ULTRASTRUCTURE OF THE CHORIONIC VILLI IN THE TERM BABOON (*Papio* sp.) PLACENTA

by

Carol Ann Baker
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Carol Ann Baker

APPROVED BY

Tammie Irene Hughey, PhD
Supervising Professor

Sister Mary Lucy Corcoran
Reader

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INTRODUCTION

There is a void or, at best, only limited ultrastructural information in almost all fields of the biological sciences. The area of placentation is no exception. Since the ultimate goal of many scientific endeavors is the contribution to the vital field of human health, this investigator feels that much information can be gained through the utilization and study of the nonhuman primates in scientific research. The baboon (Papio sp.) has been shown to be quite similar to the human from many aspects (30,31).

Some work has been done on the biological structure and ultrastructure of primate fetal placentae, however, most of it has been limited to man (3,4,14,25,26,27). Ramsey and Harris (20) have reported their observations on the macaque fetal placenta. The literature on the histological structure of the baboon placenta during the fetal period of gestation is also quite limited. Breschet (8) and Turner (24) reported limited observations on single specimens; Coventry (10) described the placenta of a

baboon killed at 4 months of gestation; Hilleman (15) described a specimen obtained near term; Houston and Hendrickx (17) have reported their observations on the fetal vasculature of full-term baboon placentae; and recently Houston (16) reported a detailed consideration of observations on the development of the baboon placenta during the fetal period of gestation. As can be noted, the literature on the histological structure of the baboon fetal placenta is limited and there have been no reported observations on the ultrastructure of the baboon fetal placenta. Several detailed considerations on the fine structure of hemochorial placentae (1,5,6,12,18,22, 23,26,27,28,29), especially of the human placenta, have been published and are useful in the comparison of the baboon term chorion frondosum with that of the human.

It is felt that the ultrastructure as well as the histological structure of the nonhuman primates must be investigated and described. This would benefit not only comparative studies, but also basic research by contributing to our foundation of knowledge. Only in this way

can the bases be set from which other scientific reseachers can investigate and elucidate the normal as well as the pathological processes involving and/or related to placentation, and ultimately contribute these to the benefit of man.

The purpose of this paper is to describe the ultrastructure of the chorion frondosum of the baboon fetal placenta at or near term gestation (175 ± 11 days).

MATERIALS AND METHODS

Baboon placentae were obtained near term gestation (175 ± 11 days) by Cesarean section. Immediately upon removal, small pieces of placental tissue were taken from the central portion of the chorion frondosum and placed in cold 5% glutaraldehyde[1] fixative buffered with 0.1 M cacodylic acid[2] (pH 7.3). The tissue was then cut into 1 mm. cubes and transferred to fresh glutaraldehyde fixative. Post-fixation was carried out in 2% osmium tetroxide[3] (OsO_4) cacodylate buffered to pH 7.3. The tissue was dehydrated progressively in ethyl alcohol. Embedding was done

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[1]Glutaraldehyde (25% in water): Eastman Organic Chemicals, Distillation Products Industries, Rochester 3, New York.

[2]Sodium Cacodylate $3H_2O$ (Sodium Dimethyl Arsenate): K and K Laboratories, Inc., Plainview, New York.

[3]Osmium Tetroxide: Mallinckrodt Chemical Works, St. Louis, Missouri.

in BEEM[4] capsules with Epon 812[5] used as the embedding medium. Polymerization was carried out with progressively increasing heat over a 72 hour period. The step-wise methods of fixation, processing, and embedding are shown in Figure 1.

Figure 1*

1) Glutaraldehyde Fixative (x3) . . . . . 3 hours
2) 0.1 N Cacodylate buffer (x3) . . . . . .30 minutes
3) 2% Osmium tetroxide (x2) . . . . . 1 hour
4) Cacodylate buffer (x2) . . . . . 1 hour
5) 25% Ethanol (x2) . . . . . .15 minutes
6) 50% Ethanol (x2) . . . . . .15 minutes
7) 70% Ethanol (x2) . . . . . .15 minutes
8) 80% Ethanol (x2) . . . . . .15 minutes

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[4]BEEM Capsules: Better Equipment for Electron Microscopy, Ernest F. Fullman, Inc., Box 444, Schenectady, New York 12301.

[5]Epon Resin 812: Fisher Scientific Company, Chemical Manufacturing Division, Fair Lawn, New Jersey.

9) 95% Ethanol (x2) . . . . . 30 minutes

10) 100% Ethanol (x2) . . . . . 1 hour

11) 100% Ethanol and Propylene oxide (1:1) (x2) 1 hour

12) Propylene oxide (x2) . . . . . 1 hour

13) Propylene oxide and Epon 812 (3:1) . . . . 1 hour

14) " " " " " (1:1) . . . . 1 hour

15) " " " " " (1:3) . . . . 1 hour (vacuum)

16) Epon 812 without DMP-30[1] (catalyst) . . . overnight (vacuum)

17) Embed tissue in Epon 812 with CMP-30

18) Place Epon blocks with tissue in oven:

a) 38°C . . . . .24 hours
b) 60°C . . . . .24 hours
c) 70°C . . . . .24 hours

*In steps numbered 1-8 the solutions should be kept in an ice bath or at 0°-4°C.

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[1]DMP-30: 2,4,6-Tri(dimethylaminomethyl) phenol, Fisher Scientific Company, Chemical Manufacturing Division, Fair Lawn, New Jersey.

The Epon blocks were trimmed with glass knives, "thick" sections of approximately 1 micron thickness were cut and mounted on conventional glass slides for light microscopy. The tissue sections were stained with Paragon Multiple Stain[1] for 30 seconds using heat and borax as a mordant, rinsed in distilled water, air dried, and coverslipped. This tissue was studied under the light microscope as a means for orientation. From selected areas of the tissue, ultrathin sections (500-900 Angstroms thick) were cut with a diamond knife on an LKB 8802-A Ultramicrotome. The approximate thickness of the sections was determined by observing the interference colors (silver to gold). The sections were mounted on 200, 300, or 400 mesh copper grids without a supporting film and placed on filter paper to dry.

The tissue sections were double-stained with saturated

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[1]Paragon Multiple Stain: Paragon C and C Company, Inc., 190 Willow Avenue, Bronyx, New York 10454.

alcoholic uranyl acetate[1] and lead citrate[2] (21). The lead citrate staining was carried out in a relatively CO_2-free atmosphere by staining in a covered petri dish which contained sodium hydroxide (NaOH) pellets. This prevents precipitation of the stain.

Electron photomicrographs were made on an Hitachi HU-11C electron microscope at an accelerating voltage of 50,000 volts. The photographic darkroom techniques involved standard photographic developing and printing procedures with the exception that a "point source" light was used in the Durst EM-45 enlarger and a rather "hard" paper (Kodabromide F-5 or F-6) was used in printing the electron micrographs. Kodak D-19 Developer was used to develop the negative plates, and the prints were developed in Kodak Dektol Developer.

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[1]Uranyl Acetate (Crystals) $UO_2(C_2H_3O_2)_2 \cdot 2H_2O$: Mallinckrodt Chemical Works, St. Louis, Missouri

[2]Lead Citrate: Mallinckrodt Chemical Works, St. Louis, Missouri.

RESULTS AND DISCUSSION

In the baboon (Papio sp.) a single, discoidal, villous, placenta is formed (16) which is of the hemochorial variety according to Grosser's classification (13). The chorionic villus of the baboon placenta is a relatively delicate, bulbous structure. The trunci chorii or major stem villi are columnar extensions of the chorion which arise from the fetal surface of the placenta. These villous trunks divide repeatedly forming the rami chorii which also divide, branching into the ramuli chorii. Arising from all levels of these columnar extensions are free terminal microvilli which are exposed to and protrude into the intervillous (maternal) blood space (16).

The chorionic villus rests in part on the epithelial basement membrane, and in part, it articulates with intervening cytotrophoblast which, in turn, rests on the basement membrane (Fig. 2,3). In no instance is the cytotrophoblast (Langhans cells) exposed to the maternal blood space, but rather there is always a single layer of

intervening syncytiotrophoblast (Fig. 4,5). In the terminal chorionic villus of the term baboon placenta it appears that the Langhans cells occur singly or in small groups of two or three cells. This cytotrophoblastic tissue rarely intervenes between a fetal capillary and the syncytiotrophoblastic tissue, but rather is found in areas adjacent to or away from the fetal capillaries. The core of the term chorionic villus contains fetal capillaries which are embedded in a connective tissue stroma. This stroma consists of ground substance, fibroblasts, collagenous fibers (Fig. 6) and occasional Hofbauer cells.

It is supposed that the most active transfer of substances occurs in the near-term or term placenta. The placental barrier (Hemochorial placenta) in the thinnest areas consists of a thin lamina of syncytiotrophoblast and its associated epithelial basement membrane, some collagenous fibers, and the fetal capillary which consists of a basement membrane lined with endothelium (Fig. 7). The placental barrier in the term baboon placenta is structurally similar

to that of the human (26). In the human cytotrophoblast is believed to undergo regression and degeneration toward the second half of gestation and is thought to lose its functional role (27). The ratio of cytotrophoblast to cyncytium suggests a similar regression and degeneration in the term baboon placenta.

