The Ultrastructure of the Mesenteric Lymph Node of the Rat[1,2]

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Although the ultrastructure of lymphocytes and monocytes from peripheral blood has been described (Kautz and De Marsh, '54; Bernhard, Haguenau and Leplus, '55; Low and Freeman, '58) the lymph nodes themselves have received little attention. Recently, Moe ('60) described by abstract the ultrastructure of lymph nodes in mice and Sorenson ('60) reported a similar study on rabbits. Bernhard and Granboulan ('60) and Granboulan ('60) described some features of the lymph node, emphasizing in particular the development of lymphocytes and plasma cells. The ultrastructure of mature plasma cells has been described by Braunsteiner, Fellinger and Pakesch ('53a, '53b and '57), Stoeckenius and Naumann ('57), and Thiéry ('58).

Many problems remain which merit continued study. With respect to reticular cells these include determination of the different types of cells, their developmental interrelationships, their relationship to fibers and their structural participation in phagocytic activity. In regard to lymphocytes, the ultrastructural modifications occurring during development of mature forms are not fully known. The origin of plasma cells remains under debate and their fate has not been fully revealed. It is to these problems that this study has been addressed.

MATERIALS AND METHODS

The lymph nodes of 37 young female Sprague-Dawley rats of 200 gm body weight were used. Under ether anesthesia pieces approximately 1 mm^3 in size were cut from mesenteric lymph nodes and fixed immediately in either 1% osmium tetroxide solution (Palade, '52) or in 2.4% potassium permanganate (Luft, '56). Both solutions were buffered with 0.14 M veronal acetate to pH 7.4. Sucrose was added to the OsO_4 at a concentration of 45 mg/ml of the fixative (Caulfield, '57). Fixation in OsO_4 was carried out at 0°C and in $KMnO_4$ at room temperature.

Dehydration of tissues fixed in 1% OsO_4 was performed at the temperature of fixation until the last change of 95% ethanol when the tissues were brought back to room temperature. Dehydration of the $KMnO_4$-fixed tissues was done at room temperature. In both cases dehydration was completed within two hours.

Purified methacrylate was used as the embedding medium, 2% Luperco CDB (50% 2,4-dichlorobenzoyl peroxide with dibutyl phthalate) being added as catalyst to 20% methyl methacrylate in n-butyl methacrylate. The methacrylate infiltrated tissue was de-aerated by subjecting the gelatin capsules containing tissue and embedding medium to negative pressure prior to polymerization. The methacrylate was polymerized for 12 to 24 hours at 60°C. After mounting on grids some of the sections were stained with lead hydroxide, lead acetate, uranium acetate or phosphotungstic acid (Watson, '58).

OBSERVATIONS

In the subsequent description, subdivision of cells into types will be avoided as much as possible in order to minimize the possibility of erroneous classification. The

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features observed with the light microscope have been used as the starting point for the identification of cells. Thus, under reticular connective cells will be described all of those cells which would be so classified if the light microscope were used.

The usual double membrane structure of the nuclear envelope was clearly visible in most cell types. Pores were also observed in the nuclear membrane. In the lymphocytic and plasma cell series, obscurely demarcated channels separated the peripheral condensations of electron-dense material and led out to the nuclear pores, creating through them continuity with the surrounding cytoplasm.

Reticular cells

Nondifferentiated reticular cells. The nondifferentiated reticular cell was found in cortical nodules and medullary cords. It was irregular in shape (fig. 2), usually being elongate with cytoplasmic processes which insinuated themselves between adjacent cells. The cell membrane was indistinct and when in contact with other cells, its visualization was frequently difficult. The cytoplasm of the nondifferentiated reticular cell was characterized by irregular density, small areas near the periphery being almost clear and giving the cytoplasm a somewhat mottled appearance.

The cytoplasmic organelles were poorly developed as compared with other cell types to be described. The endoplasmic reticulum was composed of rare vesicles or small flattened sacs scattered randomly in the cytoplasm (figs. 3 and 4). These sacs were occasionally dilated so that the caliber of the cisternae was somewhat variable. Some dense granules which appeared to be ribosomes were present but they were not numerous. They usually formed small aggregates but occasionally were associated with the endoplasmic reticulum.

Mitochondria were few in number (fig. 3). They were oval to ellipsoid in shape, although often the contour was quite irregular. Their size was variable but many of them were quite small in comparison with the size of the nucleus. The internal structure of mitochondria was exceedingly irregular, cristae being poorly developed and randomly arranged. In some cases, the matrix was quite electron-lucent. That this feature was not due to poor fixation was indicated by the well-preserved cristae and limiting membranes in these mitochondria as well as in the mitochondria of adjacent cells. Dense bodies of lesser diameter than that of mitochondria were distributed sparsely in the cytoplasm. They were quite homogeneous and resembled the microbodies of other authors (Rouiller and Bernhard, '56).

The Golgi apparatus could not be identified conclusively in photographs of many cells. A paranuclear accumulation of small vesicles located in a matrix denser than the remainder of the cytoplasm (fig. 2) appeared to be the basic component of the Golgi body. The Golgi apparatus in the "primitive" cell of the rabbit lymph node has a similar structure (Sorenson, '60).

The shape of the nucleus in the nondifferentiated reticular cell varied from spherical to ellipsoid. The nucleoplasm consisted of fine electron-dense structures in a less dense matrix. These dense structures aggregated peripherally and formed a very thin rim along the inner membrane of the nuclear envelope. Otherwise they were distributed randomly throughout the nucleus. Irregularly-shaped electron-lucent areas also characterized the nucleoplasm. A poorly formed nucleolus was seen in some cells.

Reticular cells associated with fibers. The structure of cells located adjacent to fibers varied considerably and it is probable that many inadequately discerned transitional forms existed between the nondifferentiated reticular cell and the reticular cell associated with fibers. The fiber-associated reticular cell was found in sinuses as well as in cortical nodules and medullary cords. It was distinguished from the nondifferentiated cell by the greater density of both cytoplasm and nucleoplasm, as well as by finer details to be described (figs. 5 and 7). The main body of the cell had an irregular contour with a thin rim of cytoplasm surrounding the nucleus. However, from this part of the cell extended long attenuated cytoplasmic processes which encompassed the collage-

nous fibers.[3] The plasma membrane extended inwards to surround the fibers, the contour of the membrane suggesting that the cytoplasm had rotated around the long axis of the fiber (figs. 5 and 7). The cell membrane was usually clearly defined even alongside fibers (figs. 5 and 8), although in some locations it was indistinct. Occasionally, fibers were so deeply enfolded by the cell that they were brought close to and indented the nucleus (fig. 7). Nevertheless, the fibers were always separated from the nuclear membrane by cytoplasm.

The endoplasmic reticulum present in the perinuclear cytoplasm consisted of randomly distributed small flattened sacs or tubes which, partly because of the extreme density of the cytoplasm, were not easily discerned. In the cytoplasmic processes adjacent to fibers the endoplasmic reticulum was drawn out into extensive flattened sacs which were oriented parallel to the fibers (figs. 6 and 8). Ribosomes were present in small numbers throughout the perinuclear cytoplasm. However, in the peripheral cell processes which covered the fibers they were more numerous and almost all were associated closely with the endoplasmic reticulum (fig. 8).

Mitochondria were frequent and often clustered around the cell center.[4] They were less frequently present in cell processes. Mitochondria tended to be quite elongate and contained numerous prominent and regularly arranged cristae. The matrix was uniformly dense. Facing the cell center the nuclear membrane was often indented. Mitochondria were found in these indentations and bore a close positional relation to the nuclear membrane. Mitochondria-containing areas of the cytoplasm also revealed "microbodies" whose size equaled or was less than that of the mitochondria (figs. 5 and 7). Inclusions similar to fat droplets were also found occasionally. The structure of the Golgi apparatus was not clearly revealed. In some cells it consisted of a cluster of small thick-walled vesicles in the perinuclear cytoplasm (fig. 5), while in others it included also groups of parallel membranes.

The nuclear membrane was somewhat wrinkled (fig. 7). The nucleoplasm consisted of electron-dense structures superimposed on a mottled matrix which was denser than that in the nondifferentiated reticular cell, the greatest density occurring near the nuclear membrane. The nucleolus was large (fig. 7).

Flattened *endothelioid* cells were found at the outer edge of some sinuses, lying against collagenous fibers. Their relationship to the fiber-associated reticular cell was not fully clarified. Thinned out cytoplasm extended out away from the nucleus of this cell and made close overlapping contact with adjacent cells. $KMnO_4$ fixation revealed with unusual clarity many infoldings of the cell membrane on both the luminal and fiber-facing surfaces. Associated with these infoldings were a number of vesicles, especially in the thinned out portions of the cell. As compared with the reticular cells associated with fibers, endoplasmic reticulum was poorly developed and there were few ribosomes. The sparse mitochondria tended to aggregate at the ends of the flattened nucleus. Cristae were less numerous and regularly arranged than in the mitochondria of reticular cells associated with fibers. A small number of "microbodies" with a dense matrix were present. The elongate nucleus resembled that of the fiber-associated reticular cell in the structure of its nucleoplasm. With $KMnO_4$ fixation the peripheral nucleoplasm appeared denser than that more centrally located.

Phagocytic reticular cells. Reticular cells containing phagocytized bodies were found in the cortex and medulla. Their cytoplasm was voluminous with processes that extended between other cells. Phagocytic reticular cells often bridged across a sinus, making contact with cells associated with fibers.

The external cellular membrane folded inwards, particularly along the borders facing the spaces of sinuses. Thus, the outer membrane seemed to become con-

[3] Since electron microscopic studies indicate an identity between the essential fibrils of collagenous and reticular (argyrophilic) fibers, in this paper reticular fibers are designated as being collagenous.

[4] The term "cell center" is used to designate only the general area of cytoplasm near the nucleus in which were located the centrioles, centrosome and Golgi apparatus.

tinuous with endoplasmic reticulum (fig. 10). The endoplasmic reticulum was extensive and diffusely distributed in an irregular pattern throughout the cytoplasm. Portions of the endoplasmic reticulum possessed attached ribosomes; others did not (fig. 11). In regions containing inclusion bodies, the cisternae were associated with a greater number of ribosomes (fig. 10) and some were quite expansive. The endoplasmic reticulum was folded around some mitochondria in close apposition to them. Mitochondria were spherical to ellipsoid and of variable size. Their cristae exhibited an irregular arrangement but, nevertheless, were organized more regularly than those of the nondifferentiated reticular cell (fig. 11). The Golgi apparatus consisted of clusters of double membranes and small vesicles. The clusters were found in multiple foci in and around the cell center (figs. 9 and 10).

