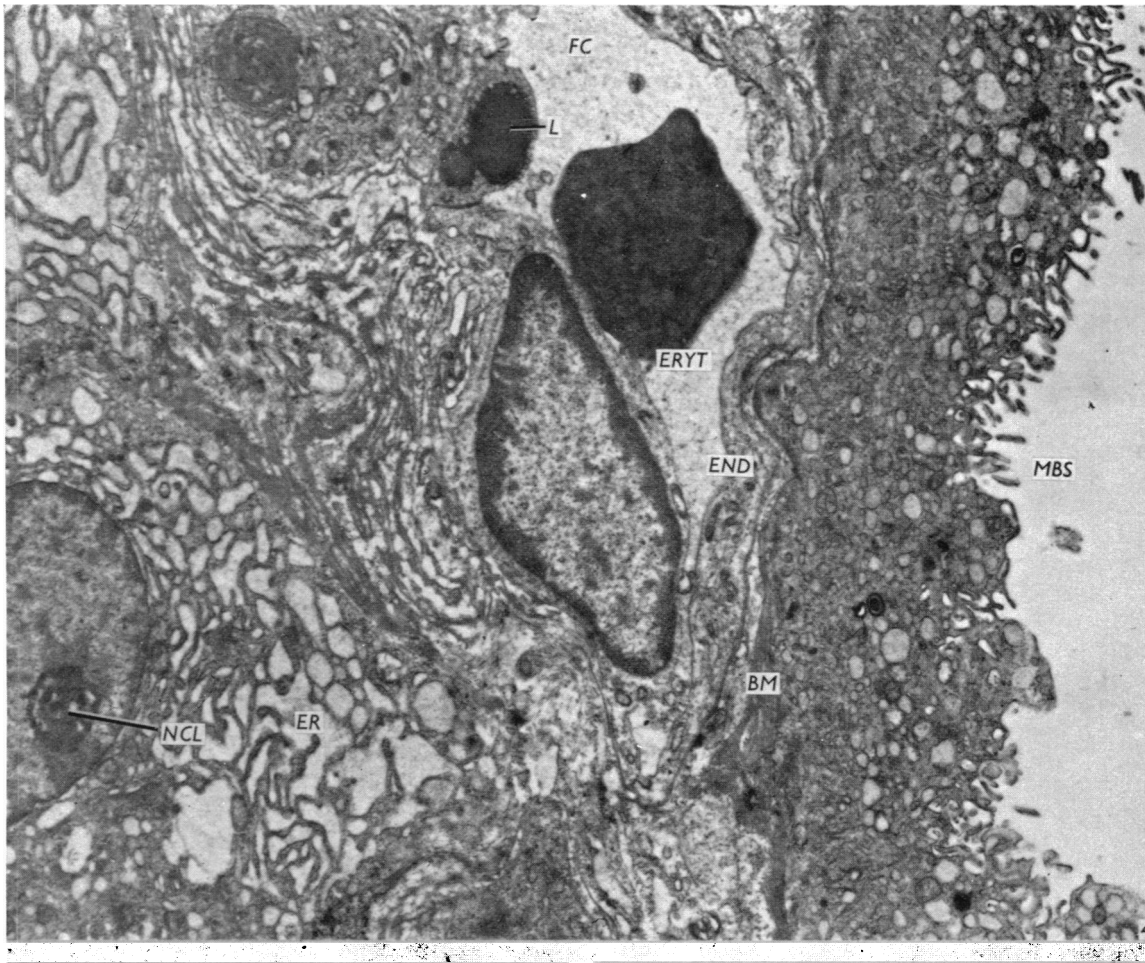


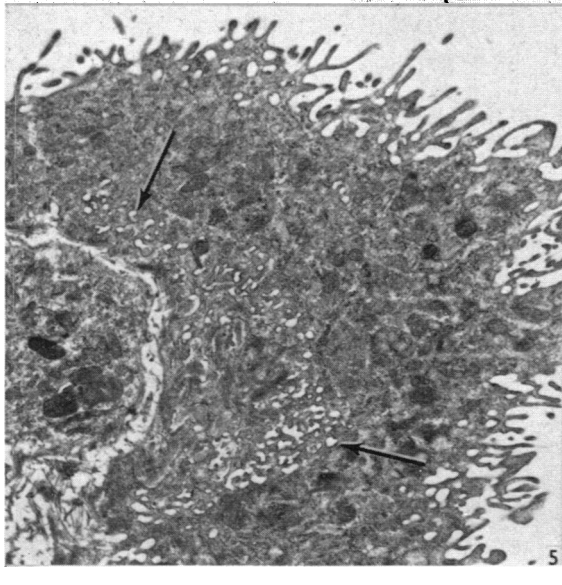


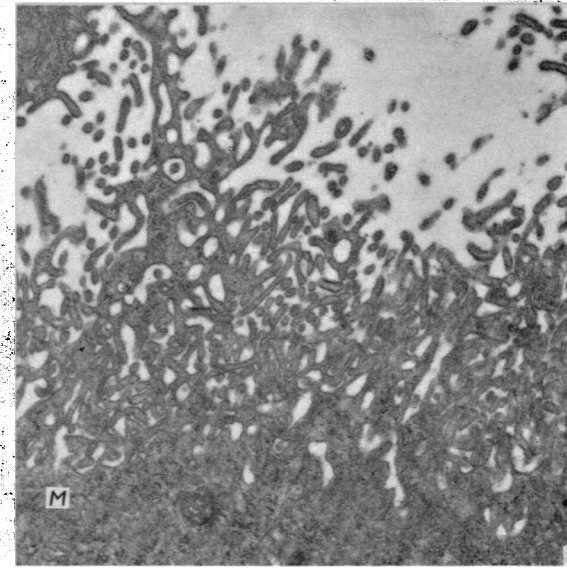


ENDERS—ELECTRON MICROSCOPIC