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FINE STRUCTURE OF THE PHOTORECEPTOR CELL OF THE EARTHWORM, *Eisenia foetida*

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Abstract

The photoreceptor cell of the earthworm, *Eisenia foetida,* occurs on the body wall among epidermal cells. Against HESS's report on *Lumbricus terrestris* (1925), it was not found on the nerves to the skin near their terminations. It is as tall as the other epidermal cells. A large sac packed with microvilli occupies the central part of the cell. The sac is interpreted to be the photoreceptive organelle. Some cilia are seen among microvilli; they lack central filaments. The photoreceptor opens at the cell apex under cuticle.

Many deep invaginations or infoldings of the outer cell membrane are seen, including in them processes from the surrounding supportive cells and from the basal cell. Desmosomes are seen on the invaginations as well as on the outer cell surface. Bottoms of some invaginations attain just outside the photoreceptor wall (Pl. Fig. 8). This suggests their possibility of having a role in speed-up of conduction of the optic impulse generated on the receptor wall to the outer cell surface.

In the cytoplasm, there are three kinds of vesicles. The first have amorphous contents of varying density, are often multivesicular, and the large ones of them are sometimes double-membraneous with clear contents. Concerning their character, various possibilities may be conceived, lysosomes and other formations derived from the mitochondrion and so on. They are the most abundant. The second are the dilated endoplasmic reticulum, and are in most cases irregular in form. And the third are the smallest, most being smaller than 90×120 mμ, and resemble Golgi or pinocytotic vesicles.

The Golgi apparatus developes well and occurs near the nerve root and around the nucleus, which is in the basal part of the cell. Golgi vesicles are found in great number. Minute round pockets on the receptor wall are rarely met with (Pl. Fig. 12). So far it is difficult to decide whether they are pinocytotic or excretory.

Ribosomes occur in abundance around the nucleus, making rough endoplasmic reticulum. They are not so rich around the photoreceptor.

Bundles of tonofilaments are seen in the cytoplasm (Pl. Fig. 10, 11), but they are not so numerous as to form neurofibrillar network. They seem to give mere mechanical support to the cell.

The nerve process leaves the cell body at the high nuclear level (Pl. Fig. 1, 2, 3). It descends down to the basal lamina and forms half desmosomes there, and then joins the epidermal nerve which runs between epidermal cells and the basal lamina.

Between the photoreceptor cell and the basal lamina, there exists the basal cell without exception. It has a relatively clear cytoplasm. The endoplasmic reticulum and ribosomes in it are not so rich as in the other epidermal cells. It includes characteristic granules of high electron density, smaller than 260×450mμ. The cell embraces apically the photoreceptor cell and basally the epidermal nerve and basal extremities of the other epidermal cells with its cytoplasmic processes.

Introduction

The photoreceptor cell of the earthworm, *Lumbricus terrestris*, was investigated by Walter N. Hess (1925) with the light microscope. According to him, photoreceptor cells occur on the body wall, among epithelial cells, and some aggregate on certain of nerves to the skin near their terminations; they are of round shape and shorter than half the height of the other epidermal cells, they have lens and retinella in their cell bodies as the optic organelles; lens are ellipsoidal or elongated and bent, being circular in all cross sections; network of neurofibrils fills the cytoplasm and is more densely arranged around lens, and here forms retinella; the nerve process leaves the cell at its basal end; and light is refracted by lens and focussed on retinella. Hess's opinion was accepted by Stephenson (1930) on Oligochaeta, and by Mann (1962) and Nagao (1967) on Hirudinea.

According to modern physiology (A. L. Hodgkin and A. F. Huxley, 1939–'53, and others), nerve impulse is conducted along the plasma membrane of the nerve fiber, and not along the neurofibril; and the latter is interpreted to give mere mechanical strength to the cell.

It is the purpose of the present study to clarify microstructures of the photoreceptor cell of the earthworm, *Eisenia foetida*, and to correlate them with the theory of the modern physiology.

Materials and Methods

Epidermis of the earthworm *Eisenia foetida* was cut carefully into pieces 1–2 mm cube, fixed for 2 hrs in cold 3 % glutaraldehyde buffered to pH 7.4 in 0.2 M s-collidine buffer, and postfixed for 1 hr with cold 1 % osmium tetroxide in the same buffer at pH 7.4. The tissue was dehydrated with increasing concentrations of ethanol, then placed in propylene oxide and embedded in Epon 812. Thick sections for light microscopy were cut at 0.5 μ and stained with 0.5 % toluidine blue or 1 % azur II-methylene blue mixture in 1 % sodium borate in distilled water. For electron microscopy, thin sections ranging from gold to gray in color were cut with glass knives on Porter-Blum MT-1 ultramicrotome. The thin sections were mounted on formvar coated copper grids, stained with 0.1 % lead citrate and saturated solution of uranyl acetate in distilled water, and examined in Hitachi HS-7 electron microscope.

General Description

General aspects of the epidermis of the earthworm, *Eisenia foetida*, are similar with those of *Lumbricus terrestris* reported by COGGESHALL (1966). The epidermis consists of an epidermal epithelium and an overlying cuticle. Underlying the epidermis are a layer of connective tissue and then the body wall musculature.

The cuticle of *E. foetida* shows sometimes an alternating series of fibrous layers embedded in the matrix, as it was reported by COGGESHALL on *Lumbricus* (1966), but such fibrous structure of the cuticle is not always observable. In the former case fibers in one layer run parallel with each other and perpendicular to those in the neighboring layers. Cuticular fibers were reported by M. D. MASER & R. V. RICE (1963) to be made of a kind of tropocollagen.

On the free surface of the cuticle, there stand numerous ellipsoidal bodies 100–130 mμ long and 35–45 mμ thick. Concerning construction of these bodies, tips of microvilli of the underlying epidermal cells may have some important role. Microvilli of the epidermal cells pierce the cuticle and their tips attain to its outer surface (Fig. 1).