The ground cytoplasm varied in density. In those regions of the cell containing many inclusion bodies, it was much less dense than that in the perinuclear area (fig. 9). Free ribosomes were distributed in small groups throughout the cytoplasm (fig. 11).

A variety of inclusion bodies which presumably represented phagocytized material were present. Although their morphology was highly diverse, they could be grouped roughly into three categories. The first type (A) attained a diameter over half that of the nucleus and possessed a moderately electron-opaque interior (figs. 9 and 10). It was irregular in shape and surrounded by an outer limiting membrane. Its matrix sometimes encompassed smaller dense round bodies which occasionally contained ferritin-like granules (fig. 15). The neighboring cytoplasm was not dense.

The second type of inclusion body (B) was distinguished by its frequent "myelin"-like formation (figs. 12, 13 and 14). The size of this body ranged upwards from that of mitochondria. The finely granular matrix in general was moderately dense, but less so than that of type A. However, some sharply circumscribed areas were extremely dense. This density appeared to arise in previously lamellated areas. This kind of inclusion body often possessed two limiting membranes, the external one being continuous with other membranes in the cytoplasm (fig. 12), while the inner membrane extended into the interior to form "myelin figures." The frequent incomplete union of two bodies suggested either fusion of two or splitting of one (fig. 13). Ferritin-like granules and crystalloids were present.

The third form of inclusion body (C) was small and ovoid or of more irregular shape. Its size approximated that of mitochondria. An electron-dense outer rim surrounded a clear center and from the outer rim projections extended inward. No external limiting membrane was seen (figs. 12 and 13). In addition to the three types of inclusion bodies described, the cytoplasm included other cellular fragments.

The nucleus of the phagocytic reticular cell possessed an irregular contour, often being elongated. The nucleoplasm was similar to that of the nondifferentiated reticular cell. A small nucleolus was seen in some nuclei.

The free rounded macrophage was structurally closely related to the fixed phagocytic reticular cell. The endoplasmic reticulum, ribosomes, mitochondria, Golgi apparatus, and inclusion bodies were quite similar in structure and distribution (figs. 16 and 17). The free macrophage was found most frequently in sinuses and was generally in contact with reticular cells which surrounded fibers. The cell reached a diameter of over 15 μ. The plasma membrane was frequently infolded and the cytoplasm was often raised up in pseudopod-like projections beside these invaginations (fig. 16). Some cytoplasmic processes were finger-like and touched those of other cells (fig. 17). The infoldings of the outer membrane extended deeply into the interior and appeared to give off small vesicles at the deep end. Although of variable structure, the inclusion bodies were usually of type B. The nucleus was eccentrically placed, and contained nucleoplasm of variable density. The density of the cytoplasm varied in different cells and in different parts of the same cell. The peripheral cytoplasm and that in the processes frequently had a hydropic appear-

ance. The cytoplasm contained many vacuoles of varied sizes most of which were empty. The vacuoles reached their greatest size at the periphery (fig. 17).

Lymphocytic cells

On the basis of differences in size, ultrastructure and nucleocytoplasmic ration, lymphocytic cells were divided into lymphoblasts, medium-sized lymphocytes and small lymphocytes to facilitate description (fig. 1). As is true with features seen with the light microscope, the ultrastructural characteristics did not permit sharp subdivision of these cells into developmental stages.

Lymphoblasts. Figure 19 illustrates a lymphoblast while the cell shown in figure 18 appears to be intermediate in development between the nondifferentiated cell and lymphoblast. In contrast to the primitive reticular cell, the lymphoblast (fig. 19)

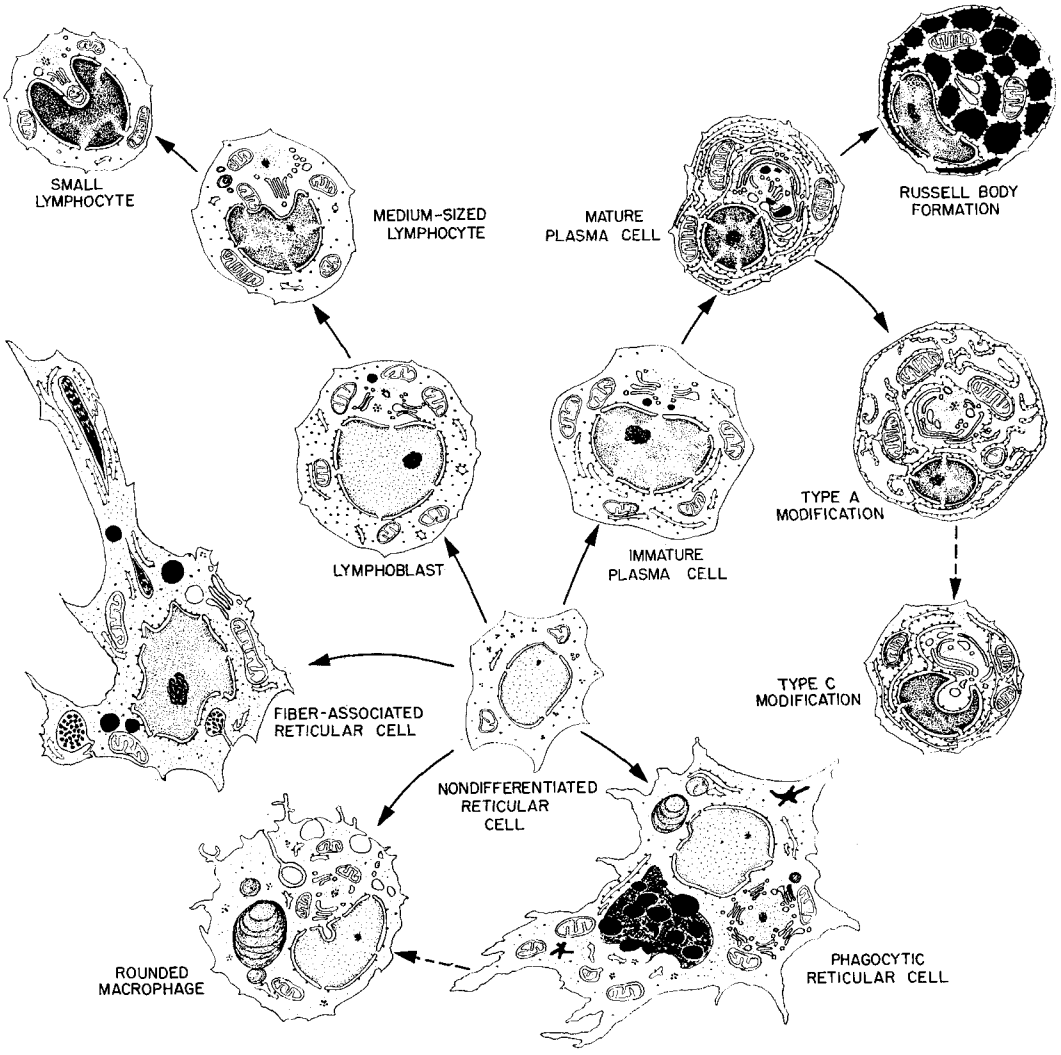

Fig. 1 Cellular interrelationships in the lymph node. Although the cellular transformations shown in this figure are indicated by the arrows to be unidirectional, the author recognizes that a purely morphological study does not reveal direction of change with certainty and that some of the transformations shown may move in the opposite direction also.

was more rounded in shape and usually possessed a greater volume of cytoplasm in relation to that of the nucleus. In areas where cells were crowded the cell membrane was contorted and vaguely defined.

The endoplasmic reticulum, consisting of flattened sacs or tubules, was irregularly and sparsely distributed. However, it was much more extensive than that of the nondifferentiated reticular cell. Similarly, ribosomes were somewhat more frequent, most of them being distributed freely and only a few being attached to the endoplasmic reticulum. Mitochondria were ovoid and tended to accumulate near the cell center (fig. 19). Their cristae were fairly numerous but irregularly arranged. The matrix was generally dense. With increasing maturity of the cell (figs. 18 and 19), cristae were more compactly arranged within a more uniformly dense matrix. Occasional small dense "microbodies" were present.

The Golgi apparatus, located in the cell center, consisted of clusters of short parallel double membranes stacked together. Near the parallel membranes and elsewhere in the cell center were small vesicles. Other larger vacuoles were associated with the Golgi complex. A paired centriole was located near the center of the area. The ground cytoplasm supporting the centrioles was somewhat denser than elsewhere in the cell and was devoid of ribosomes.

The nucleus was rounded and flattened on one side. The nucleoplasm was considerably denser than that in the nondifferentiated reticular cell. Large nucleoli were clearly revealed.

Medium-sized lymphocytes. Since the transformation of lymphoblasts to mature lymphocytes was characterized by gradual structural change, the ultrastructure of the medium-sized form will be described, chiefly in terms of its contrast with the lymphoblast. The volume of cytoplasm in relation to that of the nucleus was reduced. The medium-sized lymphocyte was rounded but when free of contact with other cells, its periphery presented irregular projections (fig. 20). The most striking ultrastructural characteristics were apparent in and about the cell center and in the nucleus.

The endoplasmic reticulum was poorly developed and when visible, consisted of small flattened sacs or tubules. Ribosomes were reduced in number and distributed singly and in clusters throughout the cell; less commonly they were attached to the endoplasmic reticulum or outer nuclear membrane (figs. 20 and 21).

The changing structure of mitochondria constituted one of the most distinctive features of lymphocytopoiesis. Of oval form, they were distinguished by the regularity and sharpness of their membranous constitution (fig. 21). Some of them were elongated. The cristae were uniformly oriented on the same plane and evenly spaced one from the other. Direct continuity of the lamellae of the cristae with the internal lamella of the outer limiting membrane was established at some points. The thickness of the outer limiting membrane was less than that of the cristae. Some cristae extended almost completely across the interior of the organelle. The matrix was uniformly dense. Not all mitochondria possessed such regular internal organization. Occasional ones were almost devoid of cristae; others presented bizarre arrangements of the cristae. Some "microbodies" were present.

Mitochondria were clustered in and around the cell center (figs. 20 and 21). Many established direct contact with the nucleus. Facing the cell center the nucleus exhibited one or more infoldings of its outer membrane, some of them being quite deep. These infoldings often encompassed mitochondria. At such points of intimate contact the outer membranes of both mitochondria and nucleus were blurred and poorly defined. When more than one mitochondrion appeared within the indentation of the nucleus, the deeper one was smaller and exhibited less regular internal structure (fig. 23, insert). Similarly, cristae were less well-defined in those portions of mitochondria proximal to points of contact with the nucleus than in the more distal portions.