SYNCYTIAL TROPHOBLAST

The syncytiotrophoblast in the term baboon placenta varies in thickness, but tends to be quite thin over the fetal capillaries. Bremer (7) has equated these membranous areas or "epithelial plates" with Bowman's capsule of renal glomeruli. The nuclei of the syncytium often concentrate in clusters of two or more and only occasionally are they found in the syncytiotrophoblastic cytoplasm overlying the more superficial fetal capillaries. The syncytiotrophoblast is devoid of cell borders which would subdivide the cytoplasm, therefore it is a true syncytium. This appears to exclude any potential extracellular space which would directly connect the maternal blood space with the fetal placenta.

The cytoplasm of the syncytiotrophoblast is quite complex and highly differentiated. The syncytial trophoblast appears more electron-dense than the cytotrophoblast with a greater number of cellular organellae. Although the syncytium has an overall appearance of being electron-dense, the background or true ground substance is actually electron-thin.

Electron-dense osmophilic granules (lipid droplets) are seen only occasionally in the term syncytial cytoplasm, and when present, they are always enclosed by a membrane. The few osmophilic lipid bodies noted appear near the base of the syncytium. The presence of lipid droplets at or near full term gestation is in accordance with observations on the term human placenta (25).

Typical oval or elongated mitochondria are found in the syncytium. A moderate number of cristae can be seen within the mitochondria (Fig. 8).

The syncytial cytoplasm contains numerous profiles of endoplasmic reticulum. The smooth endoplasmic reticulum consists of a single smooth membrane. The rough endoplasmic reticulum consists of a membrane which is lined with ribonucleoprotein granules (polyribosomes).

As previously mentioned, the nuclei of the syncytium tend to occur in groups and seldom intervene between the syncytial surface articulating with the maternal blood space and the underlying fetal capillary. The nuclei are moderately electron-dense with coarsely clumped chromatin

evident particularly toward the periphery (Fig. 2,3). These nuclei contain a distinct nucleolus. The nuclear membrane is slightly irregular often appearing to have "Notches" or small involutions in it. The nuclear membrane appears to consists of three relatively distinct layers (Fig. 9). The inner membrane is a distinct electron-dense structure. The outer membrane is also electron-dense, but appears to be a relatively less distinct structure. The middle membrane appears as a clear zone or electron-thin area. Nuclear pores are seen frequently in areas where the inner and outer membranes appear to have fused.

Typical Golgi bodies are seen scattered throughout the syncytial cytoplasm (Fig. 8). Micropinocytotic vesicles are numerous and evenly distributed throughout the syncytium. Desmosomes are found at certain points of contact between the syncytiotrophoblast and the cytotrophoblast (Fig. 10) as well as between adjacent Langhans cells.

Syncytial Microvilli

The brush border or terminal villi of the free surface of the syncytial trophoblast exhibits peninsular promontories

(Fig. 2,3). These promontories occur not infrequently, however, they do appear to be more numerous and conspicuous in some areas than in others. As seen in the human placenta (5), the height of the syncytial microvilli of the baboon placenta varies considerably. The general shape of the microvilli may be cylindrical with slightly tapered tips or claviform (clavate microvilli) with bulbous tips (Fig. 11). Only rarely are the microvilli ramified.

The microvilli are continuous with the cytoplasm of the syncytiotrophoblast, although they show a distinct internal structure (Fig. 13). On longitudinal sections they show very fine, electron-dense, linear structures which are parallel to their surface (Fig. 8,11,12). The plasma membrane of the microvilli is continuous with that of the associated syncytium. In some areas of the syncytium the microvilli are less numerous or completely absent. In these transitional and bare regions, bands of greater electron density can be noted at the plasma membrane (Fig. 4,8,16). Microfilaments are evident in the syncytial cytoplasm immediately underlying these transitional regions and lying parallel to the surface (Fig. 8). Boyd et al (5)

suggest that they may correspond to the terminal web found at the bases of microvilli in other epithelial brush borders.

At the base of many of the microvilli the plasma membrane is invaginated forming pocket-like structures termed calveolae or micropinocytotic vesicles which can also be seen deeper within the cytoplasm of the syncytiotrophoblast (Fig. 11,12). The same structures have been described in the human (12,23). "Open" or invaginating calveolae are also present at the base of the syncytium next to the epithelial basement membrane (Fig. 7,10). These structures may suggest micropinocytotic activity of the syncytial trophoblast. Previously evidence of a continuous open system of canals has not been shown. Figures 10 and 14 show structures which are suggestive of some type of canalicular system. The diameter of these structures generally agrees with that of the structures called calveolae. The structures shown appear to be open to the maternal blood space and in these particular sections they traverse over half the syncytiotrophoblast. Although it has not been previously demonstrated, this could suggest

the possibility of a canalicular system connecting the maternal blood space and the basement membrane-endothelial area or the extracellular spaces at the basal folds.

The syncytial microvilli on high magnification electron micrographs appear to have a "fuzzy" coat which is probably Bennett's (2) "glycocalyx", a specialized carbohydrate surface layer outside the plasma membrane (Fig. 11,12,13). At the base of the syncytiotrophoblast, next to the basement membrane, there are often complex infoldings of the basal plasma membrane (Fig. 15). These basal folds are also seen at the base of the syncytium in close association with the cytotrophoblast. (Syncytio-cytotrophoblast junctions). In both instances the basal folds may be either in intimate contact with the adjacent structure, or extracellular spaces may be present. These fingerlike structures or cytoplasmic processes of the syncytium are occasionally seen intervening between the cytotrophoblastic cells and the basement membrane. The extracellular spaces or cavities which may be formed appear as electron-thin areas containing no distinguishable structures or characteristics.

CYTOTROPHOBLAST

The cytotrophoblast (Langhans cells) of the term baboon placenta rests directly on the epithelial basement membrane (Fig. 4,5,10) except where the basal folds of the syncytiotrophoblast occasionally intervene. The cytotrophoblast is noticeably less electron-dense than the syncytiotrophoblast. Also the cellular organellae of the cytotrophoblast are less complex and numerous than in the syncytial cytoplasm. The mitochondria of the cytotrophoblast are more numerous than those of the syncytium, as well as appearing more electron-dense with well defined cristae (Fig. 16).

Free ribonucleoprotein granules (ribosomes) are more abundant in the cytotrophoblast, although rough endoplasmic reticulum is not quite as prevalent as in the syncytiotrophoblast. The rough endoplasmic reticulum appears quite long and narrow and is often found in close association with the mitochondria (Fig. 16). Smooth endoplasmic reticulum is much less common in the cytotrophoblast.

The association of the basal membrane of the cytotro-

phoblast with the epithelial basement membrane is more intimate than the similar association of the syncytiotrophoblast with the basement membrane. This is due to the fact that the cytotrophoblast does not demonstrate cytoplasmic processes similar to the basal folds of the syncytium which allows the presence of extracellular spaces.

The contours of the nuclei of the Langhans cells are generally more even and regular than those of the syncytiotrophoblast (Fig. 16). The structure of the nuclear membrane appears similar to that of the syncytial nuclei, i.e., an inner and outer electron-dense layer with a clear middle zone. The nuclei of the cytotrophoblast are moderately electron-dense and contain coarsely clumped chromatin; however, the nuclei are somewhat less electron-dense and the chromatin is clumped to a lesser degree than in the syncytiotrophoblast. The cytotrophoblastic nuclei contain a distinct nucleolus.

Golgi bodies generally occur in the vicinity of the nucleus. Micropinocytotic vesicles are not so abundant in the cytotrophoblast as they are in the syncytiotrophoblast.

Contact between Langhans cells and the syncytiotrophoblast as well as between adjacent Langhans cells is provided by desmosomes. In the term baboon placenta Langhans cells generally occur singly, although occasionally two such cells may appear together.

Several investigators (6,9,11) have reported in the human the presence of transition cells, i.e., intermediate stages of differentiation between Langhans cells and syncytium. No such intermediate stages were seen in the baboon.

BASEMENT MEMBRANE

The epithelial basement membrane usually appears homogeneous and, occasionally, it may appear to be formed by layers due to varying electron densities within the structure. Cytoplasmic granules may be found dispersed with the basement membrane. Also the basal folds of the syncytium occasionally protrude into the basement membrane. The basement membrane often tends to be thinner in areas where the fetal capillaries are more superficial.

CHORIONIC (FETAL) CAPILLARIES

In the term baboon placenta the chorionic capillaries tend to be superficial, lying close to the maternal blood space with only a thin intervening layer of syncytiotrophoblast. There is a capillary basement membrane which is thinner, less distinct, and in part slightly less electron-dense than the epithelial basement membrane. The lumen of the fetal capillary is lined by a single layer of endothelial cells. Desmosomes provide contact between adjacent endotehlial cells (Fig. 5,10,15). At this point of contact marginal folds which are polypoid projections of endothelial cytoplasm are quite common (Fig. 5). The tight endothelial cell junctions suggest that the transport of substances across the fetal capillary barrier must be through the cytoplasm.