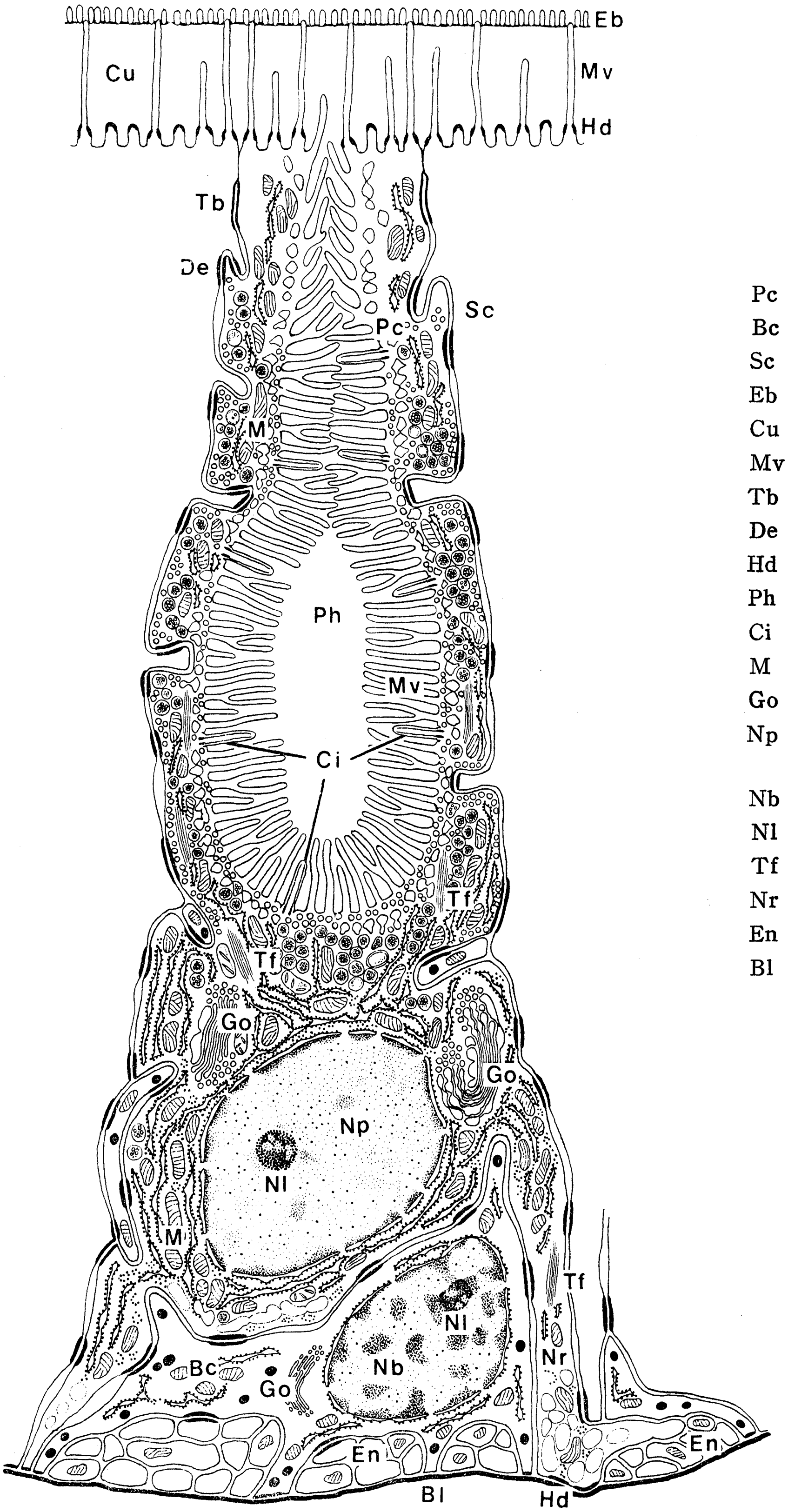
The epidermal epithelium that underlies the cuticle is 30 to 60 μ thick. It is lined with a basal lamina 150 A thick. It consists of three major cell types, as reported by COGGESHALL on *Lumbricus*; the supportive cell, the mucous cell, and the basal cell. The supportive cell and the mucous cell extend from the cuticle to the basal lamina, and the basal cell is confined to the basal regions. In addition, there are some kinds of sensory cells, including photoreceptor cells and others.

The Photoreceptor Cell

Photoreceptor cells of *Eisenia foetida* occur on the body wall, among epidermal cells. They do not group to make the visual organ like eye spots. Against HESS's report on the earthworm, *Lumbricus terrestris* (1925), they were not found on the nerves to the skin near their terminations.

The photoreceptor cell of *E. foetida* is as tall as the other epidermal cells (Pl. Fig. 1). The photoreceptor organelle occupies the central part of the cell. It is a large sac packed with microvilli. It opens at the free cell surface. It becomes narrow toward the opening (Pl. Fig. 4 & 5). Microvilli in the photoreceptor are 150–80 mμ thick. They branch frequently (Pl. Fig. 8, insertion). Microvilli grow on the photoreceptor neck wall and on the apical free cell surface as well as on the photoreceptor body wall (Pl. Fig. 5).

Some short cilia occur on the photoreceptor wall among microvilli. They lack the central filaments (Pl. Fig. 13). Each cilium has a centriole-like basal body at its base.



Pc Photoreceptor cell
Bc Basal cell
Sc Supportive cell
Eb Ellipsoidal bodies
Cu Cuticle
Mv Microvilli
Tb Terminal bar
De Desmosomes
Hd Half desmosomes
Ph Photoreceptor
Ci Cilia
M Mitochondrion
Go Golgi apparatus
Np Nucleus of the photoreceptor cell
Nb Nucleus of the basal cell
Nl Nucleolus
Tf Bundle of tonofilaments
Nr Nerve root
En Epidermal nerve
Bl Basal lamina

Fig. 1. The photoreceptor cell of *Eisenia foetida* and a basal cell under it.

The cytoplasm (Pl. Fig. 10 and others) is crowded with three types of vesicles. The first is round or ellipsoidal, and has contents of varying density. The large ones of this type attain $1.0 \times 0.7\,\mu$ in size, are very often double-membraneous (Pl. Fig. 10, arrows), and have clear contents. Usual ones of this type are smaller than $0.7\,\mu$, and single-membraneous; their dark contents have tendency to coalesce, and are very often multivesicular. They look like the lysosome, but it is also possible that they may be another structure derived from mitochondria. The second is the partial dilations of the endoplasmic reticulum, and is in most cases irregular in form (Pl. Fig. 10 & 14). And the third is the smallest, being smaller than $170 \times 120\,\mathrm{m}\mu$, and resembles Golgi or pinocytotic vesicles (Pl. Fig. 6, 7, 9, 12 & 13). Two vesicular pockets on the photoreceptor wall of Pl. Fig. 12 are 80 and 50 mμ in size. They may be regarded as pinocytotic pockets, but it is difficult to decide whether they are really pinocytotic or excretory.

Ribosomes are the most numerous at the basal part, around the nucleus (Pl. Fig. 10). They diminish their number around the photoreceptor (Pl. Fig. 10) and further toward the apical part (Pl. Fig. 5). The mitochondrion is distributed all through the cytoplasm.

The Golgi apparatus exists near the nucleus (Pl. Fig. 9, 10 & 11), and at the base of the nerve process (Pl. Fig. 1-3). It belongs to the usual type, and is composed of Golgi membranes, Golgi vacuoles, and Golgi vesicles (Pl. Fig. 11). Most Golgi vesicles are 80-50 mμ in size.

A few bunldes of tonofilaments are seen in the cytoplasm (Pl. Fig. 10 & 11); otherwise, no network of any fibrous structure is observable, which might be regarded as such a neurofibrillar network as described by HESS (1925).

The photoreceptor cell is connected with the surrounding epithelial cells by the terminal bar and desmosomes. In addition, there are many infoldings or indigitations of the cell membrane with which cytoplasmic processes from surrounding supportive cells (Pl. Fig. 6 and 7) and from the basal cell (Pl. Fig. 9) are closely fitted.

A nerve process leaves the photoreceptor cell at the high nuclear level, descends down to the basal lamina (Pl. Fig. 1-3), and then joins the epidermal nerve, which runs between the epidermal epithelium and the basal lamina (Pl. Fig. 2). The cytoplasm of the nerve process is clear, except the small part near the exit, where it is of the same density and of the same appearance with the cell body cytoplasm (Pl. Fig. 2 & 3).