Components of the Golgi apparatus, similar in organization to those of the lymphoblast were present in the cell center. At least, in more mature lymphocytes (fig. 20, insert), these components ex-

tended into the nuclear indentations and came into close contact with the nucleus.

In addition to the membranes of the endoplasmic reticulum and Golgi apparatus, the cell center also included other prominent vesicular structures (fig. 22). These vesicles were bordered by a membrane consisting of two electron-dense lamellae separated by a more electron-lucent layer. The interior possessed the same electron density as the external ground cytoplasm. Most of the vesicles were about 0.1 μ or less in diameter. However, some were considerably larger. Some of the larger ones contained secondary internal vesicles of similar structure (fig. 22). Larger vacuoles with a rather clear center were also present.

Particularly striking in the cell center was an extensive region of uniformly dense cytoplasm which encompassed the centriole and was designated the centrosome (fig. 21). This cytoplasm was composed of densely packed granules of low electron density. Except for a few ribosomes, the centrosome was devoid of the other structures which characterized the cell center.

The nucleus possessed densely packed electron-dense material interrupted peripherally by electron-lucent channels which led out to the pores of the nuclear membrane (fig. 20).

Small lymphocytes. In addition to its narrow rim of cytoplasm, the mature lymphocyte differed from the medium-sized lymphocyte in several respects (fig. 1). Endoplasmic reticulum was rarely observed; it consisted of vesicles of varied shapes and seldom were ribosomes associated with it or with the outer nuclear membrane (fig. 23). Aggregations of free ribosomes were distributed sparsely throughout the cell. Their concentration was somewhat less than in the larger lymphocytes (fig. 25).

The small lymphocyte contained fewer mitochondria; most of those present were located around the cell center. They were somewhat smaller and often possessed fewer cristae than those of larger lymphocytes. "Microbodies" were occasionally present. The Golgi apparatus was more restricted in extent and consisted chiefly of thick-walled vesicles (figs. 23 and 24). The centrosome, which appeared less extensive than in the medium-sized lymphocytes, encompassed the centrioles (fig. 24). Except for smaller size and fewer and more shallow infoldings of the membrane, nuclear structure was not greatly altered from that of the larger lymphocytes. The nuclear infoldings continued to contain mitochondria (fig. 24).

Plasma cells

The medullary cords contained clusters of plasma cells in various stages of development interspersed with nondifferentiated reticular and phagocytic cells, all of these types being grouped around blood capillaries (fig. 26).

Immature plasma cells. The most immature plasma cells possessed several characteristics which indicated their close structural similarity to and probable derivation from the nondifferentiated reticular cell. The most immature plasma cells were polygonal in shape and possessed indistinct cell membranes (figs. 1 and 27). The nucleus was roughly central in location and, except for patchy areas of electron-dense material, contained nucleoplasm of low density.

On the other hand, the direction of differentiation of the nondifferentiated reticular cell to a plasma cell was shown by several other ultrastructural features. The earliest indication was the appearance of elongated profiles of endoplasmic reticulum with flattened cisternae oriented parallel to the nuclear surface and in the immediate vicinity of the nucleus (fig. 27). Attached ribosomes also appeared early. With increasing maturity, the branching membranes of the endoplasmic reticulum came to extend throughout the cytoplasm, except for the Golgi area, and enclosed extensively anastomosed cisternae (fig. 28). Concurrently the number of ribosomes increased. The cisternae were narrow and contained a material of somewhat less density than that of the ground cytoplasm (fig. 28). Some ribosomes were scattered free in the cytoplasm. Another characteristic which indicated that nondifferentiated reticular cells develop into plasma cells was the appearance in the youngest plasma cells of electron-dense

material at the periphery of the nucleus (fig. 27). Subsequently, this material was aggregated into peripheral clumps around a large central nucleolus, creating the typical spoke-like pattern which is characteristic of the cell as seen with light microscopy (figs. 1 and 28). Mitochondria were ovoid and of somewhat varied size. Some contained well-developed and densely arranged cristae. "Microbodies" were frequently present. The Golgi apparatus was not a prominent feature of the younger forms (fig. 27).

Mature plasma cells. Mature plasma cells were more round in shape and the nuclear-cytoplasmic ratio was less than in younger forms. The nucleus had assumed an eccentric position and appeared to be actually smaller than in the young plasma cell (fig. 29).

The endoplasmic reticulum extended throughout the voluminous cytoplasm with the exception of the Golgi area. The anastomosing cisternae were generally flattened while some were dilated and filled with a cloudy material. The numerous ribosomes were generally associated with the outer surface of the endoplasmic reticulum. Mitochondria were large and ovoid and located in the rather dense ground cytoplasm between cisternae. Most mitochondria were situated near the cell center. Their cristae consisted of thin lamellae which were more numerous and more closely arranged than those of any other cell type.

The Golgi apparatus was large in relation to size of the cell. It consisted of several layers of double membranes which in somes cases appeared to encircle the cell center (fig. 30). In other cells the double membranes were arranged in stacks. Adjacent to these membranes were large vacuoles. In the cytoplasm of the cell center and in that just outside the parallel Golgi membranes were many vesicles which contained material of variable density. The outer wall of these vesicles appeared to be thick which, in at least some instances, may have resulted from the plane at which the vesicles were sectioned. Within the cell center were frequent dense bodies (fig. 30, D) which ranged in size from that of the small vesicles up to the size of the clear vacuoles. The larger bodies possessed irregular contours and were surrounded by dense limiting membranes. The cell center contained a few dense granules which appeared to be ribosomes (fig. 30).

The nucleus exhibited the same pattern as that of the more advanced immature plasma cell except that it was smaller and of a more regularly round contour. Also the nucleoplasm was denser but with the spoke-like pattern remaining clearly evident.

Modifications in the structure of plasma cells. Several modifications in the structure of plasma cells were observed (fig. 1). In the first type of modification (type A) the cytoplasm became voluminous, with the cisternae being greatly expanded and of irregular contour (fig. 31). The cisternae contained a flocculent material of low electron density. Mitochondria retained the structure seen in those of mature plasma cells. Being located in the narrow strands of ground cytoplasm they appeared to cause the endoplasmic reticulum to bulge into the cisternae. The dense cell center, Golgi components, and a centriole typical of the mature plasma cell, were retained.

The second form (type B) was characterized by great enlargement of the cisternae of the endoplasmic reticulum due to the accumulation within them of an amorphous material which, except for its somewhat greater electron density, was similar to that in the cisternae of mature plasma cells (fig. 32). Further condensation of this material appeared to result in formation of Russell bodies which were almost homogeneous (fig. 33), although direct transformation was not demonstrated. In such cells the intervening endoplasmic reticulum and ribosomes remained fairly distinct. The ground cytoplasm appeared only as narrow strands bordered by the endoplasmic reticulum. Mitochondria were located within these narrow strands of ground cytoplasm. The nucleus was deformed, and exhibited a rather marked increase in the density of its nucleoplasm (fig. 32).

A third type (C) of modified plasma cell differed from the preceding two in that it was much smaller and appeared to be in an exhausted state (fig. 26, P6). The cis-

ternae were narrow and contained only a small amount of flocculent material. The cell center with its associated Golgi apparatus was exceedingly dense. Ribosomes were numerous and associated with an endoplasmic reticulum which was well-developed. The nucleus was small, contained denser nucleoplasm and exhibited invaginations of the nuclear membrane. A few mitochondria remained.

DISCUSSION

The reticular cells

Maximow distinguished two types of cells associated with reticular fibers ('27), namely, a phagocytic and a non-phagocytic or nondifferentiated cell which with others was said to form a syncytium. However, morphological distinctions between these two types of cells have never been clearly established. In the spleen of the rabbit, Stoeckenius and Naumann ('57) recognized large light and small dark reticular cells with the electron microscope. The light reticular cells were interpreted to be closely similar to the primitive reticular cell of Maximow. The details of the ultrastructure of reticular cells in my study permitted their subdivision into a nondifferentiated form, one associated with fibers, and a phagocytic type.

Nondifferentiated reticular cells. Little attention has been given to the electron microscopy of nondifferentiated cells in general. Porter ('54), Munger ('58), and Bernhard and Granboulan ('60) have noted that various types of nondifferentiated cells are characterized by a lack of development in the endoplasmic reticulum, Golgi apparatus, and mitochondria and by an absence of other specialized structures. In agreement with their observations are the simplicity of the cytoplasmic membranous structures, the presence of fairly numerous ribosomes, and the poorly developed Golgi apparatus and mitochondria in the nondifferentiated reticular cell of the lymph node from the rat. In general, these observations agree with those made on this cell type by Bernhard and Granboulan ('60) in man.

The constant presence of electron-lucent foci in the nucleoplasm, mitochondria and ground cytoplasm of the nondifferentiated reticular cell may have resulted in part from damage occurring during the technical procedures. However, if this is true, the differences cited must have stemmed from the unique intrinsic constitution of the cell because adjacent cells of other types did not reveal similar alterations.

Although using a different fixative, Sorenson ('60) described a large nucleolus in the nondifferentiated reticular cell of the rabbit. It was much smaller in the rat. Since Brachet ('57) and Prescott ('59) have concluded that ribonucleic acid is synthesized in the nucleolus, the small size of this structure may indicate that ribonucleic acid is synthesized at a low rate. Although a fair number of ribosomes were present, the poor development of the endoplasmic reticulum would suggest that protein synthesis was proceeding slowly. Similarly, the lack of intramitochondrial development might be indicative of a low concentration of oxidative enzyme activity within this organelle (Green and Hatefi, '61).

Reticular cells associated with fibers. Moe ('60) described the reticulum of lymphatic sinuses in the mouse as consisting of "a tube of reticuloendothelial cells encompassing an extracellular connective tissue component. . . ." Sorenson ('60) noted that the internal framework of the lymph node in the rabbit is made up of large groups of collagenous fibers which are covered by elongated flattened endothelial or reticular cells. In my study of lymph nodes in the rat, collagenous fibers likewise were shown to be encompassed by cytoplasm throughout their extent, in fact, no fiber was observed which presented a bare surface to the lumen of a sinus or other tissue space. Thus, it has now been shown in three species that collagenous fibers composing the reticular framework of the lymph node are totally encased in cytoplasm. This arrangement leads one to expect a more continuing participation of cellular activity in the metabolism of collagen and its associated ground substance in the lymph node than may be true of fibro-elastic connective tissue. Since these fibers are the argyrophilic ones of light microscopy, the interesting possibility is raised that this cellular associa-

tion may account for their silver-staining property.