The apparent thickness of the endothelial cells depends on the state of contraction or distension of the capillary lumen. The thickness of the endothelium, of course, is greater in the area containing the nucleus. The cytoplasm of the endothelial cells contains numerous

mitochondria which often occur in groups (Fig. 15). They are distinct, electron-dense structures with numerous well defined cristae. The cytoplasm contains many free ribonucleoprotein granules and long, slender, rough endoplasmic reticulum, but few profiles of smooth endoplasmic reticulum are present. Micropinocytotic vesicles are abundant, not only within the cytoplasm, but also along the external and luminal surfaces of the endothelial cells (Fig. 7). Bundles of extremely fine filaments are dispersed throughout the endothelial cytoplasm. The nuclei of the endothelial cells are moderately electron-dense with clumped chromatin concentrated at the periphery. Nucleoli are often present.

Perithelial cells (Fig. 2) are often found in close association with the endothelial cells. The perithelial cells have electron-dense nuclei with coarsely clumped chromatin. Free ribonucleoprotein particles and profiles of rough endoplasmic reticulum are abundant in the cytoplasm.

CONCLUSIONS AND SUMMARY

The ultrastructure of the chorion frondosum of the term baboon (*Papio* sp.) is described with special reference to the cytotrophoblast and syncytiotrophoblast. The baboon chorion frondosum in the term placenta appears to be quite similar to that of the human at the same gestational period. Electron micrographs are presented which suggest the presence of a canalicular system which has not previously been reported in primates.

KEY FOR FIGURES

bf - Basal folds

C - Calveolae

cbm - Capillary basement membrane

CTB - Cytotrophoblast

D - Desmosomes

E - Endothelium

EBm - Epithelial basement membrane

er - Endoplasmic reticulum

FC - Fetal capillary

G - Golgi

IVS - Intervillous (maternal) blood space

L - Lipid

M - Mitochondria

mf - Marginal folds

mv - Microvilli

N - Nuclear envelope

Nu - Nucleus

P - Perithelial cells

RBC - Red blood cells (erythrocytes)

STB - Syncytiotrophoblast

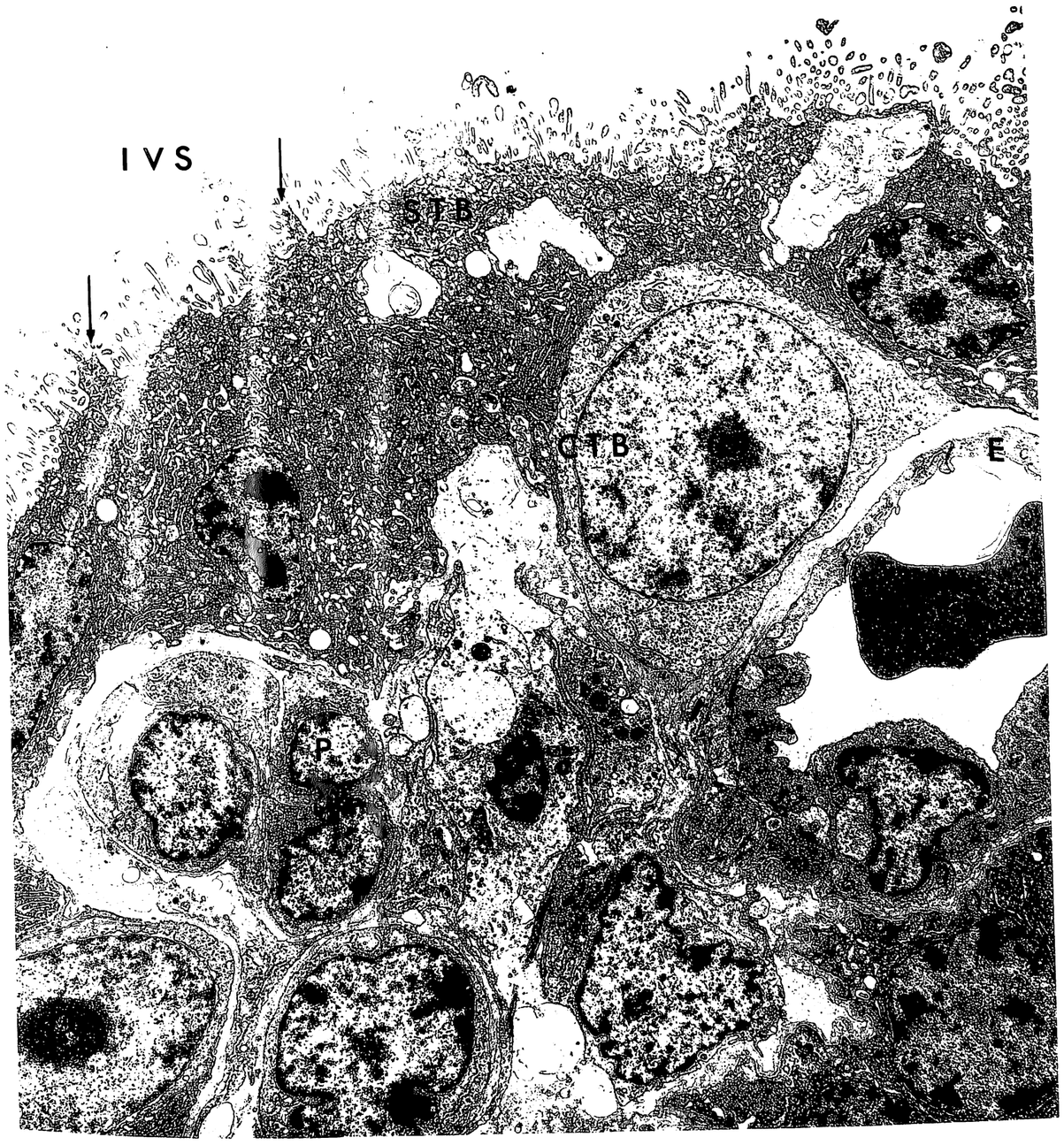


Fig. 2. Low magnification electron micrograph of baboon chorionic villus. IVS, intervillous space; STB, syncytiotrophoblast; CTB, cytotrophoblast; E, endothelial cell; P, perithelial cell; RBC, erythrocyte. Note the promontories (arrows) along the surface of the syncytium. To the left a contracted fetal capillary can be seen, to the right a distended fetal capillary. Magnification x 5,625.

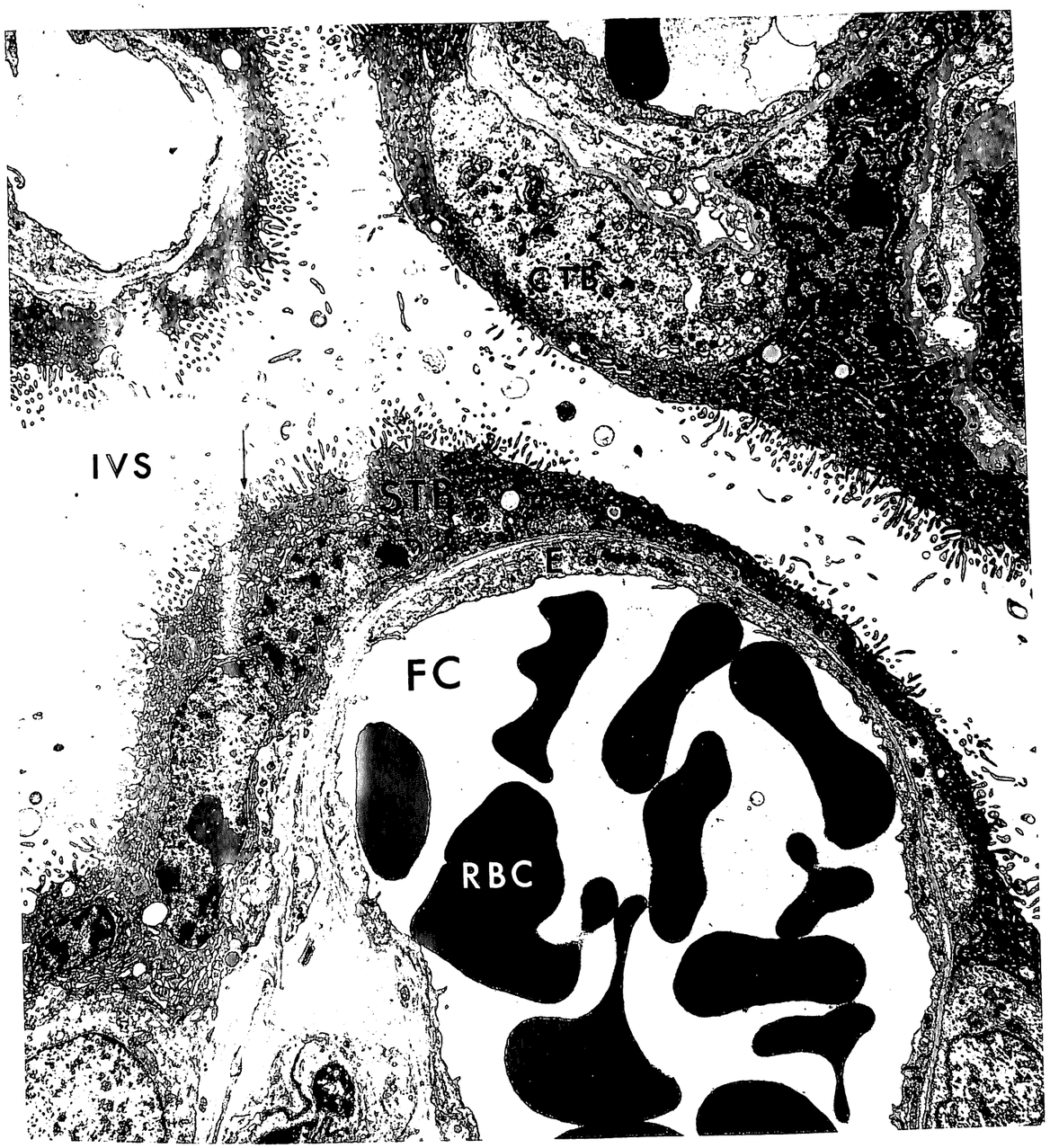


Fig. 3. Low magnification electron micrograph of chorionic villi. IVS, intervillous space; CTB, cytotrophoblast; STB, syncytiotrophoblast; E, endothelial cell; RBC, red blood cell; FC, fetal capillary. Note the syncytial promontories (arrow); the syncytial nuclei are located at the "side" of the fetal capillary. Magnification x 5,000.