The Basal Cell

One or two basal cells are observed between each photoreceptor cell and the basal lamina in sections (Pl. Fig. 1-3 & 14). The nucleus is round (Pl. Fig. 14) or elongated (Pl. Fig 1-3). Nuclear contents appear coarser than those of the photoreceptor cell, and it is very easy to distinguish these two types of nuclei. Its scanty cytoplasm contains a few organelles and appears comparatively uniform. Its peculiarity is represented by a few number of round granules of high electron density, smaller than 0.3 μ, which may be made of a kind of pigment.

The basal cell sends out many cytoplasmic processes. Downwards, these processes embrace the epidermal nerve (Pl. Fig. 14) or basal extremities of other epidermal cells (Pl. Fig. 1-3), and attain the basal lamina; and upwards, they extend along the photoreceptor cell body, and are often found in infoldings or in indigitations even apical to the nucleus of the photoreceptor cell (Pl. Fig. 9); thus supporting the cell from its basal side.

The Supportive Cell

The supportive cell around the photoreceptor is often higher in electron density than the latter (Pl. Fig. 6). It sends protoplasmic processes into infoldings or indigitations of the cell membrane of the latter. Many desmosomes are found between these two types of cells.

It was reported by COGGESHALL (1966) on ***Lumbricus***, that the supportive cell has on its free surface two types of microvilli, long and short; the formers pierce the cuticle, attain just outside it, and may have an important role in construction of the ellipsoidal bodies arranged on the outer surface of the cuticle; the latter are like stumps, and make half desmosomes with the cuticle. The same can be stated of the present species.

Furthermore, it was added by him that the supportive cell may secrete the cuticular substance in ***Lumbricus***. And it seems true also of the present species, many Golgi apparatus being observable in the apical half of the cell, which suggests its high secretory activity (Pl. Fig. 6 & 7).

Discussions and Conclusions

By the electron microscope studies on the vertebrate eye, it became clear that a stack of double membrane disks are piled up in the outer segment of the rod and cone, which is the receptive organelle derived from the ciliary process of the young visual cell (SJÖSTRAND, 1953; DE ROBERTIS, 1956; TOKUYASU & YAMADA, 1959; NILSSON, 1965). Photoreceptor cells of the invertebrates were grouped into two by EAKIN & WESTFALL (1965): ciliary and rhabdomeric. The former is derived from ciliary processes as in vertebrates and is found in echinoderms, chaetognates, and coelenterates. The latter is composed of microvilli or alike protoplasmic processes, and is observed in arthropods, annelids, molluscs, and platyhelmintes.

The photoreceptor cell of the earthworm belongs to the rhabdomeric type. In

Eisenia, the photoreceptor is a large open sac, from the wall of which a crowd of microvilli and some cilia grow. The microvilli often branch. The cilia are simple and lack central filaments. They are too few in number to allow them some direct role in the photoreceptive activity. Their function is uncertain.

Against HESS's description about ***Lumbricus terrestris*** (1925), the photoreceptor cell of *Eisenia foetida* is as tall as the surrounding epidermal cells. Its receptor sac opens at the cell apex. No neurofibrillar network is seen, except a few bundles of tonofilaments running in the cytoplasm, which may support the cellbody. It is clear that the cell has no such structure as retinella described by HESS.

Now it is made clear that there are two types of photoreceptors in the annelids: closed type of ***Lumbricus*** and ***Hirudinea*** on the one hand and open type of ***Eisenia*** on the other. Concerning the conduction of the optical impulse generated on the receptor wall, following suggestion may be made. Optical impulse generated by the chemical change of the photoreactive substance arranged on the microvillus membrane may be conducted from the receptor wall to the outer cell membrane round the cell apex, where the receptor opens, or through deep invaginations of the outer cell membrane attaining just outside the receptor wall. In *Eisenia* there is no transverse membrane system found by the present authors in Hirudinea (now under preparation), which connect the receptor wall with the outer cell membrane.

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Explanation of Plate Figures

Key to abbreviations

Bc: basal cell. Ci: cilium. Ct: connective tissue. Cu: cuticle. En: epidermal nerve. Er: endoplasmic reticulum. Go: Golgi apparatus. Gm: Golgi membrane. Gva: Golgi vacuole. Gve: Golgi vesicle. M: mitochondrion. Mc: mucous cell. Mu: circular muscle layer. Mv: microvilli. Nb: nucleus of the basal cell. Nr: nerve root of the photoreceptor cell. Np: nucleus of the photoreceptor cell. Ph: photoreceptor. Sc: supportive cell. Tf: a bundle of tonofilaments.

Explanation of Plate I

1. Epidermis of *Eisenia foetida*, illustrating four kinds of cells: photoreceptor cell (Pc), basal cell (Bc), mucous cell (Mc), and supportive cell (Sc). × 4.600

Explanation of Plate II

2. Another section through the nerve root of the same photoreceptor cell. Here, the nerve root turns into the epidermal nerve (En) which runs between the epidermal cells and the basal lamina. × 7.000

3. The third section through the nerve root of the same photoreceptor cell. The order of these three successional sections is Pl. Fig. 2-1-3. × 5.800

Explanation of Plate III

4. Photoreceptor opens at the cell apex. It is filled with microvilli and some cilia. × 4.600

5. Apical part of a photoreceptor cell. Two deep infoldings of the cell membrane are seen. × 22.500

Explanation of Plate IV

6. An oblique section of a photoreceptor cell through its apical level, illustrating many deep infoldings or indigitations which include cytoplasmic processes from surrounding supportive cells (Sc). × 10.800

7. The same as above. Several Golgi apparatus (Go) develop well in the apical half of the surrounding supportive cells (Sc), which suggests high secretory activity of these cells. In this micrograph, there is no difference in cytoplasmic density detween the photoreceptor cell and the supportive cell. × 10.800

Explanation of Plate V

8. A cross section of a photoreceptor cell through its middle part, showing a deep infolding attaining just outside the photoreceptor wall (arrow). × 18.000
Insertion illustrates branching of a microvillus. × 23.000

9. Deep invaginations at the level of nucleus, which envelop two kinds of processes, one from the surrounding supportive cells, and the other from the basal cell; the latter is clearer than the former, and includes characteristic granules of high density (arrow) x 10.800

Explanation of Plate VI

10. Cytoplasm of the photoreceptor cell is crowded with three kinds of vesicular formations: the first, those with contents of varying density; the second, dilated endoplasmic reticulum; the third, those resembling Golgi or pinocytotic vesicles. Bundles of tonofilaments are seen (Tf). Ribosomes are abundant in the nuclear region. Two Golgi apparatus (Go) are seen. × 9.200

11. Golgi apparatus occurs around the nucleus (Np), and is composed of Golgi membranes (Gm), Golgi vacuoles (Gva) and Golgi vesicles (Gve). × 32.000

Explanation of Plate VII

12. Two vesicular pockets on the photoreceptor wall (80 and 50 mμ) may be pinocytotic or secretory. Many small vesicles smaller than 120×170 mμ are seen in the cytoplasm. × 30.000