The infolding of the plasma membrane of reticular cells to surround enclosed fibers is a striking feature of these cells. Although not reported by Sorenson ('60) it is seen clearly in several of his photographs (figs. 2 and 4). This relationship raises the following intriguing possibility regarding the functional relationship of cells to the fibers. If fibrils are formed at the surface of the cell it may be inferred that the cytoplasm subsequently flows around them in a rotational pattern with respect to the long axis of the fibrils. Then enlargement and development of fibers might continue while encased by the cytoplasm. Immaturity of many of the fibers is probably indicated by the sparsity of the fibrils.

The frequent occurrence in the processes of reticular cells of a well-developed endoplasmic reticulum with many associated ribosomes has particular significance with respect to the formation of protein, a relationship which has been stressed by many workers including Porter ('53, '54), Braunsteiner and Pakesch ('55), and Palade ('56). Porter and Pappas ('59) presented convincing evidence that collagenous fibers are formed at the surface of chick fibroblasts which contain extensive endoplasmic reticulum with associated ribosomes in their elongated "pseudopodia." It appears quite probable that the similar processes of reticular cells in the rat lymph node are concerned with synthesis and deposition of tropocollagen. The frequent perinuclear ribosomes also may be related to active protein synthesis. Indeed, additional study is required to determine whether any significant structural difference exists between the fiber-associated reticular cell and the fibroblast.

The reticular cells of lymph nodes are generally regarded by histologists as existing in a syncytial arrangement. It is pertinent that in all reticular cells observed in the lymph node of the rat the cytoplasm intervening between nuclei was always compartmentalized by a cell membrane. Thus, the existence of a true reticular syncytium is highly improbable.

Phagocytic reticular cells. Phagocytosis is regarded currently as being a process essentially similar to pinocytosis (Palade, '55, '56; Bennett, '56; Karrer, '58, '60). The plasma membrane participates by folding inwards in areas where foreign particles have become attached to the cell (Karrer, '60). Enclosure of these particles is completed by the formation of cytoplasmic pseudopods (Essner, '60) or "ruffles" (Karrer, '60) adjacent to the infoldings which permit external closure of the plasma membrane. Thus, the included bodies are surrounded by a membrane which is derived from the plasma membrane and possesses the same intrinsic structure. However, there is not yet complete agreement on the general interrelations of the outer cell membrane with the internal membranes of the cell. In the splenic macrophage of the chick and rat Palade ('55, '56) concluded that the plasma membrane is continuous with the endoplasmic reticulum and Robertson ('59) observed that both membranes are of identical structure. These observations have not been confirmed and Karrer ('60) disagrees with the conclusions drawn from them. Thus, the possible relationship of the membrane surrounding inclusion bodies to endoplasmic reticulum is unresolved. In this study the limiting membrane of the type B inclusion body was continuous with other intracellular membranes which may have been a component of the endoplasmic reticulum.

Assuming the validity of the concept that phagocytosis is essentially similar to pinocytosis, several ultrastructural characteristics of the phagocytic reticular cell may be explained. The rarefaction of cytoplasm in the neighborhood of inclusion bodies, a condition not observed previously by others in other types of phagocytic cells, may have resulted from engulfment of external fluid during phagocytosis. Further, the limiting membranes surrounding inclusion bodies of types A and B, a feature observed by Karrer ('58) in alveolar macrophages of the lung, may have been derived from the cell membrane when the material was taken up. Although continuity of the limiting membrane around inclusion bodies with the cell membrane was not established in this study, frequent infoldings of the latter membrane were

seen which at their internal ends appeared to continue into vesicles.

Schulz ('58) and Karrer ('60) have arranged the different types of inclusion bodies in the probable order of their ingestion and subsequent development. Type B without "myelin" figures was described in the macrophages of the lung (Karrer, '60) as being representative of material just after its ingestion. The appearance of "myelin" figures was thought to represent a subsequent step in modification of this material. Indeed, formations of this type have been described in a wide variety of cells, some of which are not generally regarded as being phagocytes (reviewed by Miller, '60). Evidence indicates that the newly formed membranes are composed of lipoprotein (Miller, '60) of unknown origin. The presence of ferritin-like granules in this type of body indicates that at least some of the inclusions represent fragments of erythrocytes. No inclusion bodies comparable to the third type have been described previously. The small size and extreme density of this body indicate that it may have arisen from further condensation of one of the other types.

The accumulation of endoplasmic reticulum and ribosomes in the region of phagocytized bodies suggests participation of these organelles in the destruction of ingested materials by the synthesis of essential enzymes. Essner ('60) observed high acid phosphatase activity in phagocytic vacuoles following ingestion of erythrocytes. The presence of high concentrations of acid phosphatase and other hydrolytic enzymes in lysosomes may be pertinent (de Duve, '59; Straus, '59) because of the possible identity of lysosomes and inclusion bodies. The presence of rough-surfaced endoplasmic reticulum in the neighborhood of phagocytized material has not been a general observation (Miller, '60).

The formation of lymphocytic cells

Only Bernhard, Haguenau and Leplus ('55) and Bernhard and Granboulan ('60) have described the ultrastructural changes which characterize lymphocyte formation. The fine structure of the cells representing various stages in lymphocyte formation in the rat resembles in many respects that described for the human lymph node by Bernhard and Granboulan. Several additional important features were observed. The transformation of the nondifferentiated reticular cell to the lymphoblast (fig. 1) in the rat was characterized by rounding up the cell with increase in volume of cytoplasm; by cytoplasmic differentiation which included the appearance of a more extensive endoplasmic reticulum consisting of flattened vesicles; increase in the number of free and attached ribosomes; an increase in the number of mitochondria as well as in the number and regularity of cristae which were supported by a denser matrix; enhanced prominence of the Golgi apparatus; and increased density of the nucleoplasm.

In the continued development of lymphoblasts into small lymphocytes, a different trend of changes took place which, in many respects reversed the structural modifications which occurred in the development of the lymphoblast from the nondifferentiated reticular cell. With declining size of the cell and cytoplasmic volume, the endoplasmic reticulum, ribosomes, and Golgi apparatus became less prominent and the mitochondria smaller and fewer in number. Similarly, the nucleolus became smaller while the density of nucleoplasm increased. These changes can be taken to indicate a reduced rate of protein synthesis. Indeed, the mature lymphocyte gives the ultrastructural appearance of a rather inactive cell. Other ultrastructural characteristics of the lymphocyte not previously observed require further consideration.

The centrosome. The frequent occurrence of centrioles in the cell center confirms the classical observations of light microscopy. Furthermore, the exceedingly dense homogeneous cytoplasm in which the centrioles were located demonstrates the presence of cytoplasmic specialization in this area. Although the term "centrosome" has been used with varied connotations by different workers (Wilson, '53) it is probably the most desirable term for designation of this area, particularly since the region is devoid of other organelles.

Spatial relation of mitochondria to nucleus. The apposition of mitochondria to the nuclear membrane suggests (a) that

transport occurs between the two structures or (b) that mitochondria arise from the nucleus. The time-lapse cinematography of Frederic ('54) and the electron micrographs of Ornstein ('56) have revealed the more general occurrence of this relationship in other types of cells. Previous studies suggest the involvement of the nucleus in the synthesis of mitochondrial diphosphopyridine nucleotide (Brachet, '57). The possibility that transport occurs between nucleus and mitochondria appears feasible. Furthermore, the blurring of nuclear and mitochondrial membranes at these points of contact occurs so regularly that functional significance is implied. With respect to the possible origin of mitochondria from the nucleus, Brandt and Pappas ('59) showed that this occurs in some lower forms. In the lymphocyte, mitochondria encompassed by the indentation of the nuclear membrane were smaller and contained less well-developed cristae than those outside of the indentation and situated farther away from the nucleus. These variations may well suggest the maturation of mitochondria as they move away from the nucleus although origin directly from the nucleus is not necessarily indicated.

Vesicles with double electron-dense membranes. The vesicles observed in this study which possessed double electron-dense membranes may be identical with the compound vacuoles described in lymphocytes by Low and Freeman ('58) as judged on the basis of similarity in distribution and size. However, these workers did not observe the triple-layered structure of the wall as was observed in this study. No indication of the functional significance of these vesicles was obtained.

Nuclear structure. Bernhard and Granboulan ('60) described the nucleus of lymphocytes as being uniformly dense. This was not the case in this study where material of high electron density became increasingly clumped toward the periphery of the nucleus as development progressed from the lymphoblast to the mature lymphocyte. These aggregations were separated by less dense areas or ill-defined channels leading to and through nuclear pores. The nuclear channels may serve as passageways through which metabolites move into and out of the compact nucleus of lymphocytes.

The plasma cells

It is now clear that the cytoplasm of the mature plasma cell is distinguished by an extensive endoplasmic reticulum associated with a multitude of ribosomes (Braunsteiner and Pakesch, '55; Thiéry, '55, '58; Kautz, De Marsh and Thornburg, '57; and Bernhard and Granboulan, '60). The origin of the cell is less certain. According to most investigators utilizing the light microscope the plasma cell arises by direct transformation from the lymphocyte (Trowell, '58; Roberts, Dixon and Weigle, '57). Thus far convincing electron microscopic evidence for this transformation has not been presented, and was not secured in this study. The electron microscope offers a distinct advantage in resolving this dilemma because endoplasmic reticulum with its associated ribosomes constitutes a much more precise microscopic criterion for identification than does cytoplasmic basophilia as viewed with the light microscope. This criterion makes possible the differentiation of the lymphoblast from the most immature plasma cell (plasmablast). The incipient development in nondifferentiated reticular cells of endoplasmic reticulum with the distinctive form and orientation which characterize it in mature plasma cells, in addition to the early changes in nuclear structure, provide strong support for the concept that in the normal lymph node, plasma cells are derived from the nondifferentiated reticular cell. This viewpoint was advanced previously by Braunsteiner and Pakesch ('55), Thiéry ('60) and Bernhard and Granboulan ('60). Thus, it appears that the lymphocytes and plasma cells represent different cell lines arising from the nondifferentiated reticular cell and that, if lymphocytes do transform into plasma cells, the transformation might involve prior dedifferentiation toward the nondifferentiated reticular cell.

The significant development of mitochondria and the Golgi apparatus in plasma cells may be interpreted as being indicative of a metabolically active cell. A large nucleolus in other cell types has

been associated with rapid synthesis of ribonucleic acid (Brachet, '57; Prescott, '59) which can be correlated with the presence of many cytoplasmic ribosomes. These features combined with the extensive endoplasmic reticulum are the structural counterparts of active protein synthesis.