OBSERVATIONS ON THE VILLOUS HAEMOCHORIAL PLACENTA OF THE NINE-BANDED ARMADILLO (*DASYPUS NOVEMCINCTUS*)

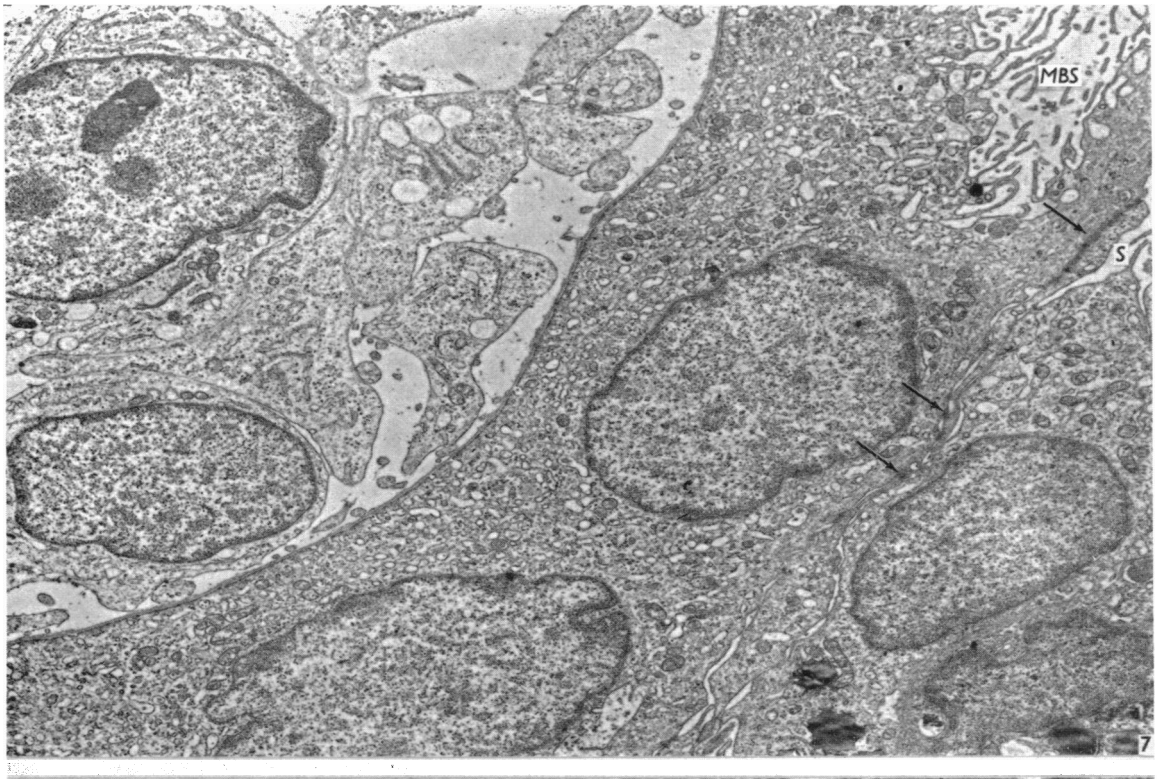
(*Facing p.* 214)