13. A cilium on the photoreceptor wall. × 20.000

Two insertions are cross sections of a cilium and its basal granule. Note nine radiations around the latter. × 30.000

14. Two basal cells are seen under one photoreceptor cell. The epidermal nerve runs between the basal cells and the basal lamina. Note dark round granules in the basal cell. × 3.600


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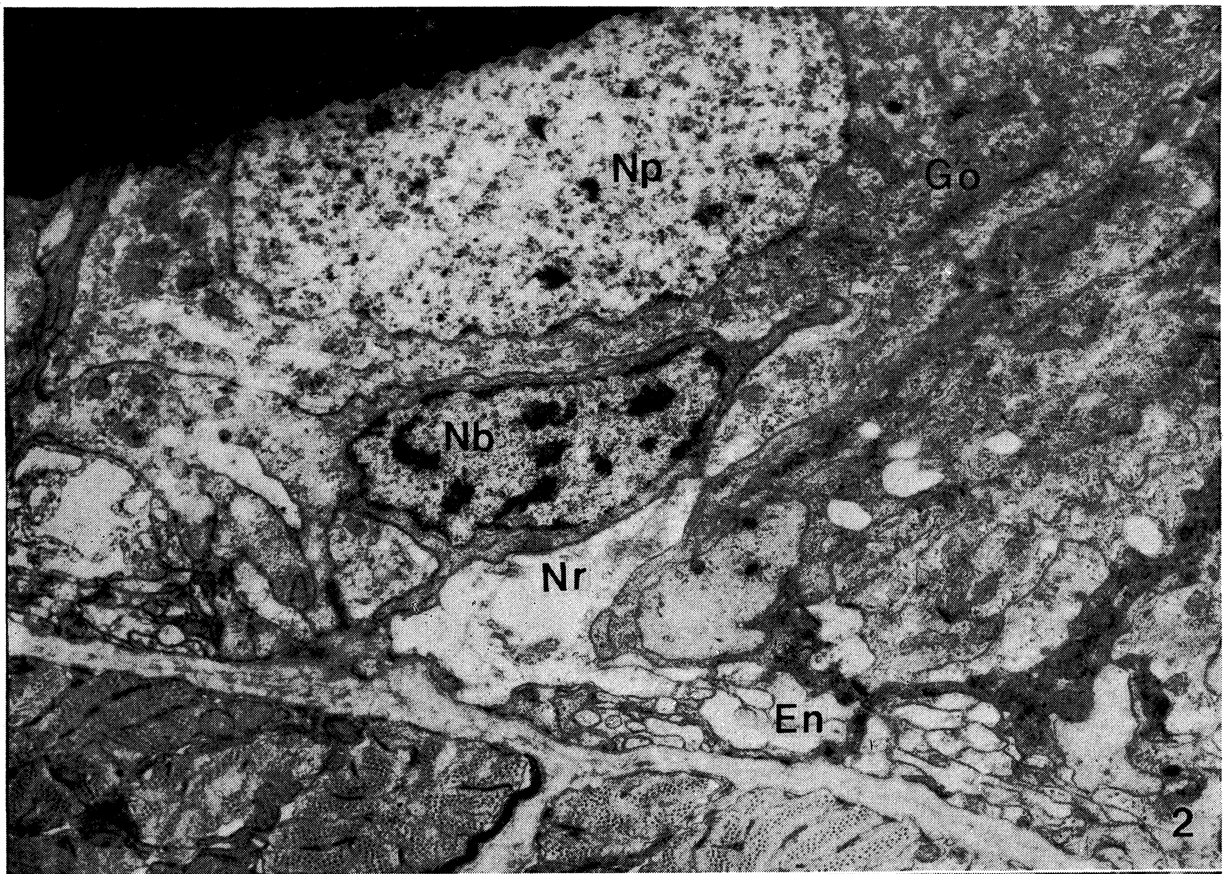
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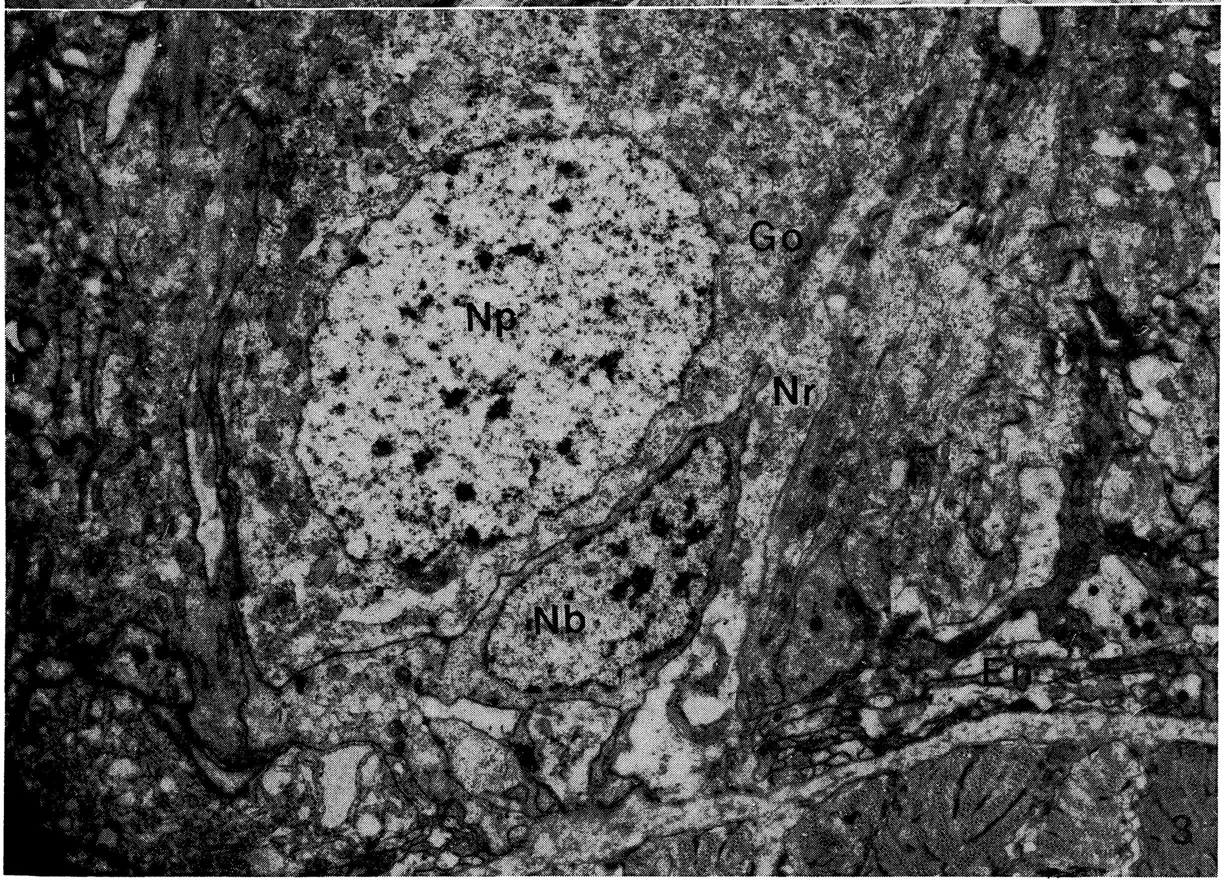
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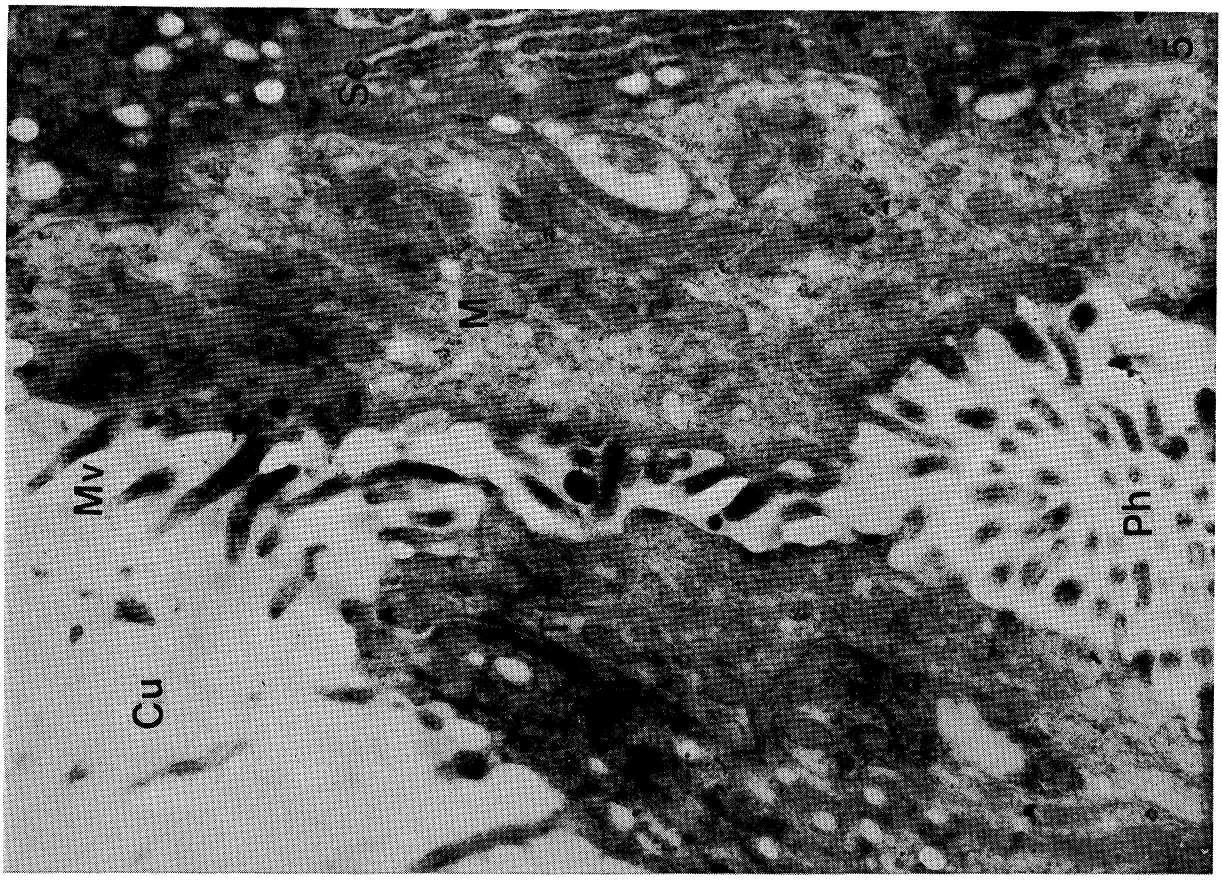