The material located within the cisternae of the endoplasmic reticulum may represent the protein synthesized by the plasma cell. Numerous studies with the light (Fagraeus, '48) and electron microscopes (Braunsteiner and Pakesch, '55; Thiéry, '55, '58) point to participation of the plasma cell in antibody formation. This concept raises the possibility that the intracisternal material may be composed of or contain antibody protein. Furthermore, Russell bodies appear to arise from a further increase in the concentration of intracisternal substance (Thiéry, '58). When the fluorescent antibody technique was applied to Russell bodies, their periphery fluoresced brilliantly (White, '54).

The frequent clusters of plasma cells around phagocytic reticular and nondifferentiated reticular cells is suggestive of a similar arrangement observed by Bessis ('58) in the bone marrow. Sorenson ('60) noted this relationship in the lymph node of the rabbit and described a unique extension of the plasma cell cytoplasm into the cytoplasm of neighboring cells which he suggested may be concerned with the interchange of substances between these cells.

SUMMARY

The ultrastructure of the mesenteric lymph node of the rat was described with emphasis being placed on cellular interrelationships. Reticular cells were divided into three types: nondifferentiated reticular cells, reticular cells associated with fibers and phagocytic reticular cells. Collagenous fibers were surrounded invariably by the cytoplasm of reticular cells. A syncytial arrangement of reticular cells could not be demonstrated. Inclusion bodies in the phagocytic reticular cells were grouped into three types. Type A was large and dense and surrounded by a limiting membrane. Type B was less dense and often contained "myelin" figures. Type C was small with an extremely dense periphery and a clear interior.

The development of lymphoblasts from nondifferentiated reticular cells was characterized by augmentation of cytoplasmic volume, expansion of endoplasmic reticulum, increase in the number of ribosomes, development in the structure of mitochondria and of the Golgi apparatus, and by an increase in the density of nucleoplasm. In development of lymphoblasts to mature lymphocytes, all of these trends were reversed except for changes in the nucleus. In addition, a prominent centrosome encompassed the centrioles. Some mitochondria were in contact with the nuclear membrane. Evidence was presented which indicates that the plasma cell differentiates directly from the nondifferentiated reticular cell. In its later stages the plasma cell underwent various forms of structural modification. Intracisternal material appeared to condense to form Russell bodies.

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Abbreviations to plates

C, cell center
CM, cell membrane
Co, centriole
Cr, crystalloid
Cs, centrosome
ER, endoplasmic reticulum
F, collagenous fiber
G, Golgi apparatus
IA, type A inclusion body
IB, type B inclusion body
IC, type C inclusion body
L, lymphocyte
Li, lipid droplet
M, mitochondria
No, nucleolus
P, plasma cell
PR, phagocytic reticular cell
V, vacuole

PLATE 1

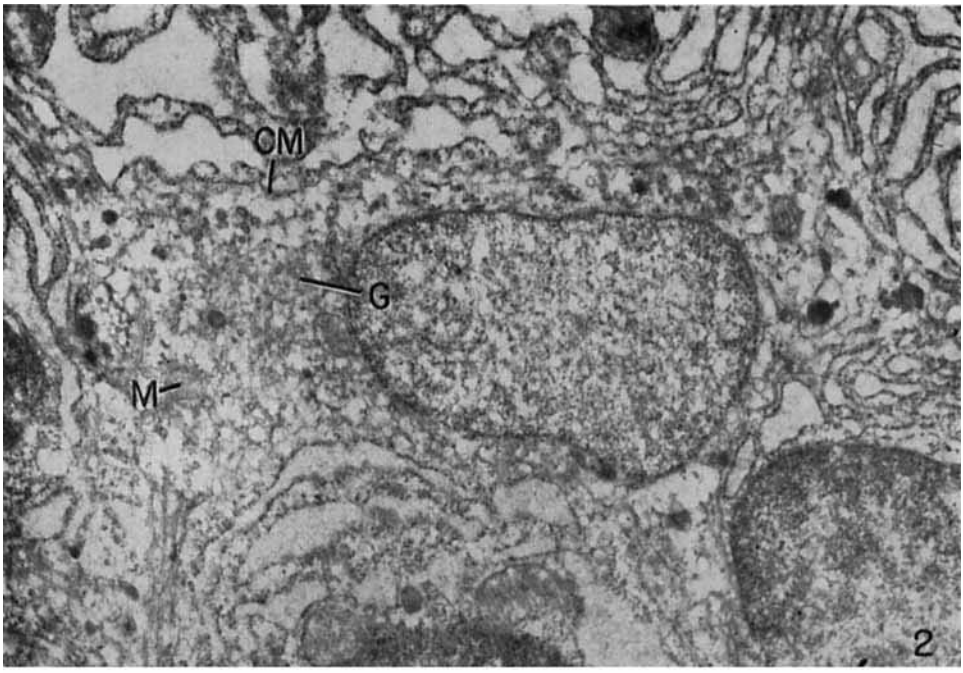
EXPLANATION OF FIGURES

Unless stated to the contrary, all illustrations are of tissues fixed in OsO_4.

2 A nondifferentiated reticular cell showing irregular cytoplasmic processes and an indistinct cell membrane. The Golgi apparatus appears to consist primarily of thick-walled vesicles. The electron-dense material of the nucleoplasm is sparsely distributed. × approximately 10,000.

3 A portion of a nondifferentiated reticular cell. Mitochondria are of irregular shape and have few cristae and a matrix of low density. The nucleus contains a small nucleolus. × 13,200.

4 Another region of the nondifferentiated reticular cell illustrated in figure 2. Here the cell membrane is more clearly defined. Present in the cytoplasm are aggregates of free ribosomes and a sparse endoplasmic reticulum. × 13,200.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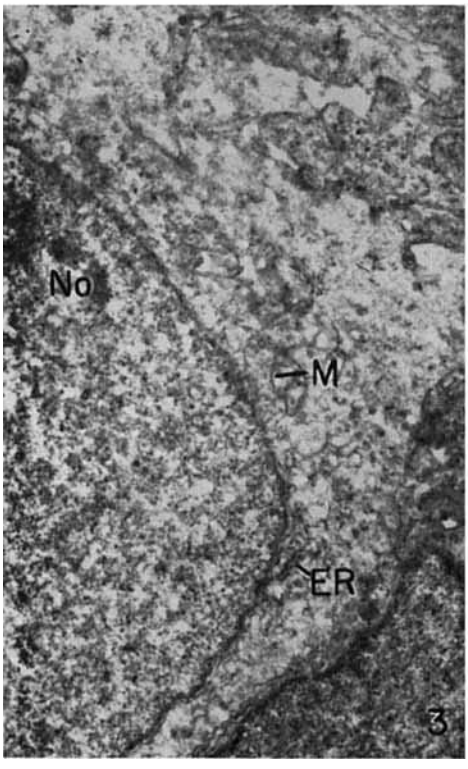
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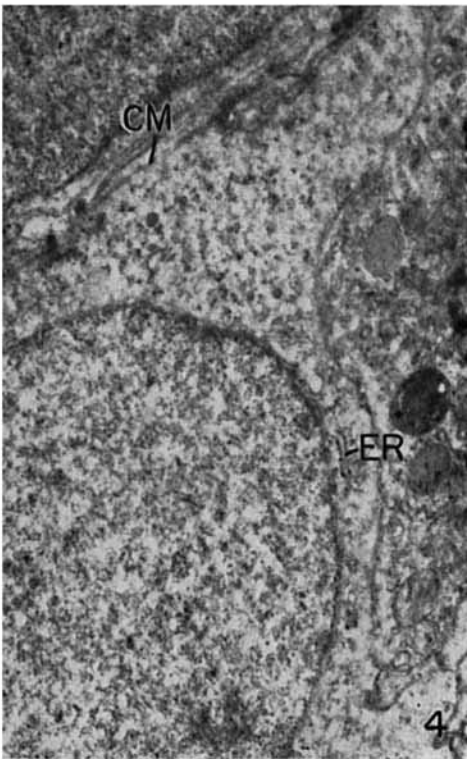
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PLATE 2

EXPLANATION OF FIGURES

5 A reticular cell associated with fibers illustrates the greater cytoplasmic density as compared with that of the nondifferentiated reticular cell (fig. 2) and of the phagocytic reticular cell. A portion of a phagocytic reticular cell is shown at the right. The cell membrane appears to be infolded (arrows) to surround bundles of fibrils. × 14,200.

6 A portion of the cytoplasmic process of a fiber-associated reticular cell showing extensive rough-surfaced endoplasmic reticulum and elongated mitochondria with numerous, well-organized cristae in a dense matrix. × 15,800.

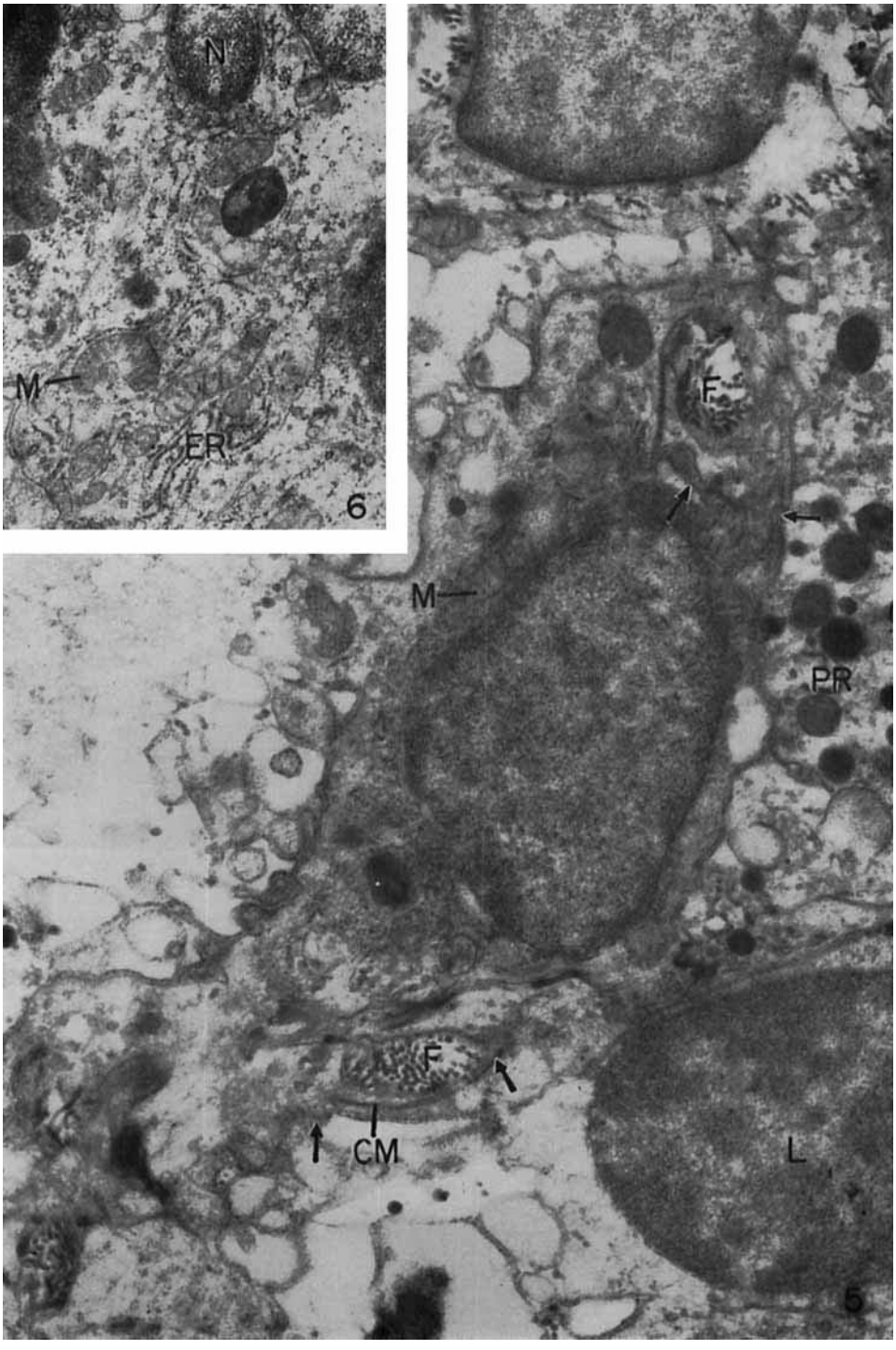
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PLATE 3