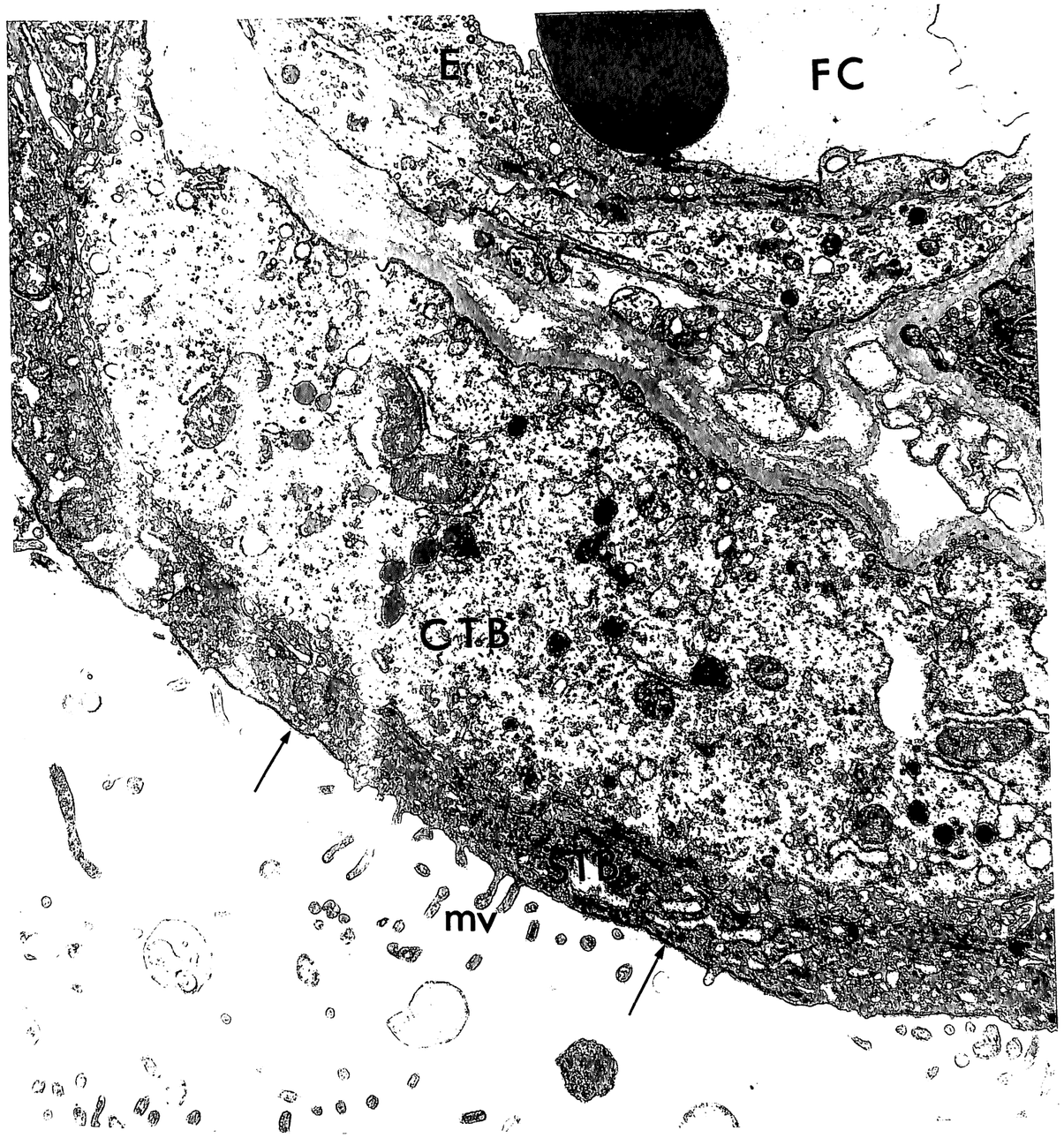


Fig. 4. Trophoblast is composed of two layers, the syncytiotrophoblast (STB) and the cytotrophoblast (CTB). Note the darkened areas (arrows) in the transitional and bare regions at the syncytial surface. mv, microvilli; FC, fetal capillary; E, endothelium. Magnification x 15,000.

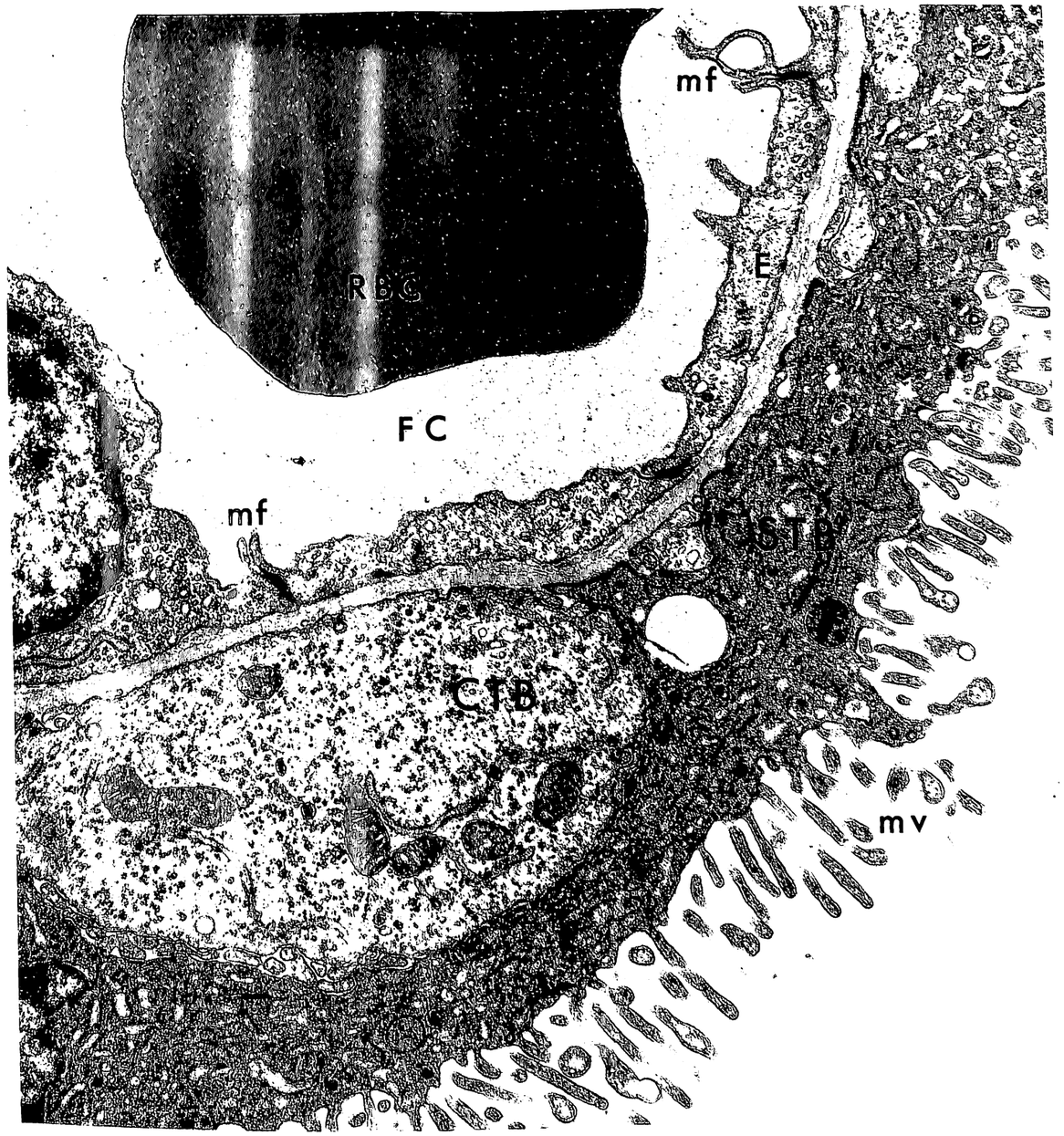


Fig. 5. At the points of connection (desmosomes) between endothelial cells, marginal folds (mf) often project into the lumen of the fetal capillary (FC). E, endothelium; CTB, cytotrophoblast; STB, syncytiotrophoblast; mv, microvilli; RBC, red blood cell. Magnification x 17,500.

Fig. 6. Collagenous fibers can be seen in which the fetal capillary (FC) is embedded. Magnification x 26,900.