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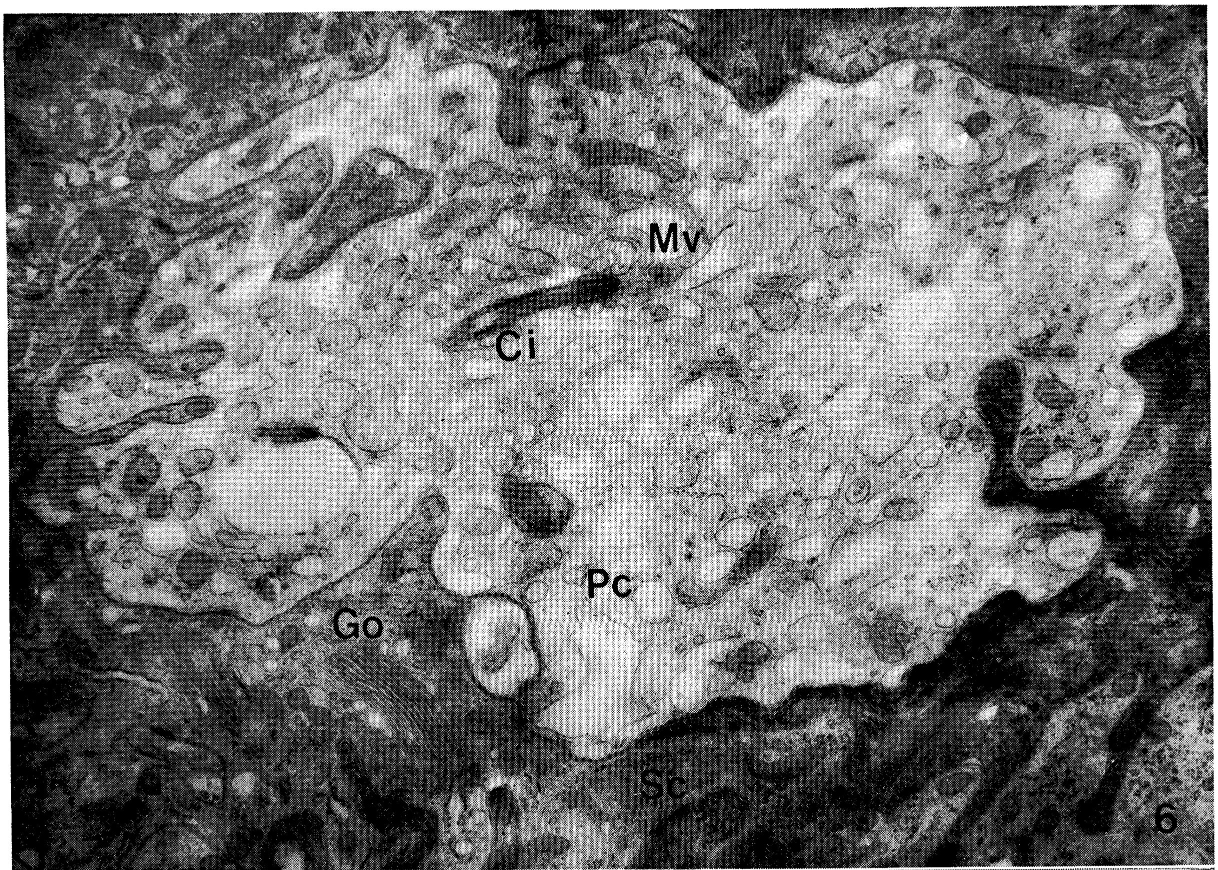
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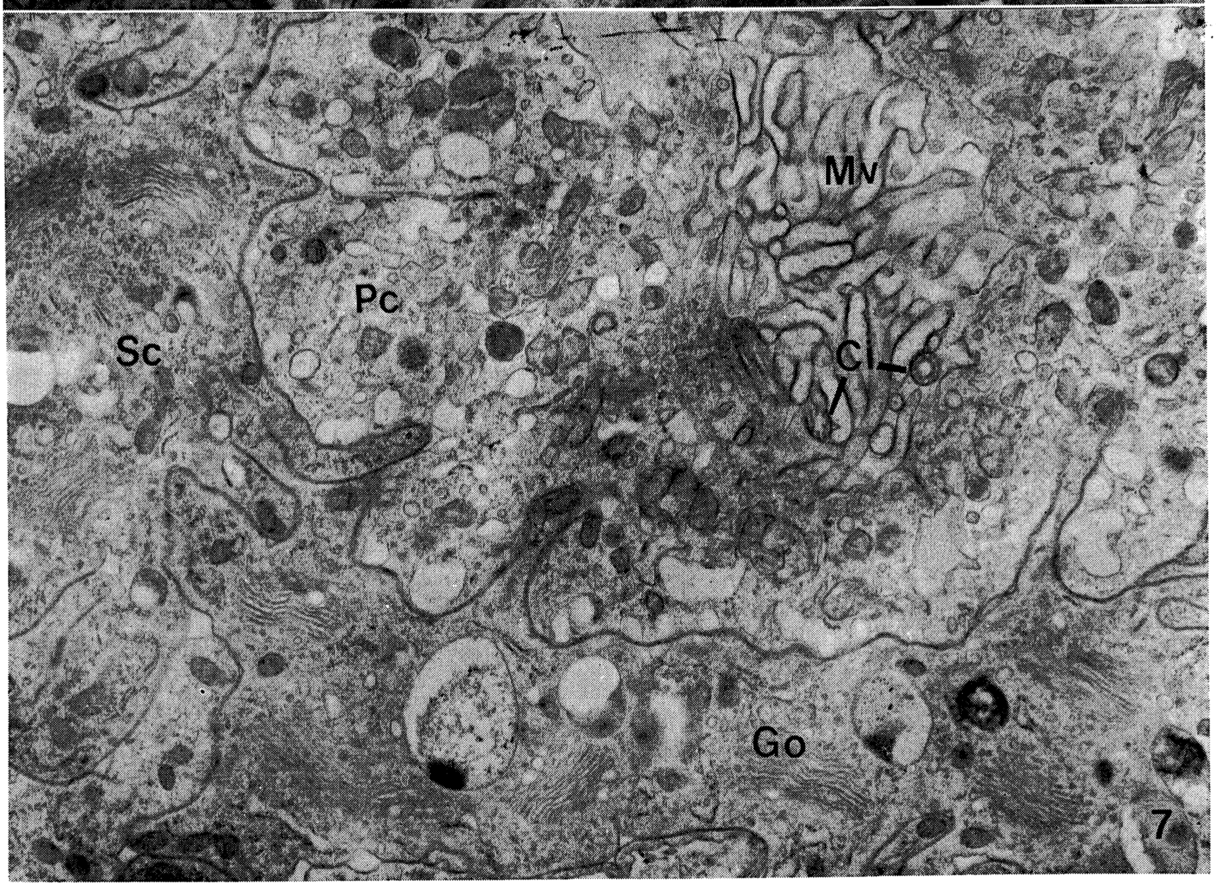
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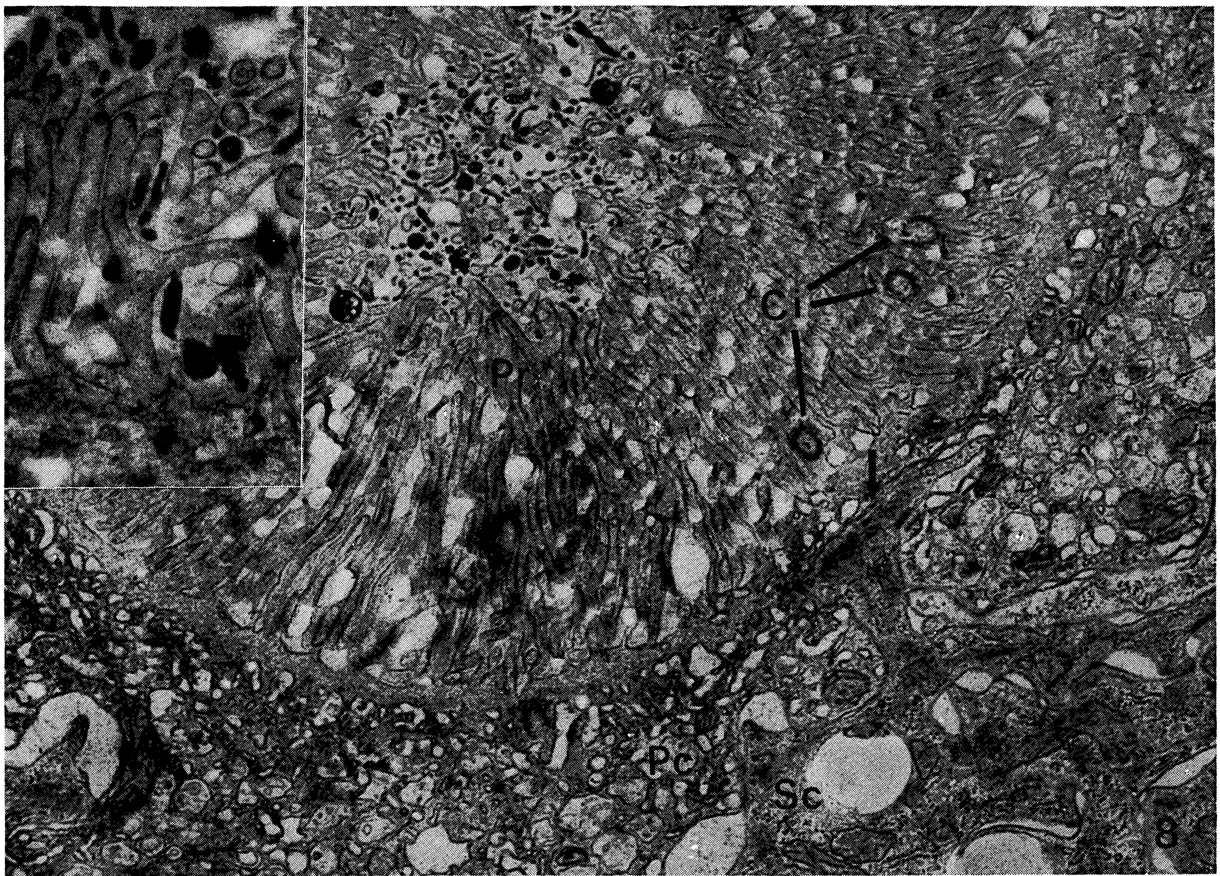