EXPLANATION OF FIGURES

7 This reticular cell is associated with fibers and illustrates the close proximity of fibers to the nucleus in addition to the numerous infoldings of the cell membrane (arrows) to encompass bundles of fibrils. These fibrils are not densely packed. Irregularity of the nuclear contour, a large nucleolus and lipid inclusions are evident. × 12,800.

8 The extensive endoplasmic reticulum with associated ribosomes extends throughout the cytoplasmic process of a fiber-associated reticular cell. The fiber is completely surrounded by cytoplasm, the two being separated by the cell membrane. × 15,600.

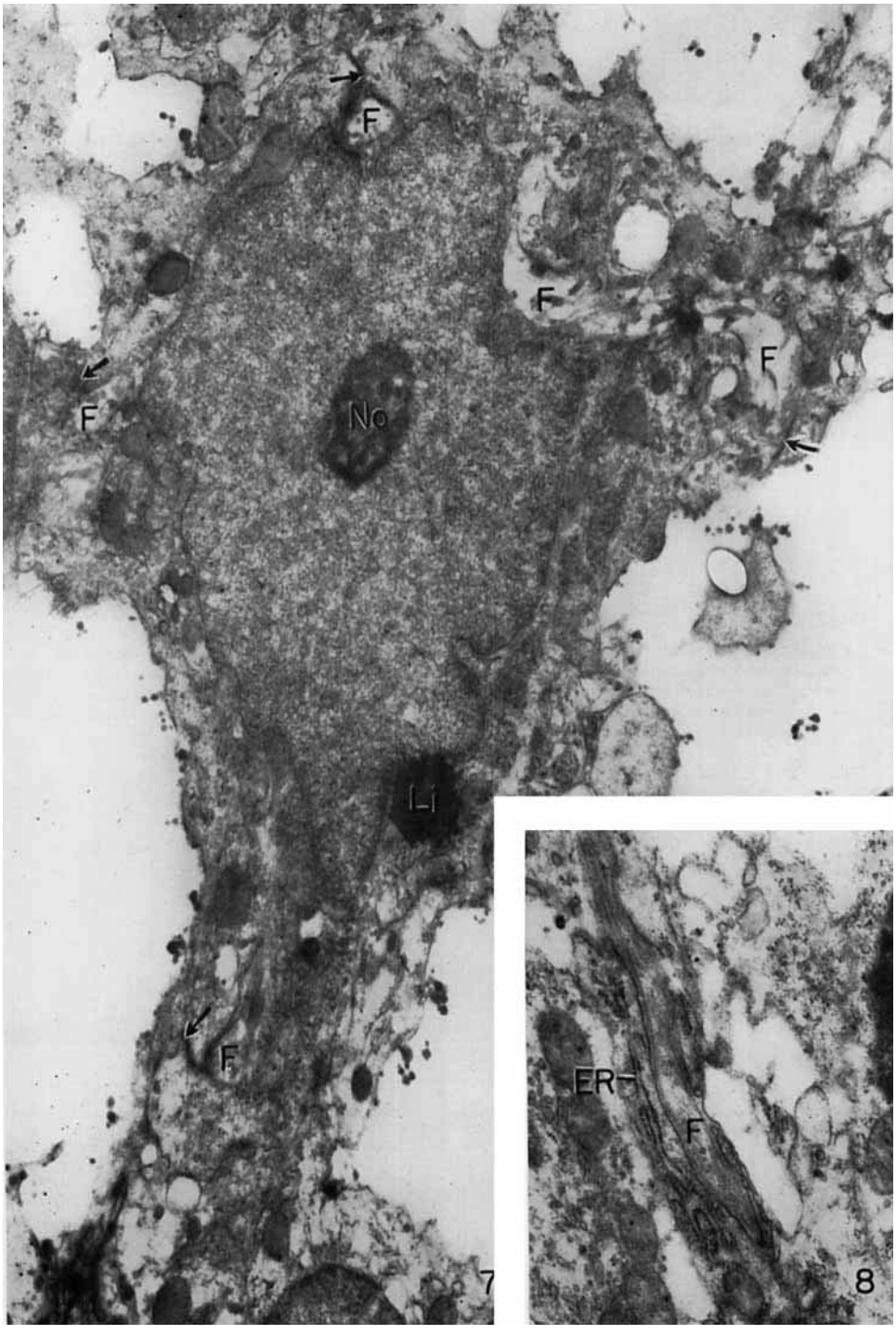
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PLATE 4

EXPLANATION OF FIGURE

9 A phagocytic reticular cell is surrounded by several plasmacytes (P_{1-5}). Much of the voluminous cytoplasm of the phagocytic cell is occupied by a type A inclusion body. Above it is a rarefied region of cytoplasm which is rich in endoplasmic reticulum. To the right of the nucleus is a prominent aggregation of Golgi components. Mitochondria are well-developed, although their size is variable. × 11,000.

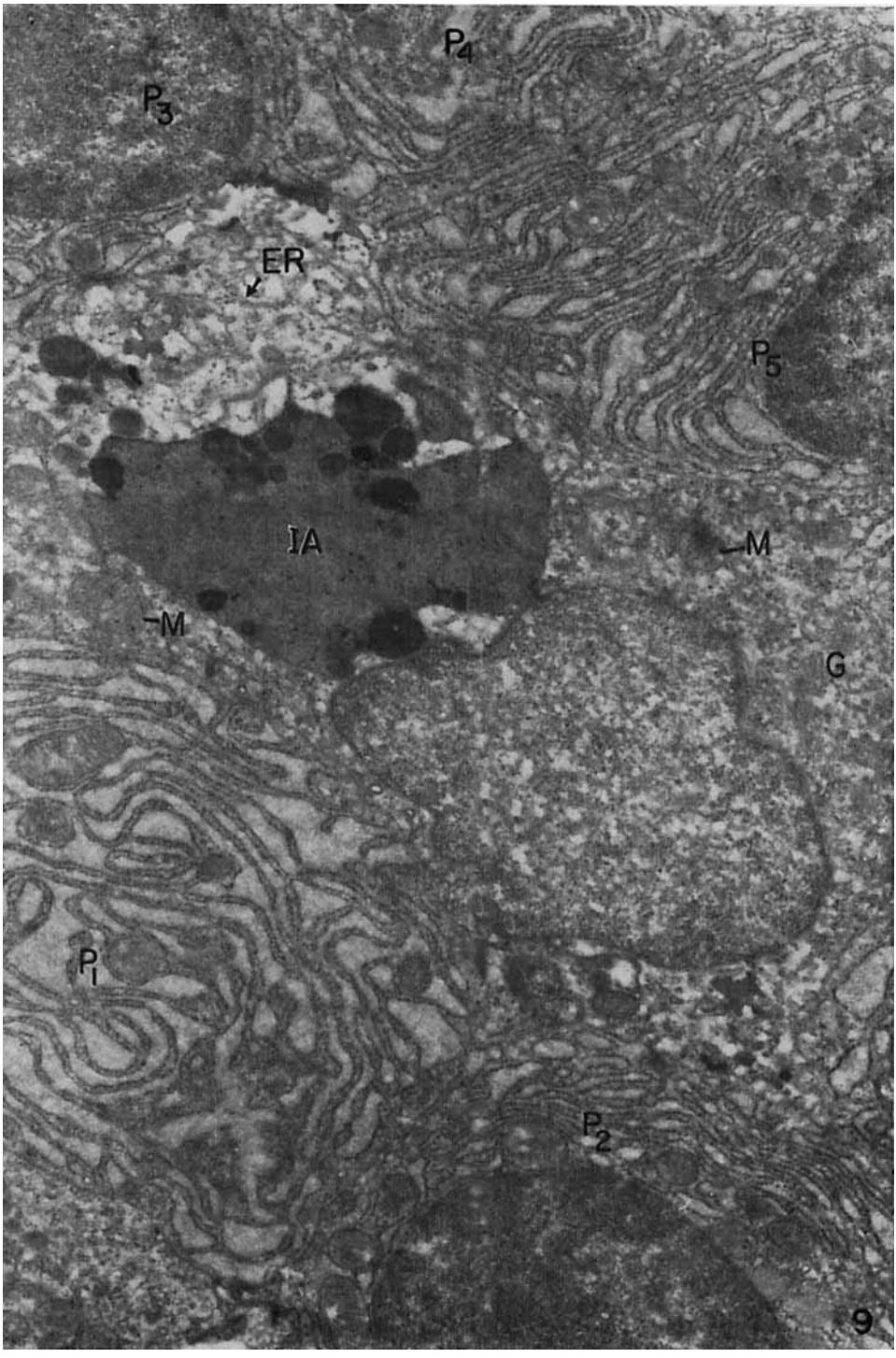
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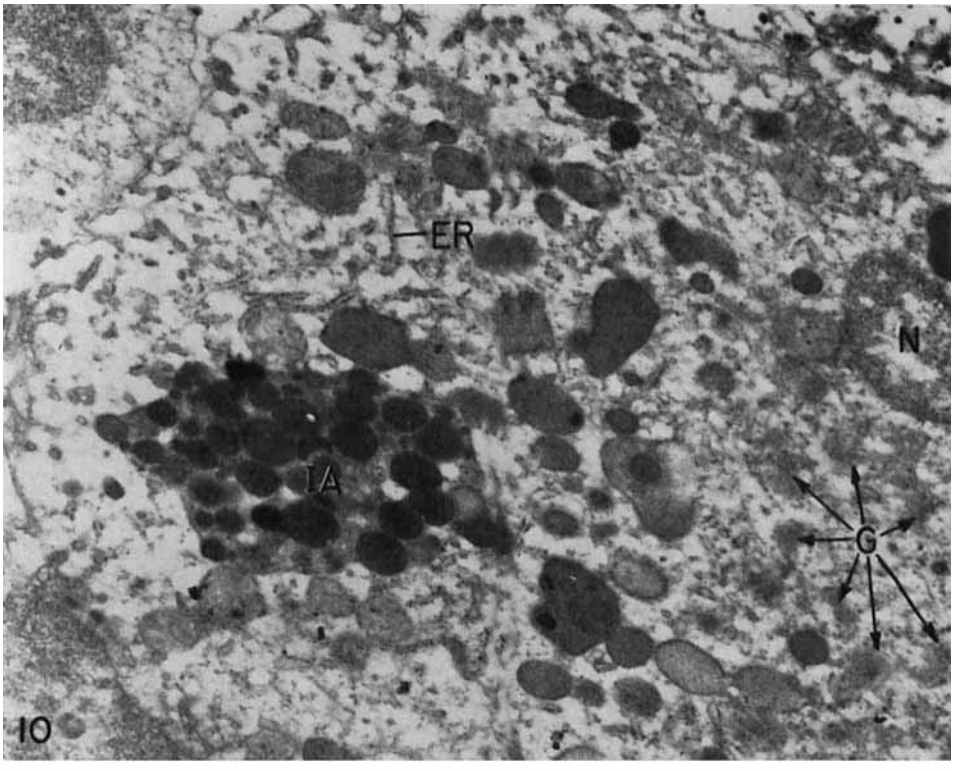
PLATE 5