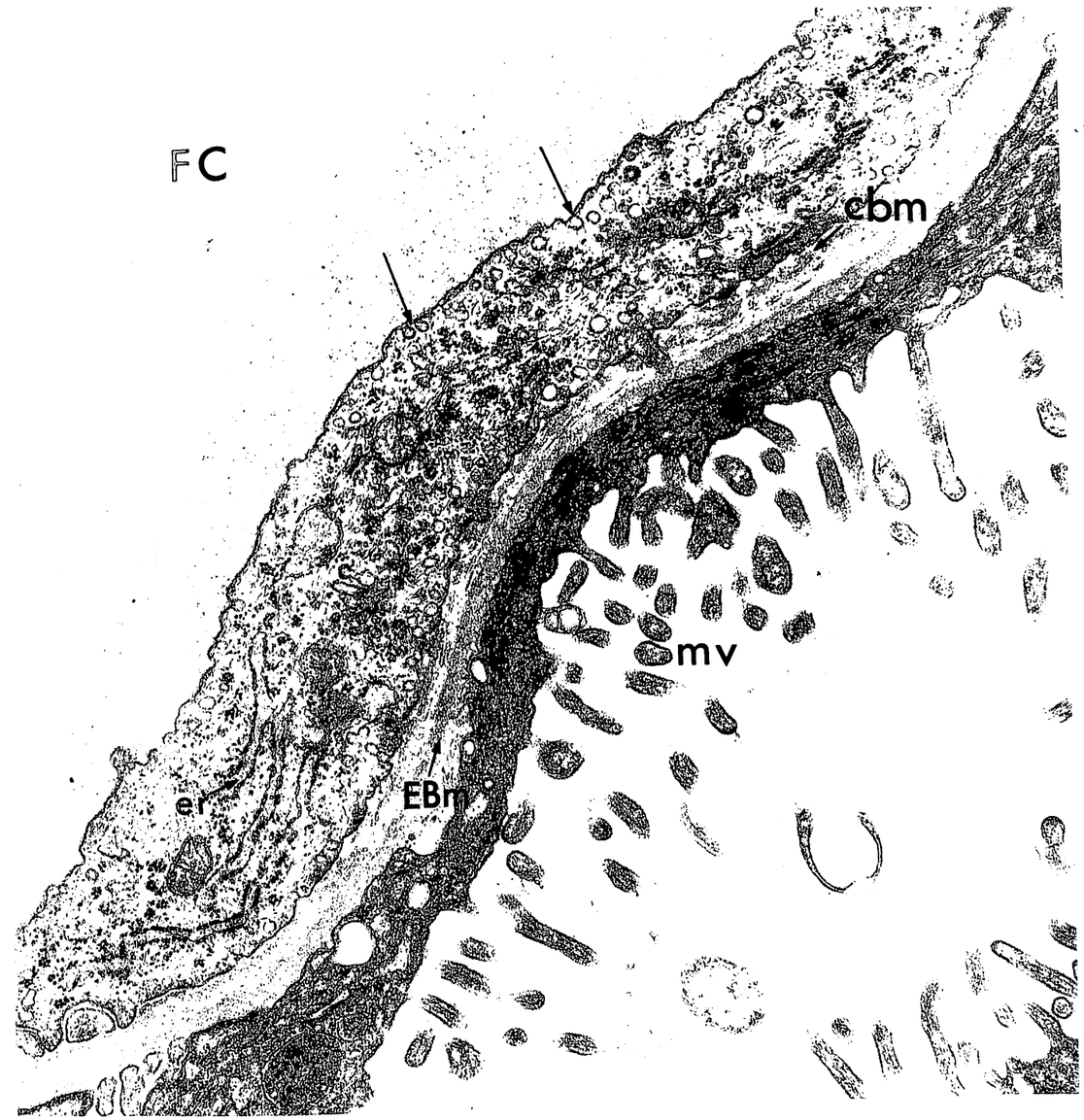


Fig. 7. Calveolae (arrows) or micropinocytotic vesicles can be seen throughout the syncytium and the endothelium. FC, fetal capillary; cbm, capillary basement membrane; EBm, epithelial basement membrane; er, endoplasmic reticulum; mv, microvilli. Magnification x 27,500

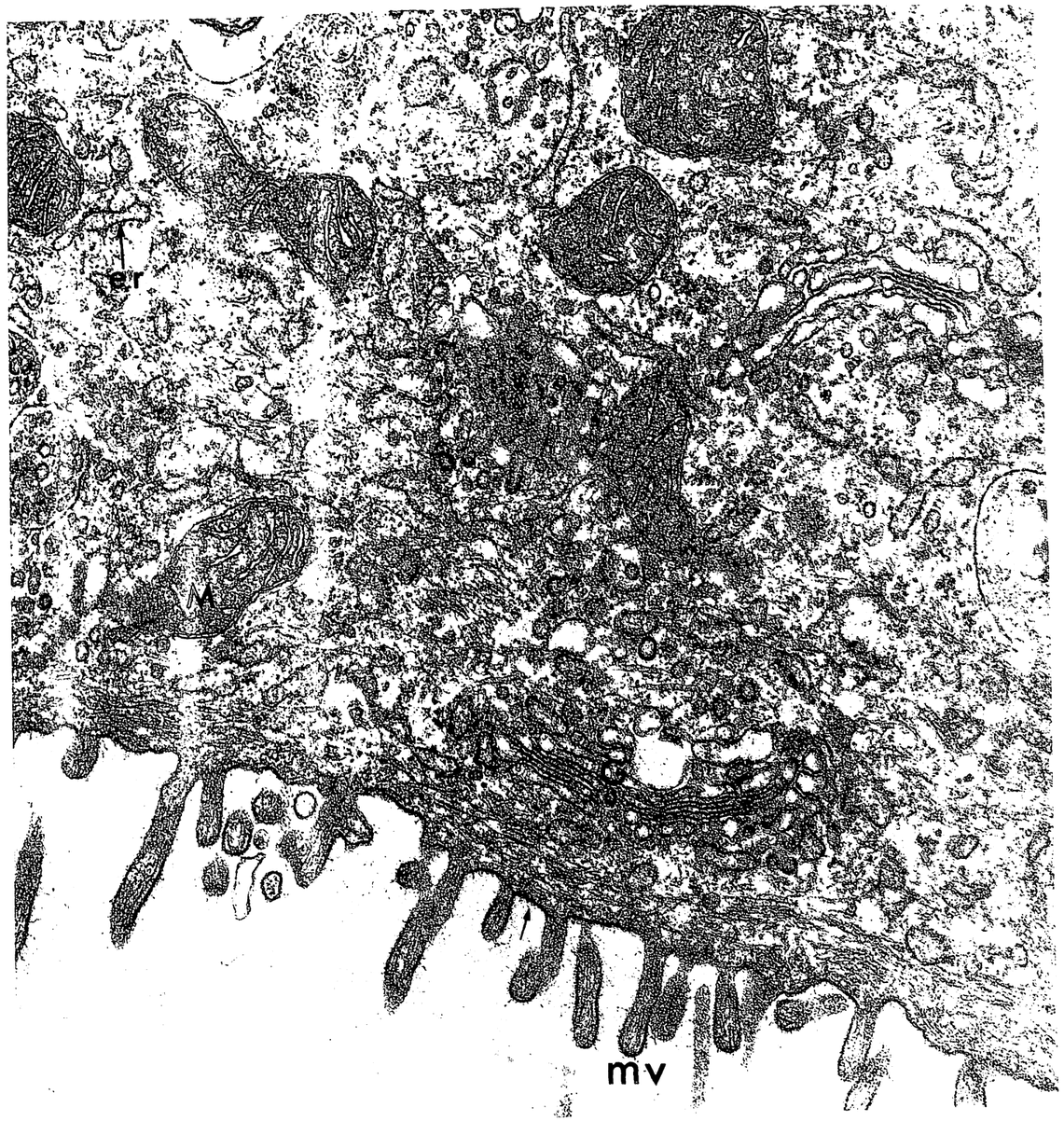


Fig. 8. High magnification of the syncytiotrophoblast shows Golgi bodies (G), mitochondria (M) with well defined cristae, dark bands (arrow) at the syncytial surface in transition regions, microvilli (mv), and rough endoplasmic reticulum (er). Magnification x 33,000.