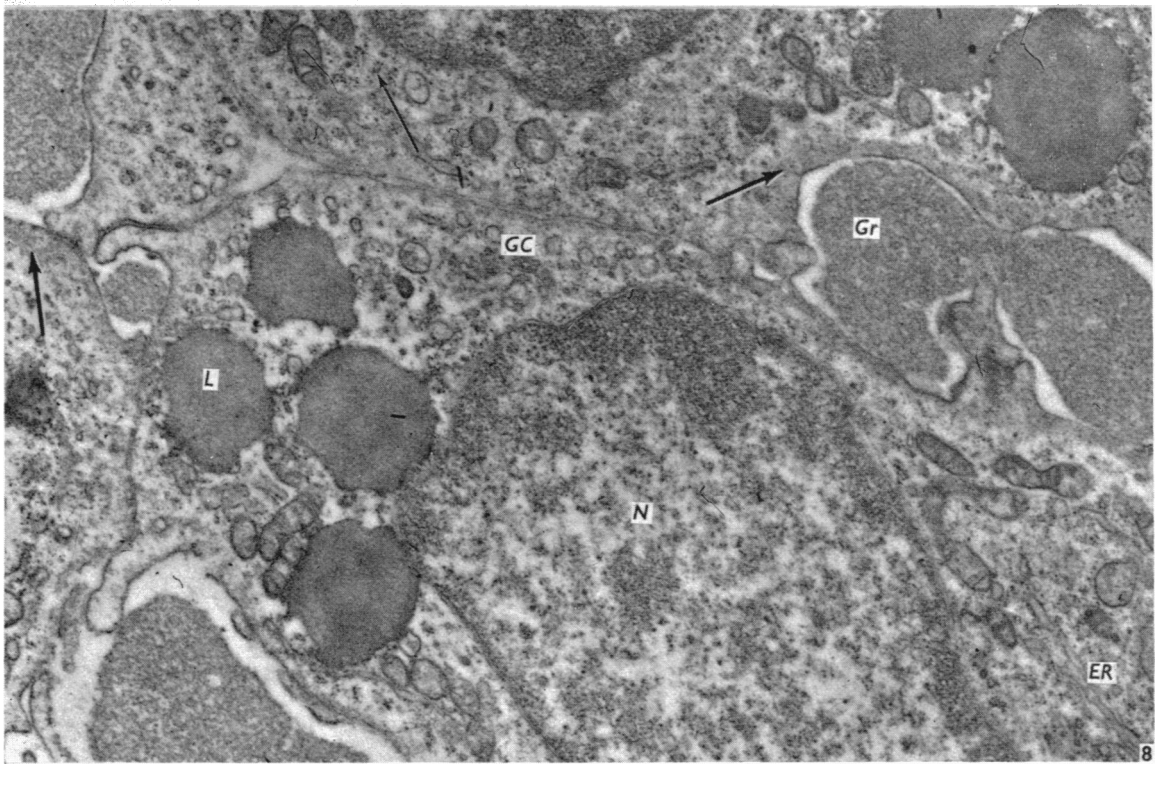




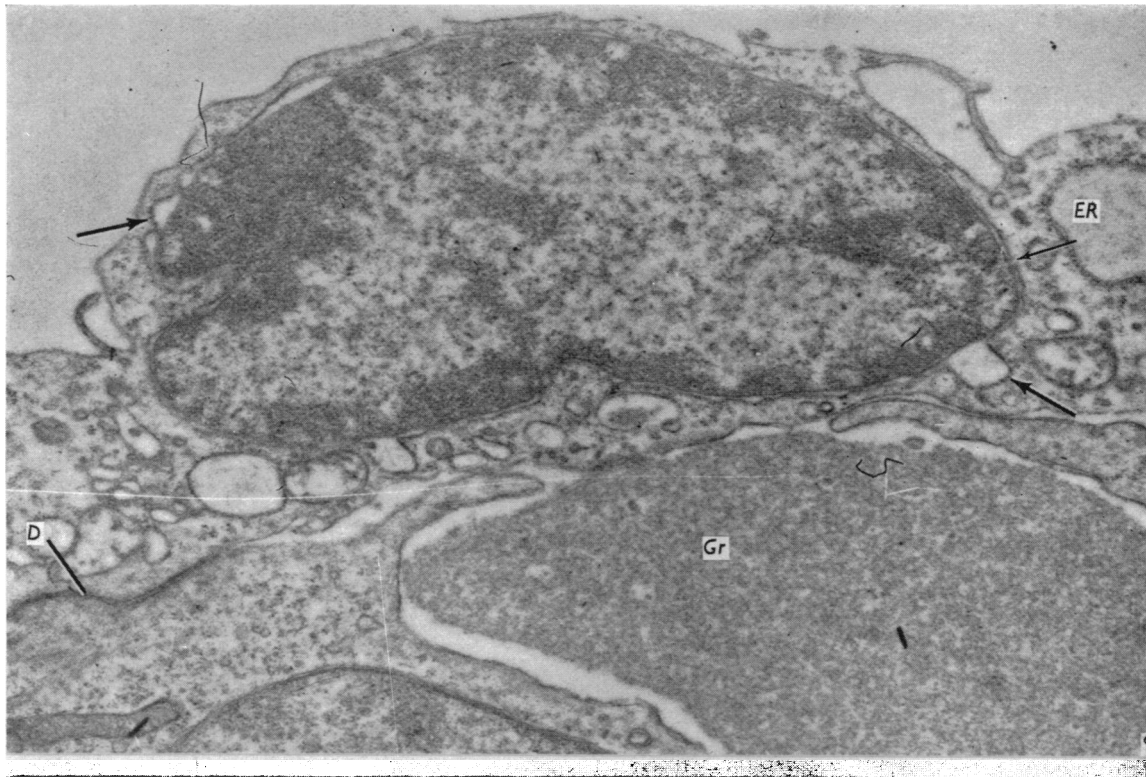


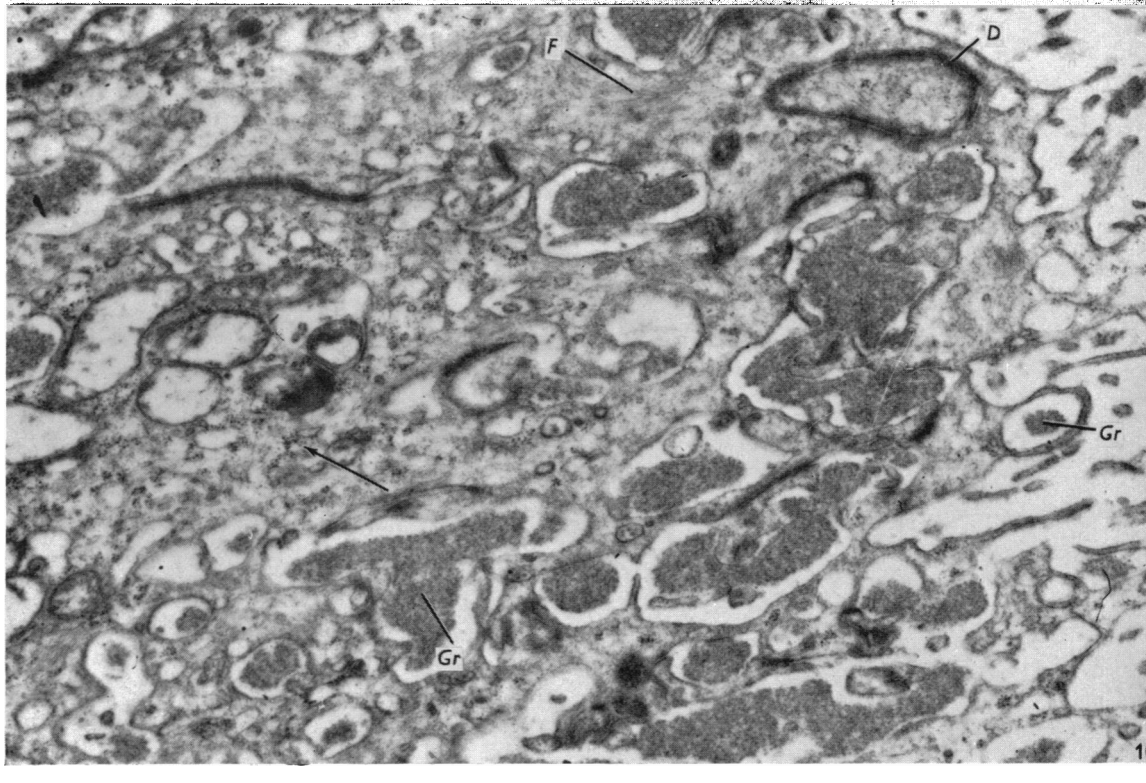
ENDERS—ELECTRON MICROSCOPIC OBSERVATIONS ON THE VILLOUS HAEMOCHORIAL PLACENTA OF THE NINE-BANDED ARMADILLO (*DASYPUS NOVEMCINCTUS*)