EXPLANATION OF FIGURES

10 A portion of the cytoplasm of a phagocytic reticular cell showing a large type A inclusion body enclosed by a limiting membrane; within the inclusion body are additional smaller dense globular bodies. Other similar bodies are contained in the rarefied portion of the cytoplasm which is rich in rough-surfaced endoplasmic reticulum. The Golgi apparatus is at the right. × 11,200.

11 A portion of the cytoplasm of a phagocytic reticular cell illustrating the irregularity in form of the cisternae. Long profiles of the endoplasmic reticulum have both smooth- and rough-surfaced portions. Free ribosomes are scattered in the form of small aggregates (arrows). Mitochondria are also irregular in structure. × 28,000.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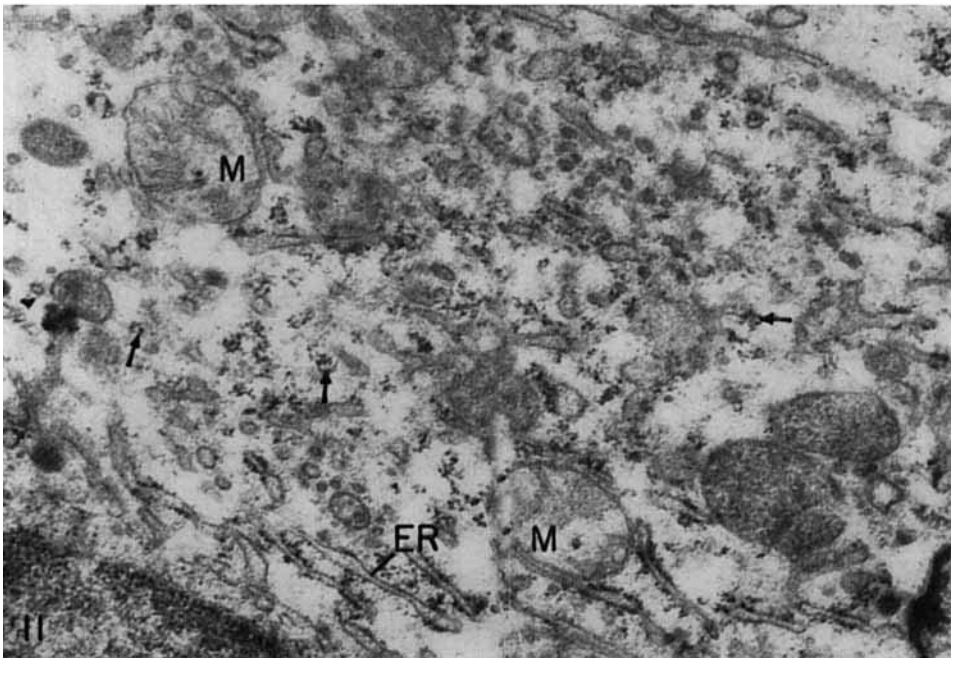
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PLATE 6

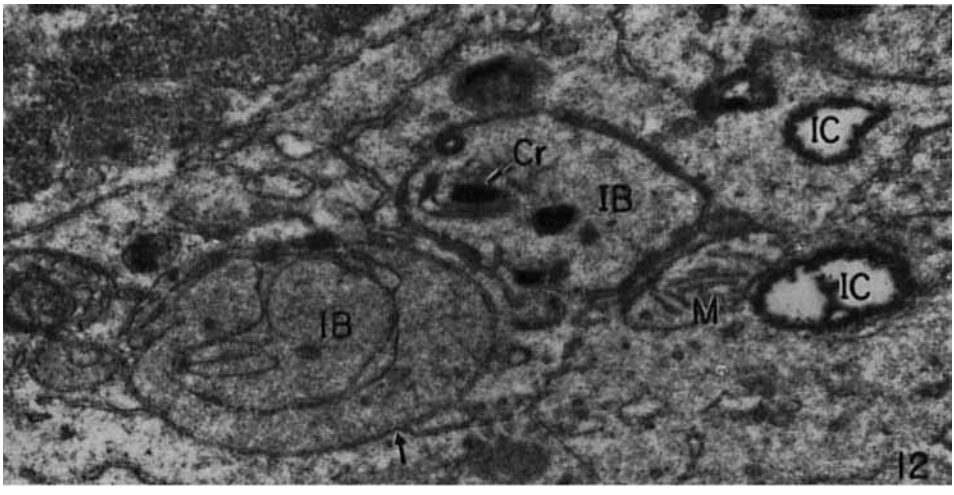
EXPLANATION OF FIGURES

12 A portion of the cytoplasm of a phagocytic reticular cell after $KMnO_4$ fixation. Two large type B inclusion bodies of low electron density are shown. The limiting membrane of the one on the left is continuous with other intracytoplasmic membranes (arrow). Small crystalloids (Cr) are seen within a type B inclusion. Type C inclusion bodies appear on the right with their clear interior and extremely dense periphery. The presence of a limiting membrane around them is uncertain. × 27,500.

13 A portion of a phagocytic reticular cell similar to that in figure 12, showing type B inclusion bodies of varying sizes. The large one at the right illustrates the formation of a "myelin" structure, while the large one at the left appears to represent either a fusion of two bodies or fisson of one. A type C inclusion body is at the lower right. × 27,000.

14 A type B inclusion body with a "myelin" figure. Fine dense particles within the body may be ferritin granules. A highly irregular pattern of cristae is seen in the mitochondrion at the right. × 30,000.

15 A portion of a type A inclusion body possesses a dense matrix in which are numerous granules (arrow), which appear to be ferritin. × 56,000.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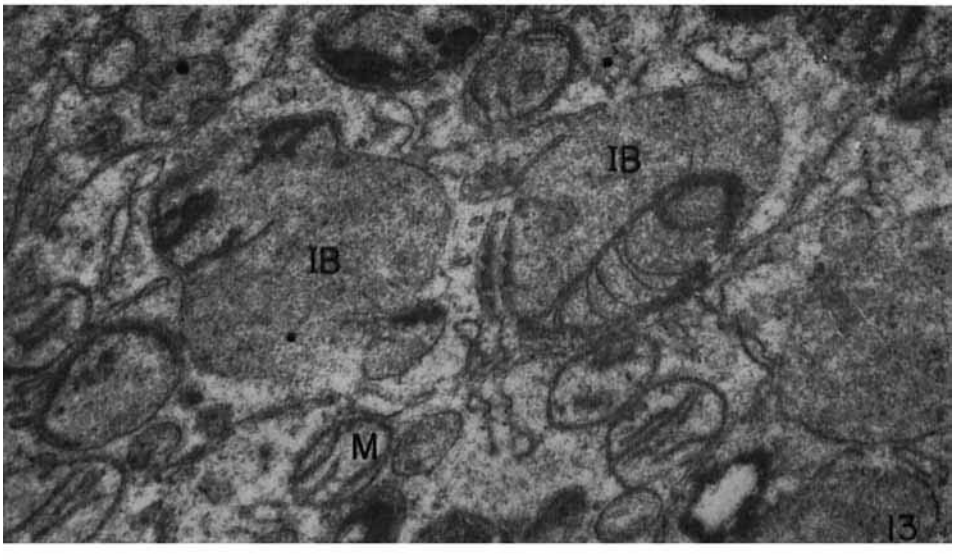
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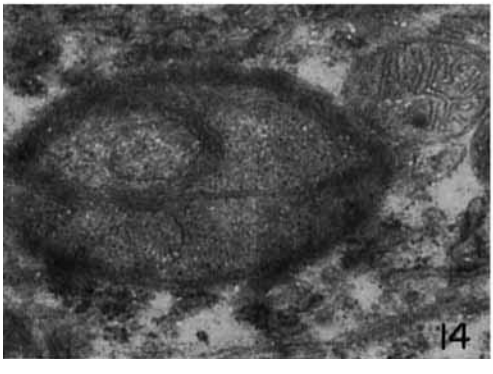
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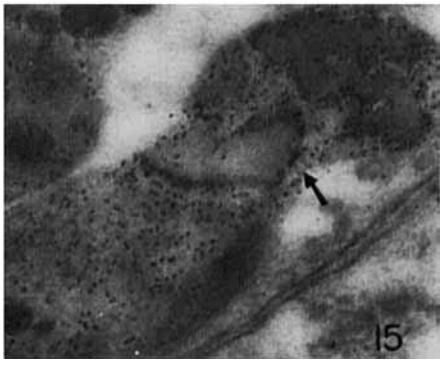
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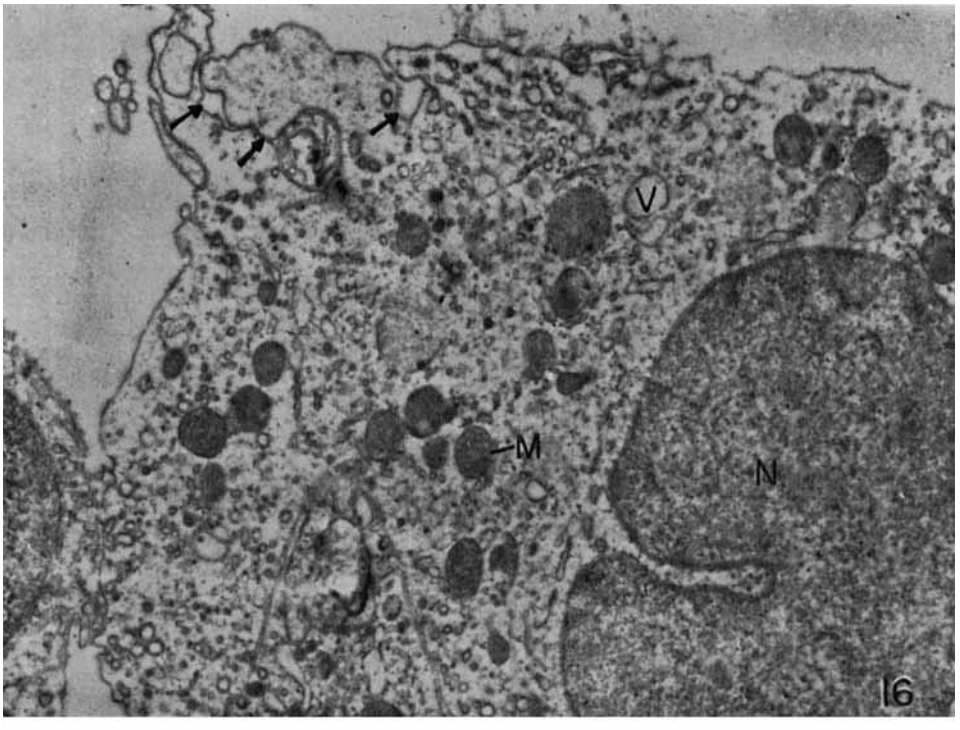
PLATE 7