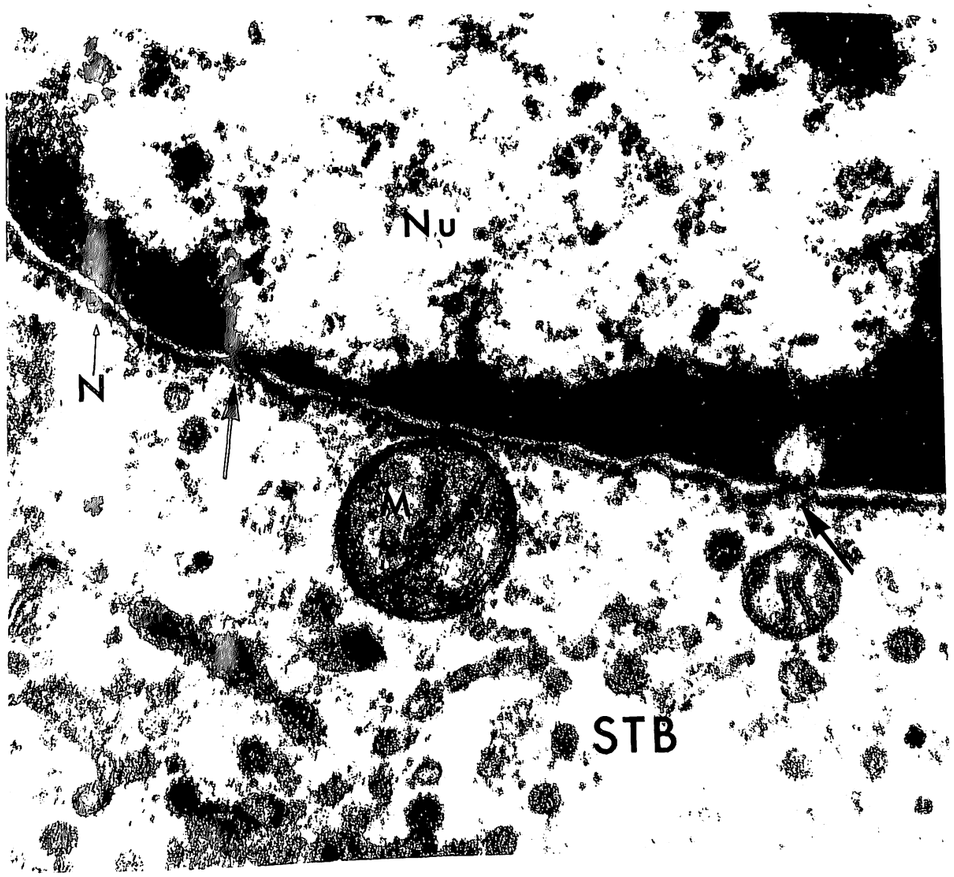
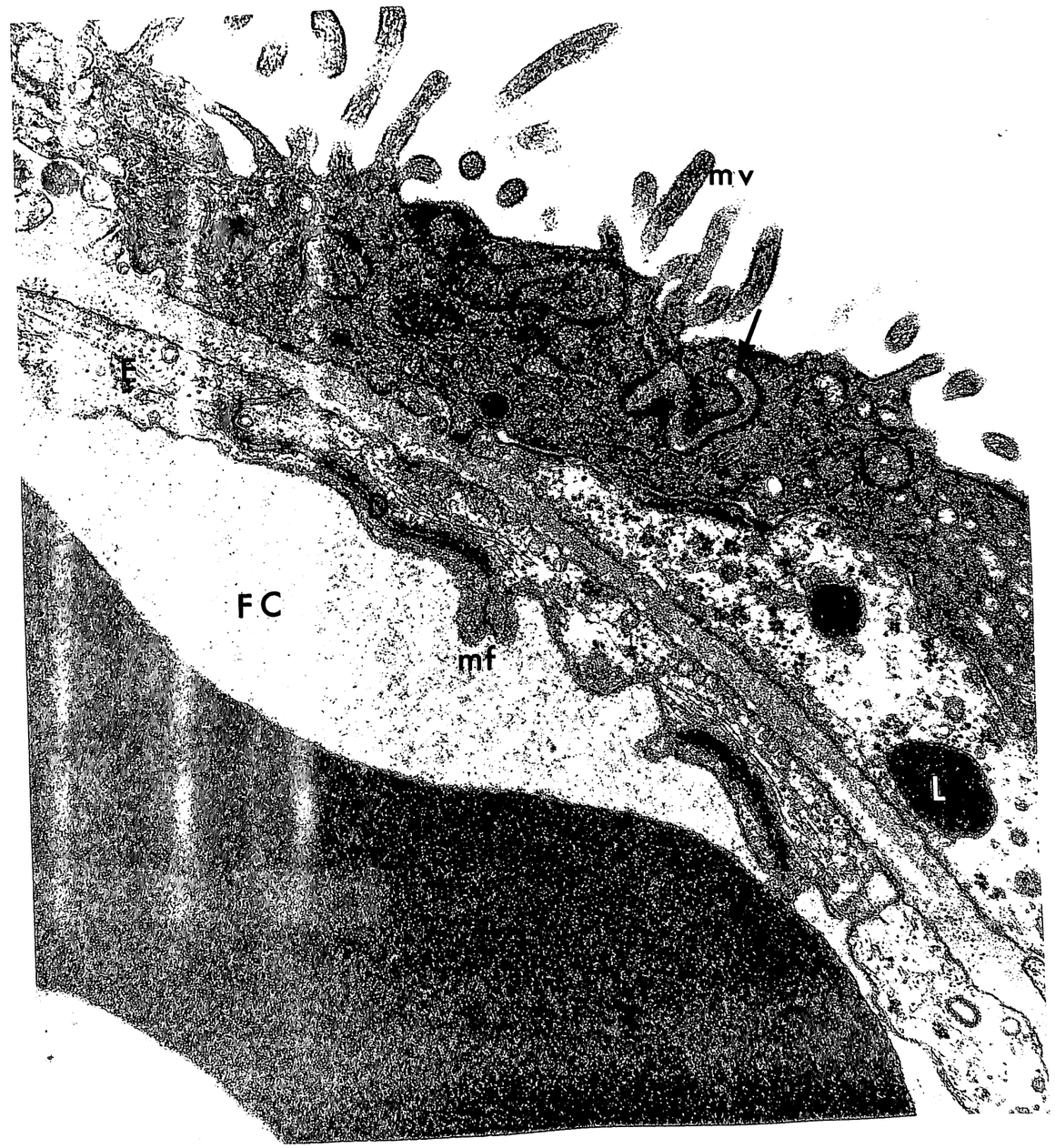


Fig. 9. Nuclear membrane (N) of syncytial nucleus (Nu) appears to contain pores (arrows). STB, syncytiotrophoblast; M, mitochondria. Magnification x 73,900.

Fig. 10. Distinct desmosomes (D) can be seen which are the means of connection between adjacent endothelial cells (E). Lipid droplets (L) are present in both the cytotrophoblast and the syncytium. A structure (arrow) possibly suggestive of a canalicluar system is present in the syncytiotrophoblast. FC, fetal capillary; mf, marginal folds; mv, microvilli; RBC, red blood cell. Magnification x 35,000.



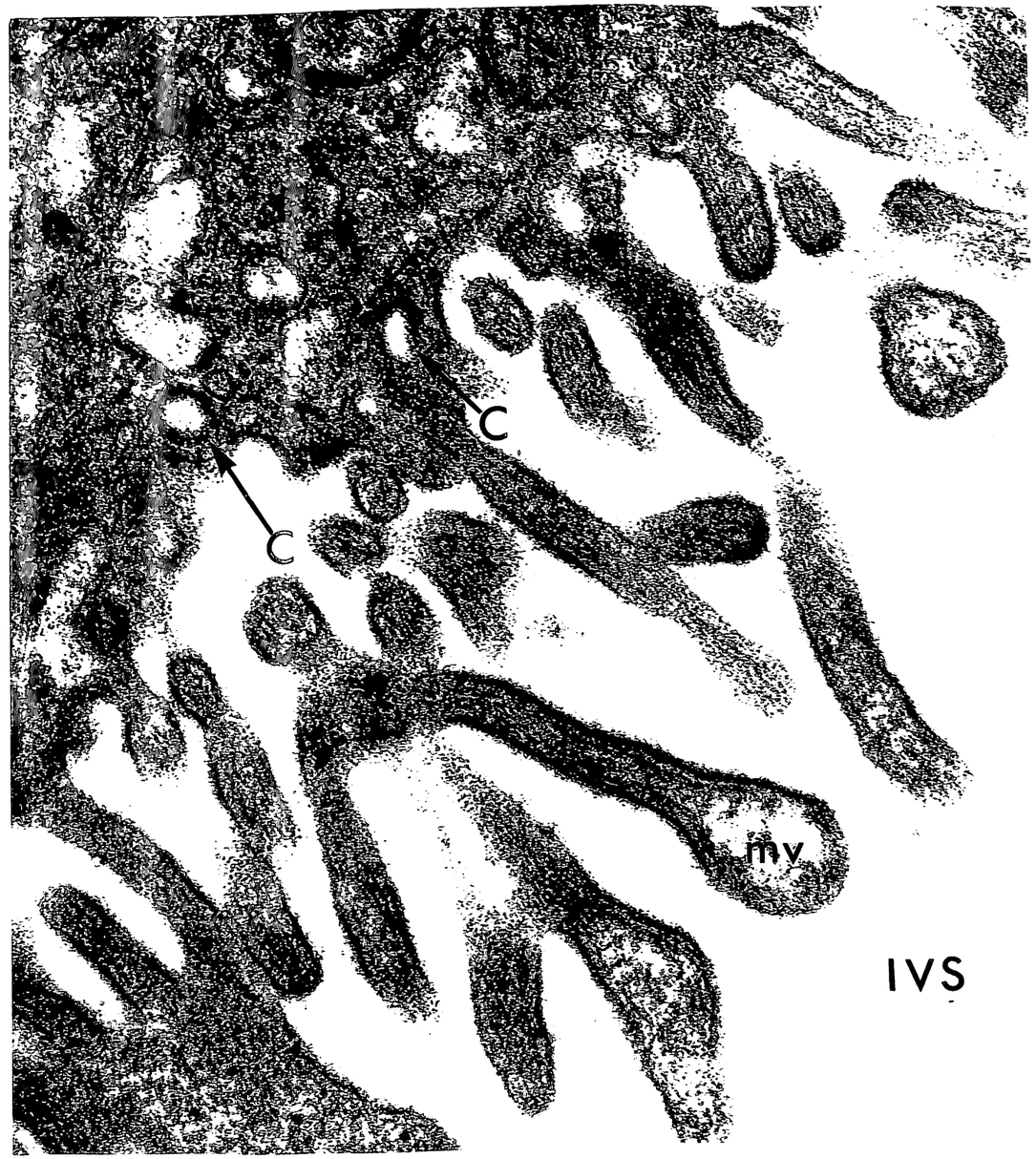


Fig. 11. High magnification electron micrograph of the syncytiotrophoblastic surface showing microvilli (mv) with bulbous tips and invaginating calveolae (C). IVS, intervillous space. Magnification x 70,000.