ENDERS—Electron microscopic observations on the villous haemochorial placenta of the nine-banded armadillo (*Dasypus novemcinctus*)





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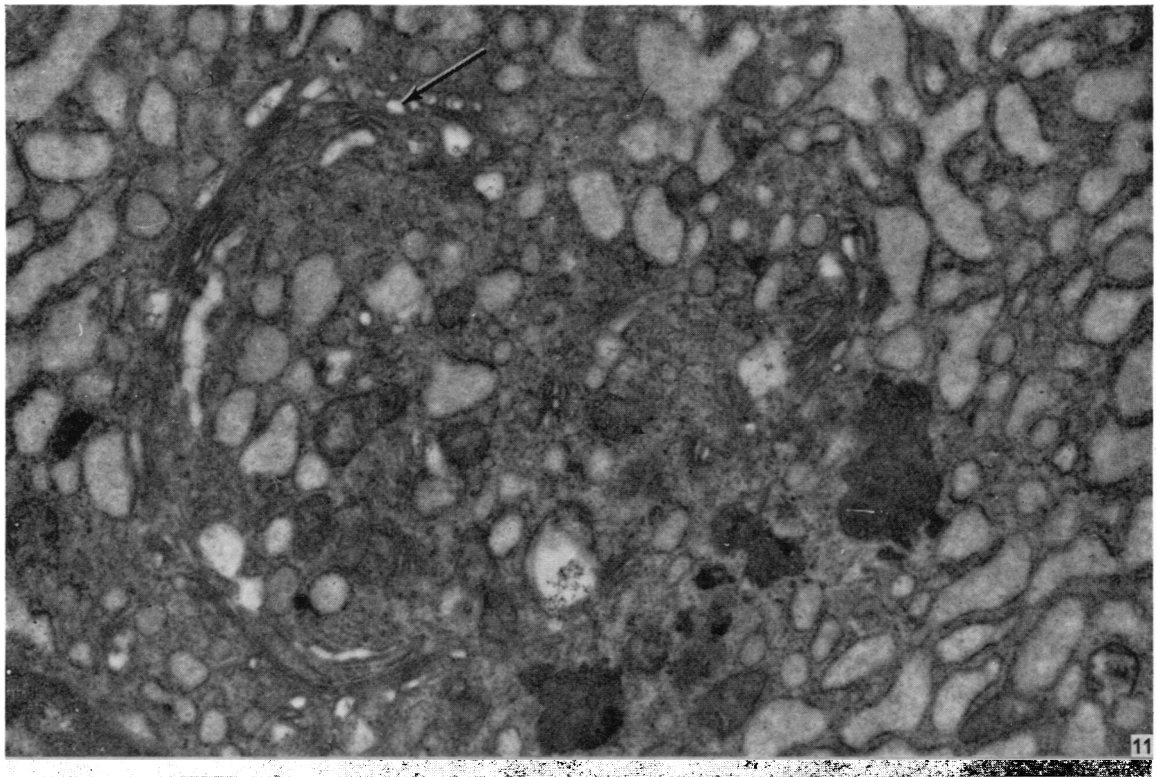
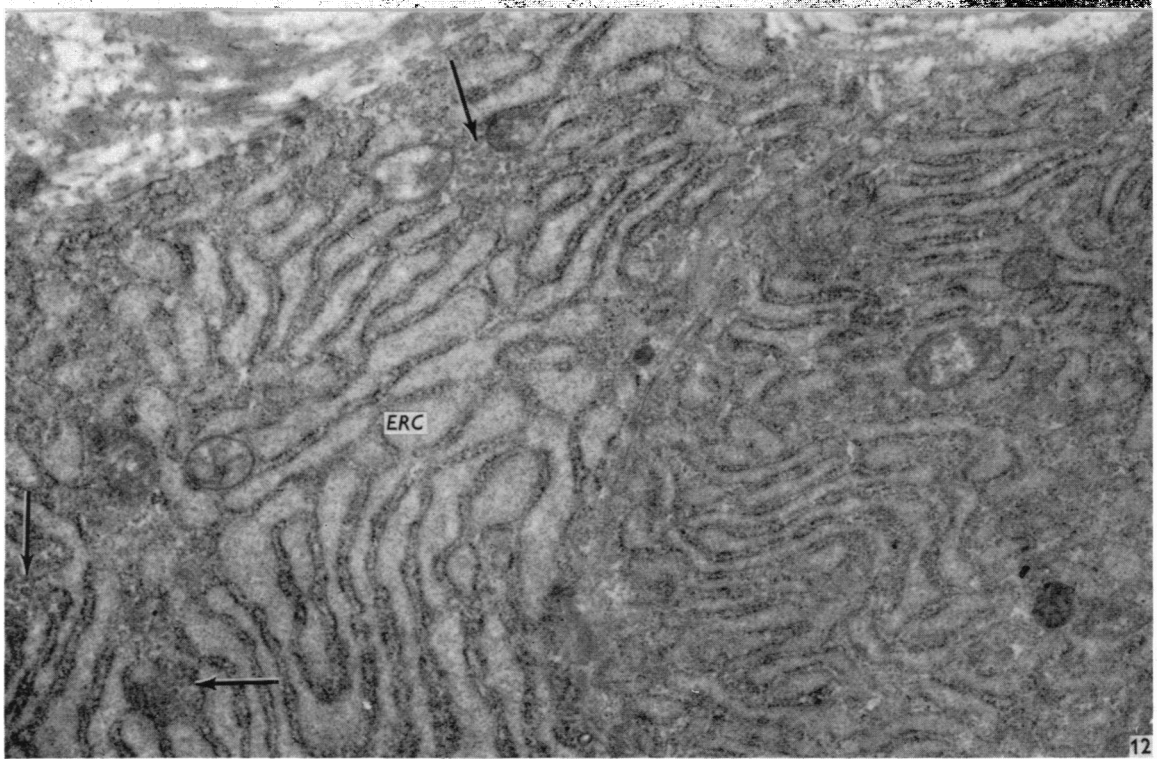
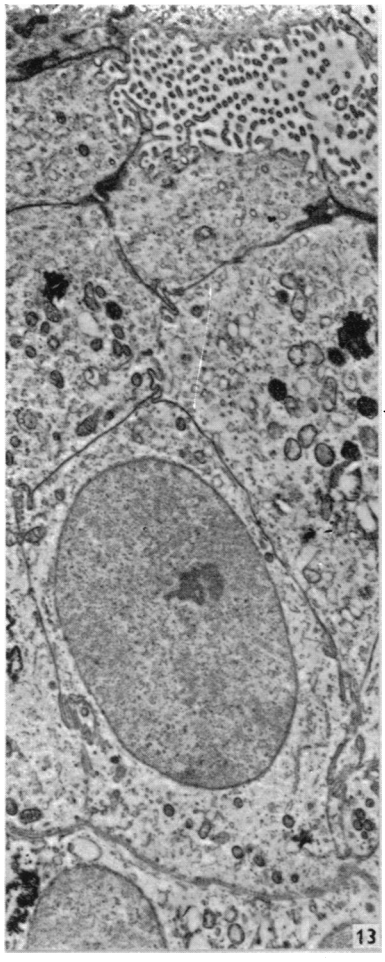
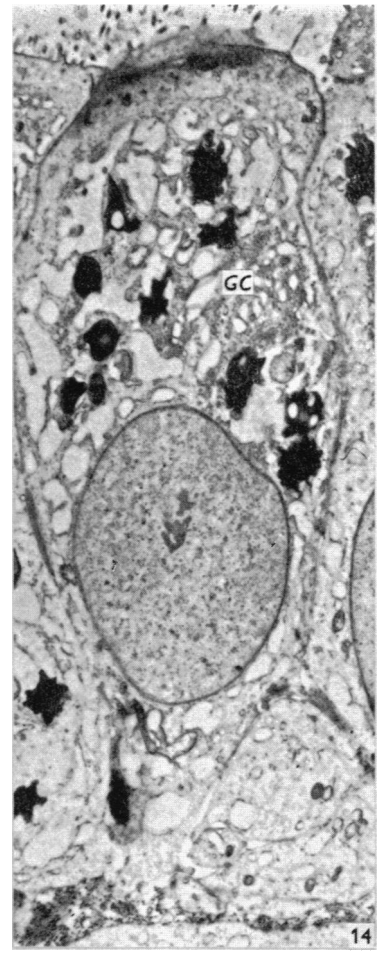
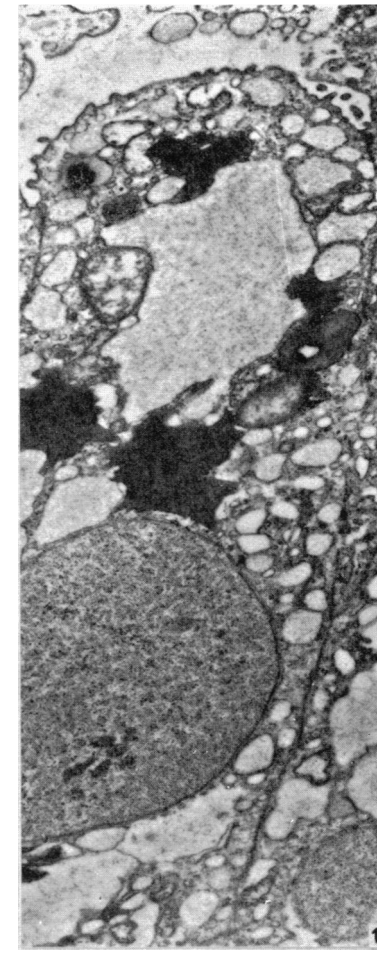