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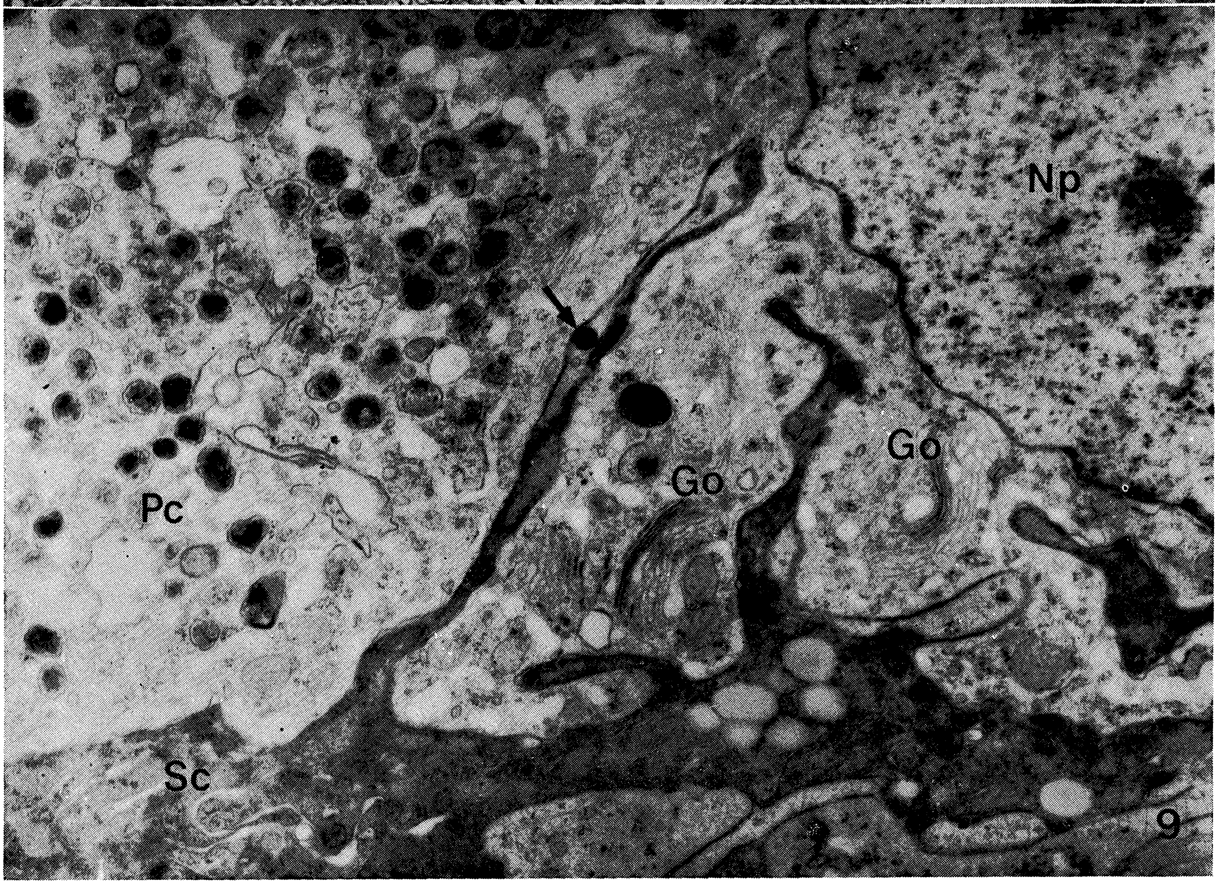