Fig. 12. High magnification electron micrograph shows calveolae (C) at the syncytial surface. The "fuzzy" coat of the microvilli may be the "glycocalyx". Magnification x 70,000.

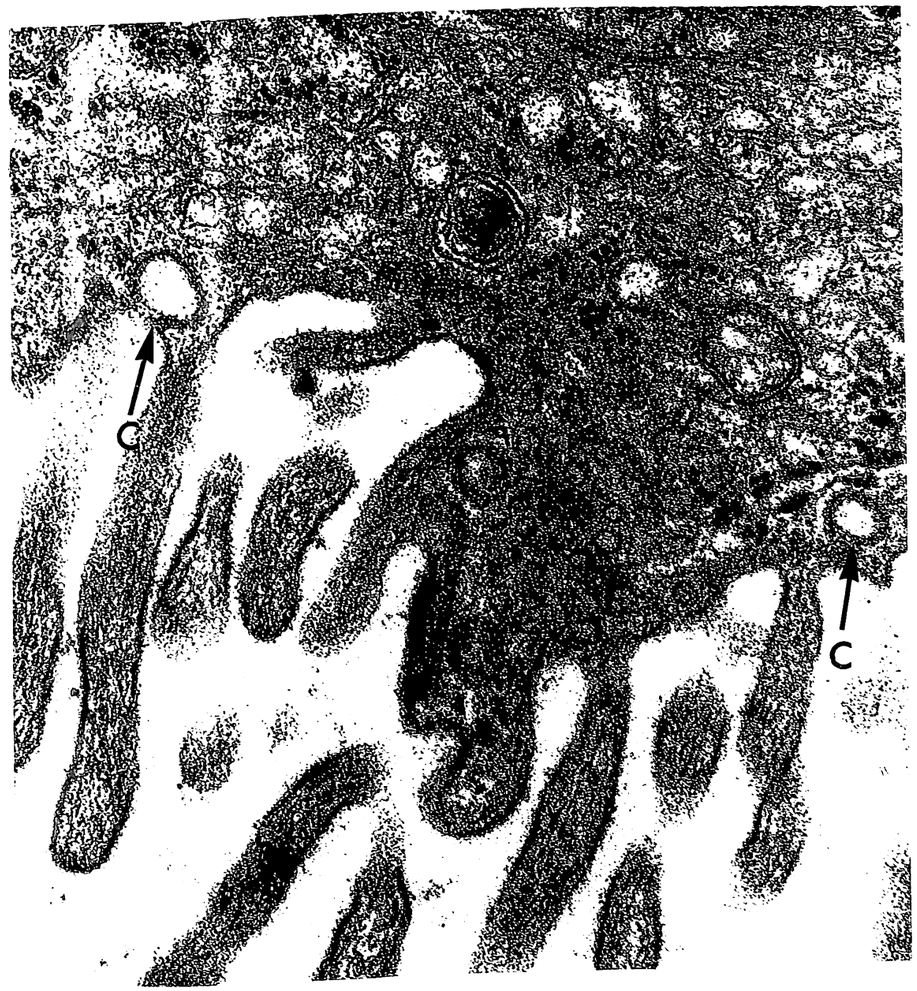
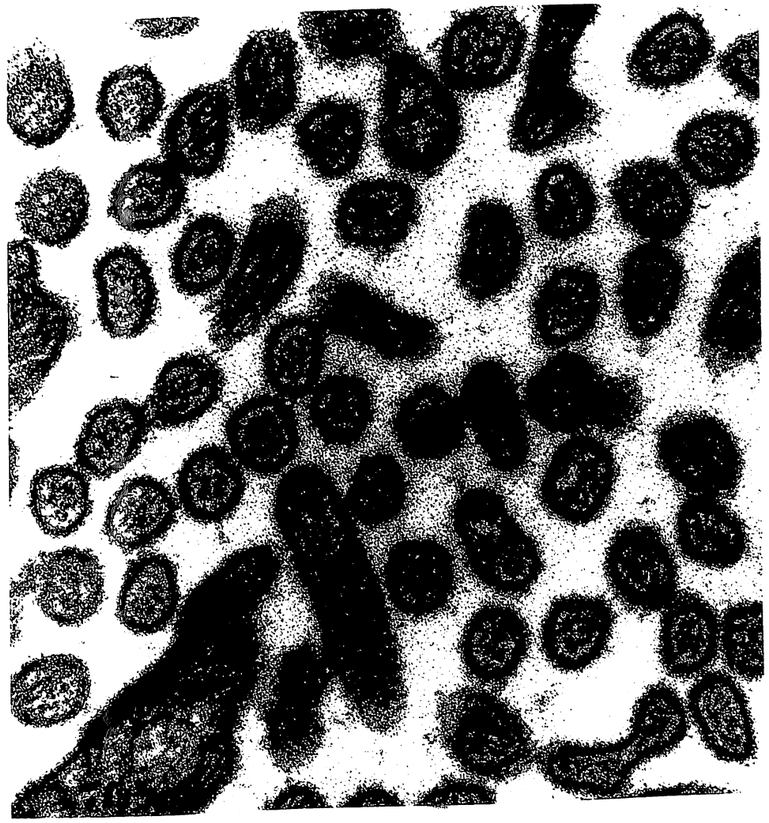


Fig. 13. Cross-section of microvilli. Magnification x 84,800.



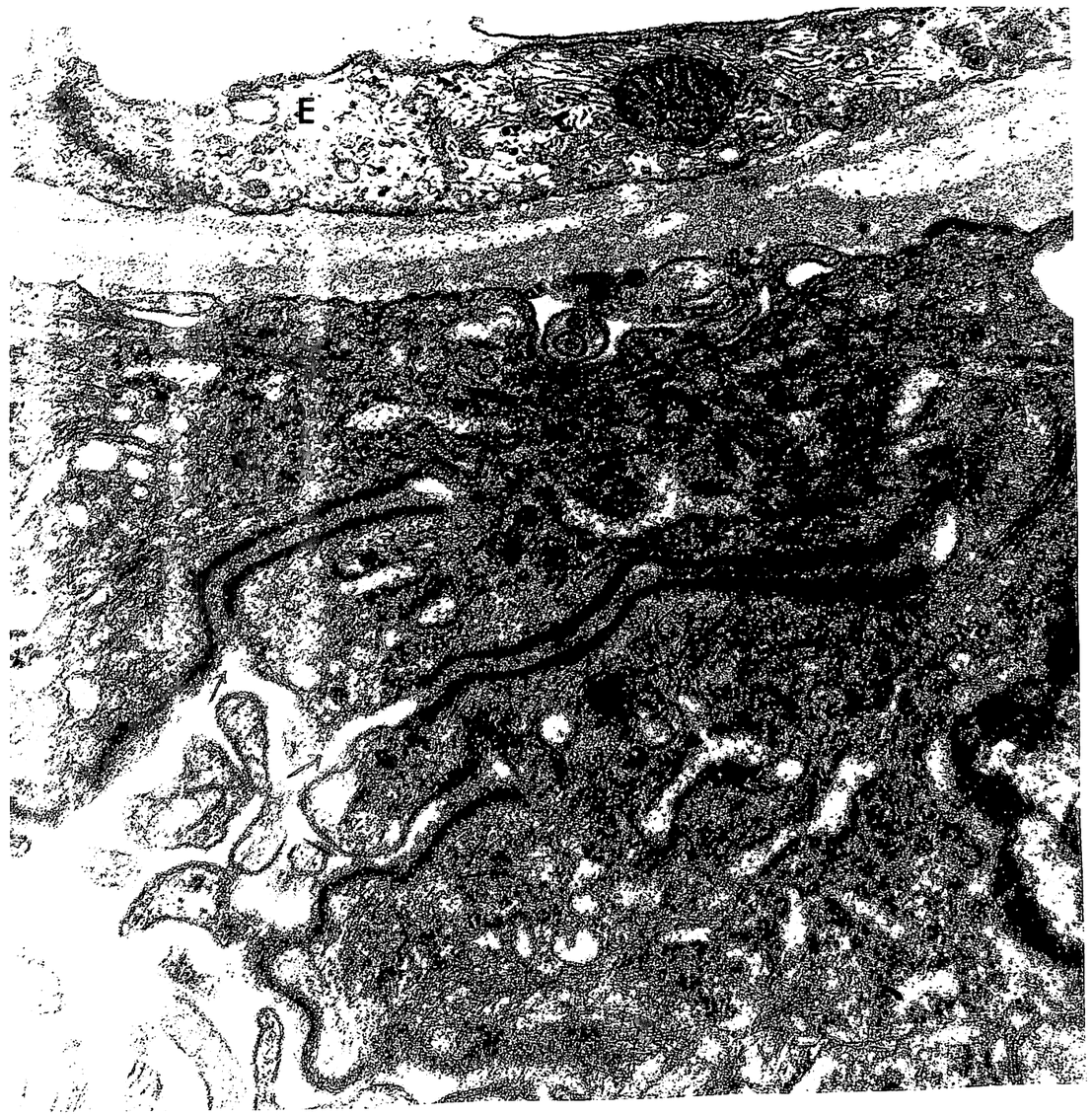


Fig. 14. Structures (arrows) in the syncytiotrophoblast are suggestive of a canalicular system of transport. E, endothelium of fetal capillary. Magnification x 45,000.