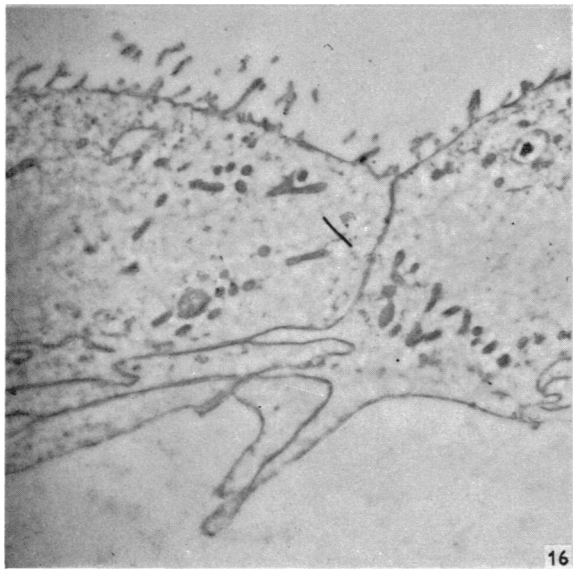


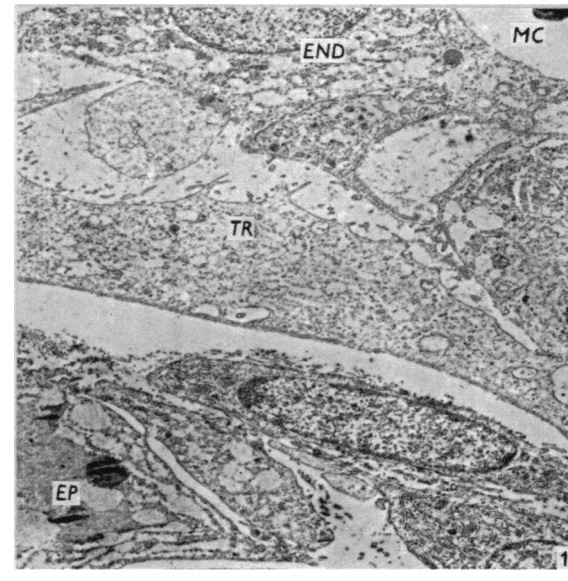
ENDERS—ELECTRON MICROSCOPIC OBSERVATIONS ON THE VILLOUS HAEMOCHORIAL PLACENTA OF THE NINE-BANDED ARMADILLO (*DASYPUS NOVEMCINCTUS*)