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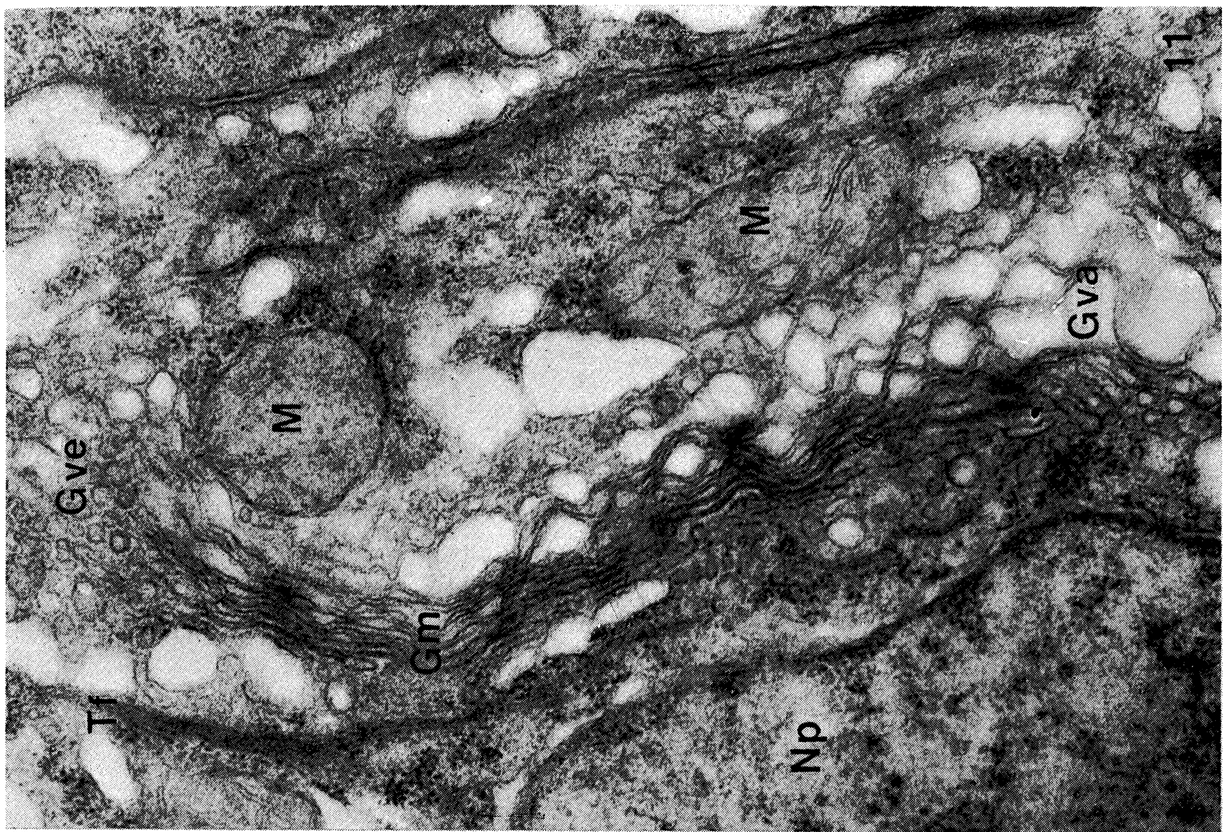
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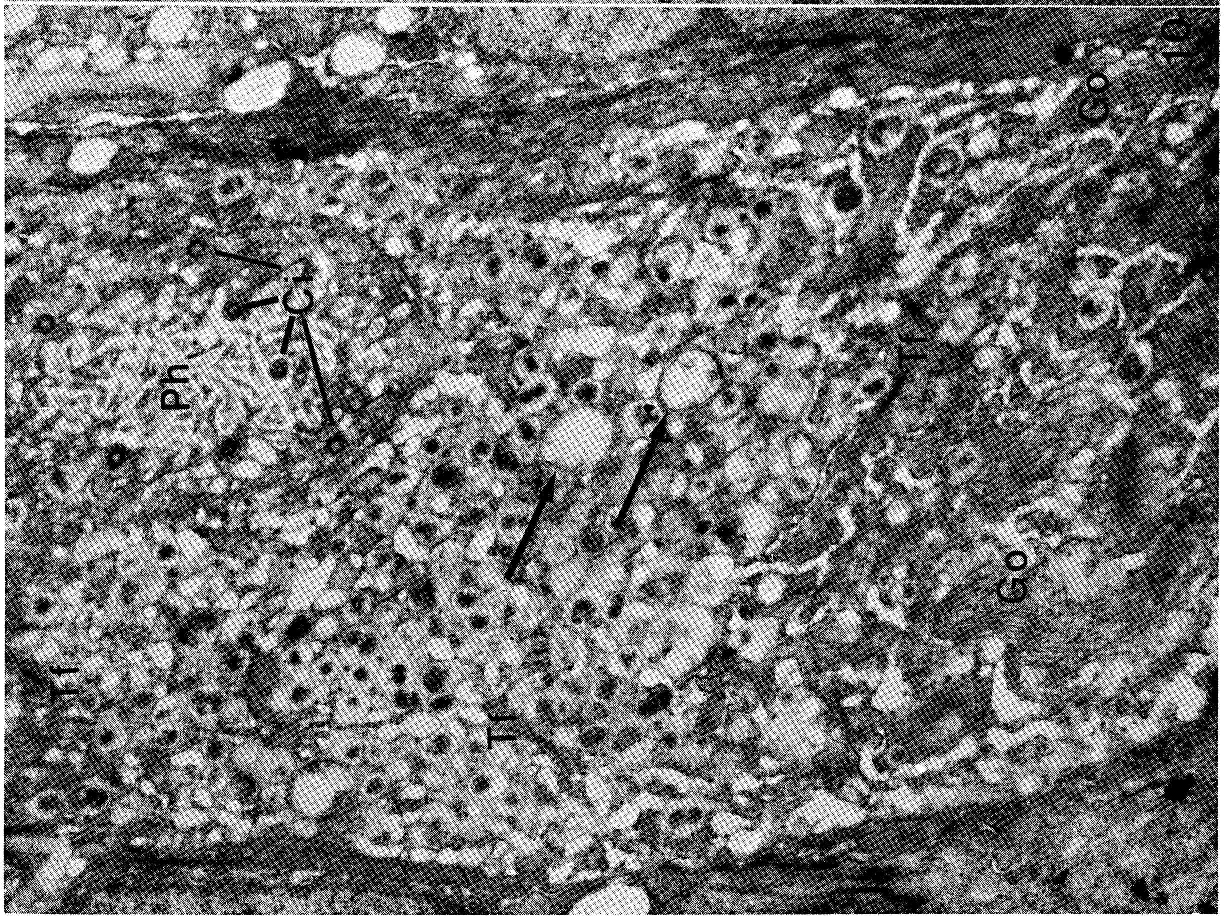
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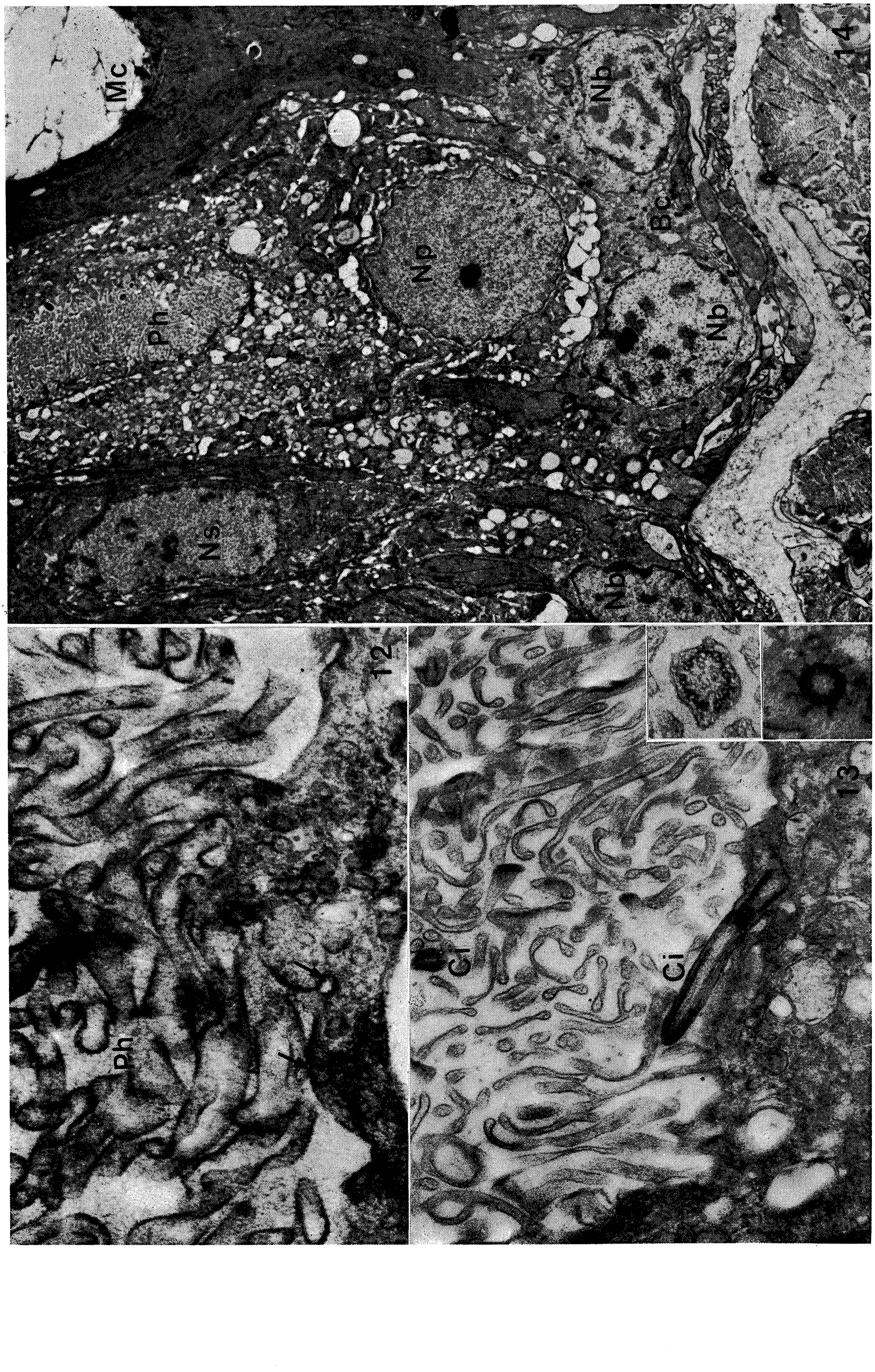
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