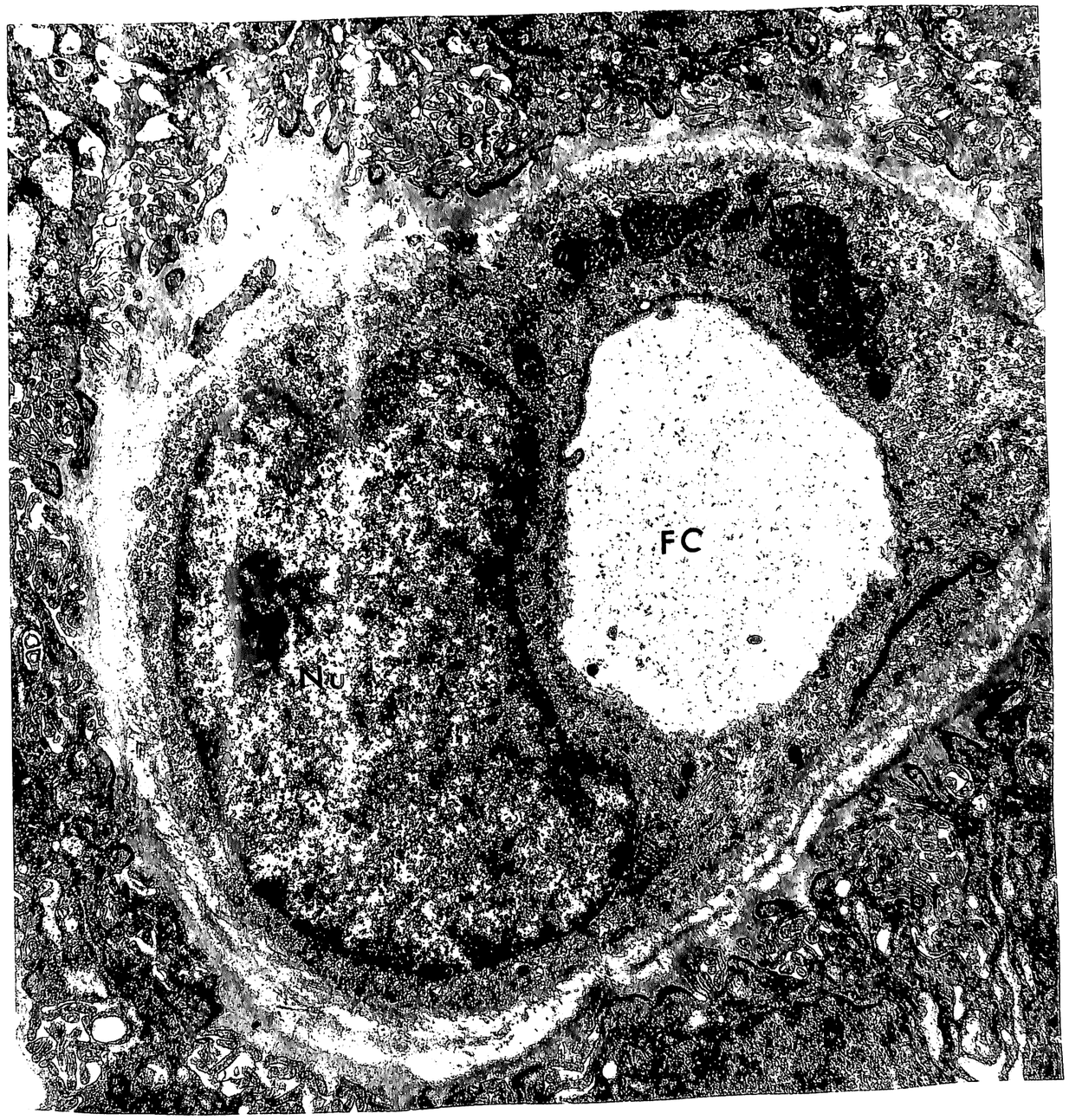


Fig. 15. Basal folds (bf) can be seen at the base of the syncytiotrophoblast next to the epithelial basement membrane. Note the fetal capillary (FC) is contracted and its cytoplasm contains groups of electron-dense mitochondria (M). A desmosome (D) is present at the junction of two endothelial cells. Magnification x 15,625.

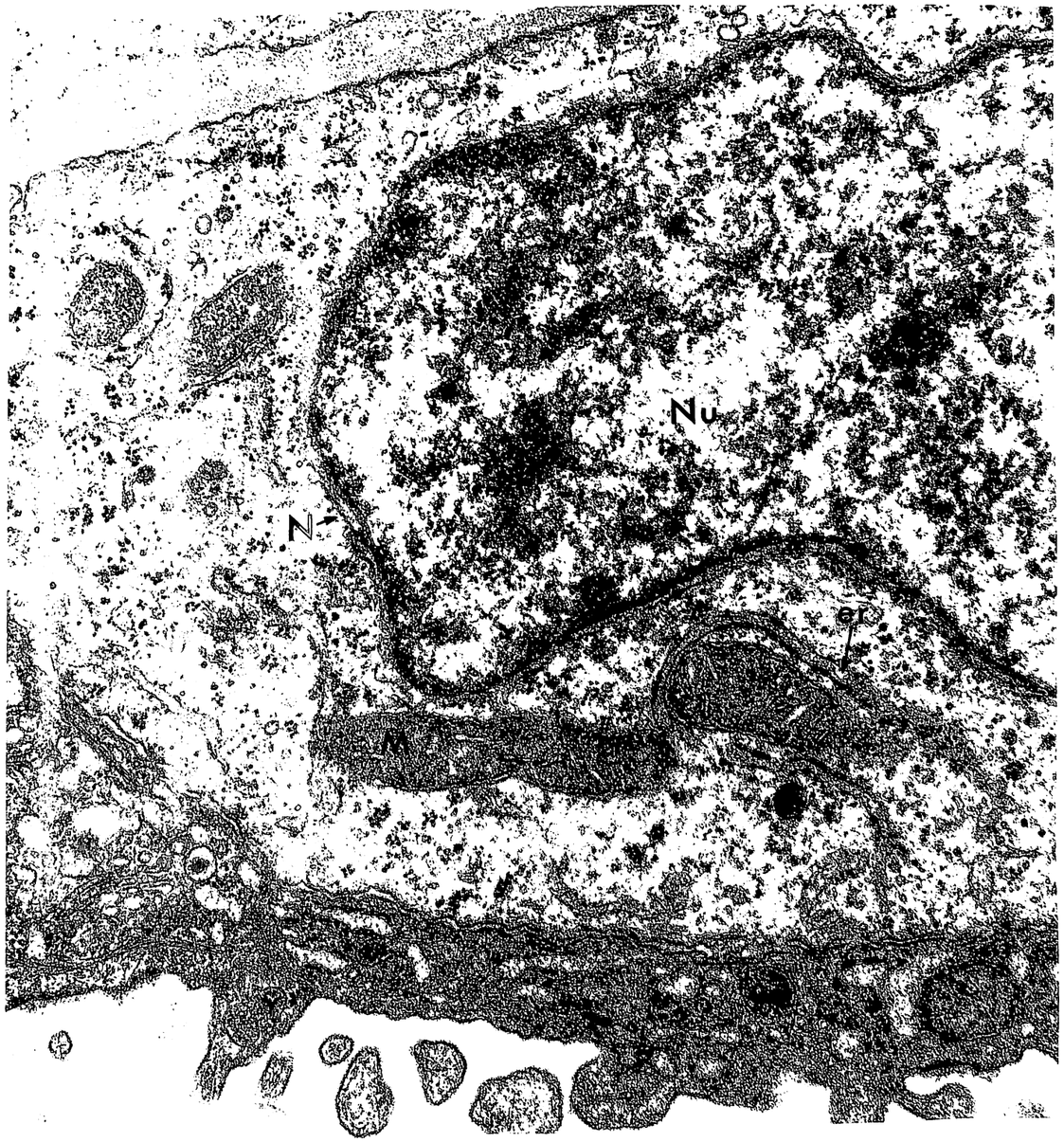


Fig. 16. High magnification electron micrograph shows syncytiotrophoblast, cytotrophoblast, and basement membranes. The cytotrophoblast contains long, slender endoplasmic reticulum (er) in close association with mitochondria (M). Nu, nucleus; N, nuclear membrane. Magnification x 35,000.

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