ENDERS—Electron microscopic observations on the villous haemochorial placenta of the nine-banded armadillo (*Dasypus novemcinctus*)

PLATE 2

Structure of the villi from the period of the mature placenta

Fig. 4. A marginal portion of a villus. In this particular region of syncytium the endoplasmic reticulum is in the form of vesicles, and the canaliculi are relatively collapsed. The nature of the placental barrier is clearly depicted, as is the modified fibroblast in the lower left corner. × 7600.

Fig. 5. In this section of the syncytium the canaliculi formed by the invagination of the basal plasma membrane are dilated and are especially clearly seen (arrows). × 8700.

Fig. 6. Tangential view of the surface of the syncytium. Note that the microvilli are relatively short compared with the earlier period of the placenta (fig. 3) but that they are numerous and highly branched. × 11,000.

PLATE 3

Fig. 7. Region of junction of the cell column with the vascular villus. At the upper left are processes of several mesenchymal cells. Cutting across the middle is the syncytial trophoblast. At the lower right are parts of two cells of the cell column. Note the desmosomes formed at points of contact between cells of the cell column and the syncytium (arrows) and the thinness of the basement membrane underlying the syncytium. × 7400.

Fig. 8. Typical cells of the cell column. Note the granulation of the cytoplasm (large arrows) next to the intercellular space, and that the cell membranes are frequently indistinct in these regions. Note also the numerous RNP granules in the cytoplasm (small arrow). × 18,000.

PLATE 4

Region of junction between the cytotrophoblast and the overlying syncytium

Fig. 9. Note that the outer nuclear membrane is reflected away from the nucleus at several spots, and that RNP granules are associated with these areas of the membrane (large arrows). A possible nuclear pore is seen at the small arrow. × 17,000.

Fig. 10. In this region there is considerable interdigitation between the cytotrophoblast, which is predominantly at the lower left, and the syncytium. Note that the attachment plaques of the desmosomes can be clearly distinguished, and that the intercellular granules have reached the surface of the syncytium at the right. The small arrow points to a cluster of RNP particles. × 18,700.

PLATE 5

Structure of the modified fibroblast of the mature placenta

Fig. 11. Golgi complex. Note that the Golgi vesicles (arrow) do not appear to contain the amorphous substance seen in the cisternae of the endoplasmic reticulum. × 18,000.

Fig. 12. Parts of two modified fibroblasts are seen. Of special interest is the presence of distinct granules within the cytoplasm (arrows). Note that the cisternae of the endoplasmic reticulum are oriented in relation to these areas of the cytoplasm. × 18,000.

PLATE 6

Figs. 13–15 depict the progressive modification of the glandular epithelial cells of the endometrium which occurs with the onset of implantation.

Fig. 13. Note that there are numerous microvilli and relatively few small lipid droplets in these unmodified cells. × 5900.

Fig. 14. The endoplasmic reticulum shows more extensive dilatation than in the preceding picture. Microvilli are still present on the surface. × 5500.

Fig. 15. The hypertrophy of this endometrial cell is exaggerated by the increase in magnification. Microvilli are reduced. Note the granulation within the large vesicle. In light microscope preparations these cells contain vast quantities of glycogen. × 8500.

Fig. 16. An electron micrograph of the abembryonic trophoderm of a blastocyst. Note the manner in which the cells interdigitate at their basal margins. The microvilli are on the outer surface of the blastocyst. Note also the absence of mitochondria from the more central regions of the cells, and the absence of any extracellular membranes. × 8500.

Fig. 17. A tongue of trophoblast is apparently invading between the already modified endothelium of the maternal capillary and the glandular epithelium. Note the collagen fibres and fibroblast lying beneath the trophoblast. × 5000.