EXPLANATION OF FIGURES

16 A portion of a rounded macrophage shows irregularity in contour of the plasma membrane which is folded inwards (arrows), suggesting the presence of pinocytotic activity. There are numerous small intracytoplasmic vesicles along with many mitochondria, an endoplasmic reticulum and some vacuoles. The nucleus is fairly electron-lucent. × 12,000.

17 A portion of a rounded macrophage which shows many peripheral finger-like projections (arrows), which make contact with others. Inclusion bodies are of type B. The largest vacuoles are peripheral. × 10,400.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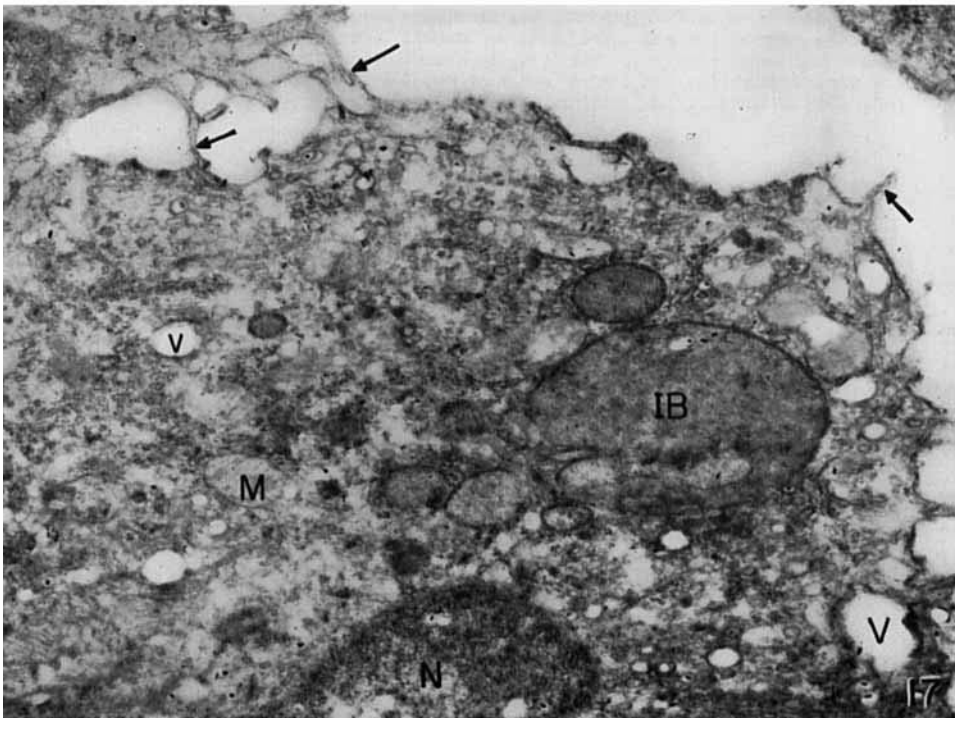
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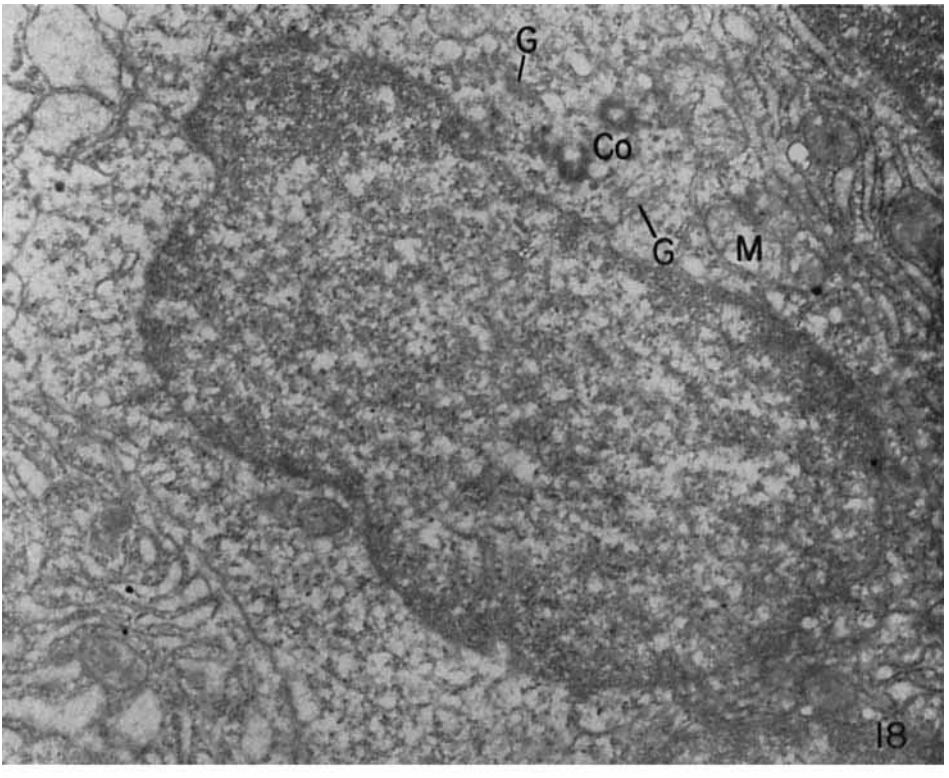
PLATE 8

EXPLANATION OF FIGURES

18 This cell is probably a transitional form between the nondifferentiated reticular cell and lymphoblast. The cell is irregular in shape. Mitochondria are large and have poorly developed cristae within a matrix of variable density. The cytoplasm contains little endoplasmic reticulum but many ribosomes. The Golgi apparatus consists of (a) stacks of double membranes many of which end in vesicles, and (b) numerous vesicles. The nucleoplasm has increased electron density. × 10,800.

19 This lymphoblast and its nucleus are rounded. Numerous mitochondria are clustered near the cell center and have a dense matrix. The endoplasmic reticulum is both rough- and smooth-surfaced and is fairly abundant. Although the plane of section did not pass through the cell center, some of the Golgi components are discernible at the right side of the flattened nuclear face. The nucleolus is conspicuous. × 8960.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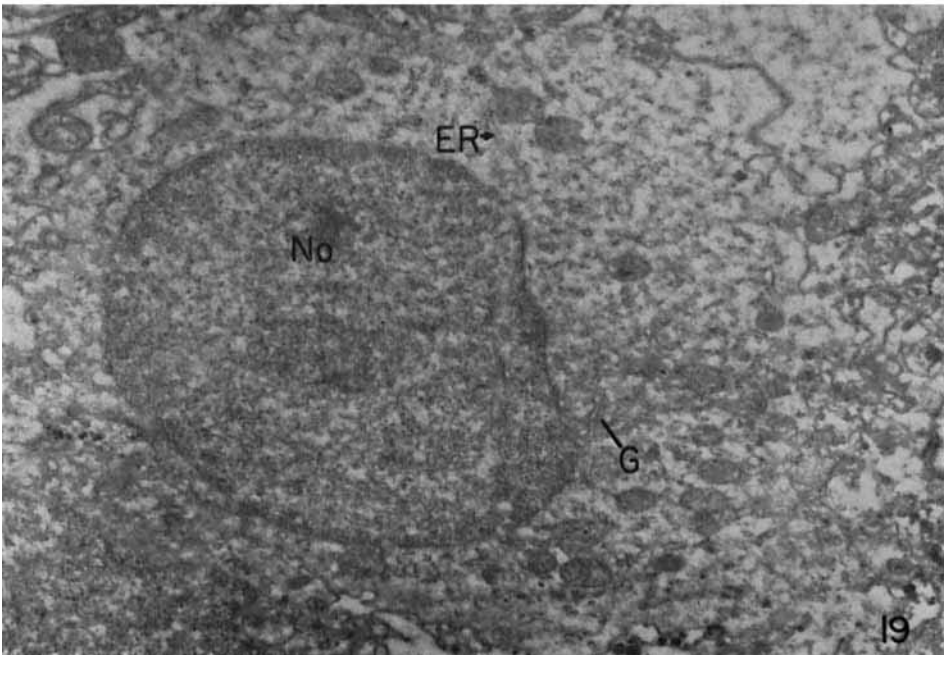
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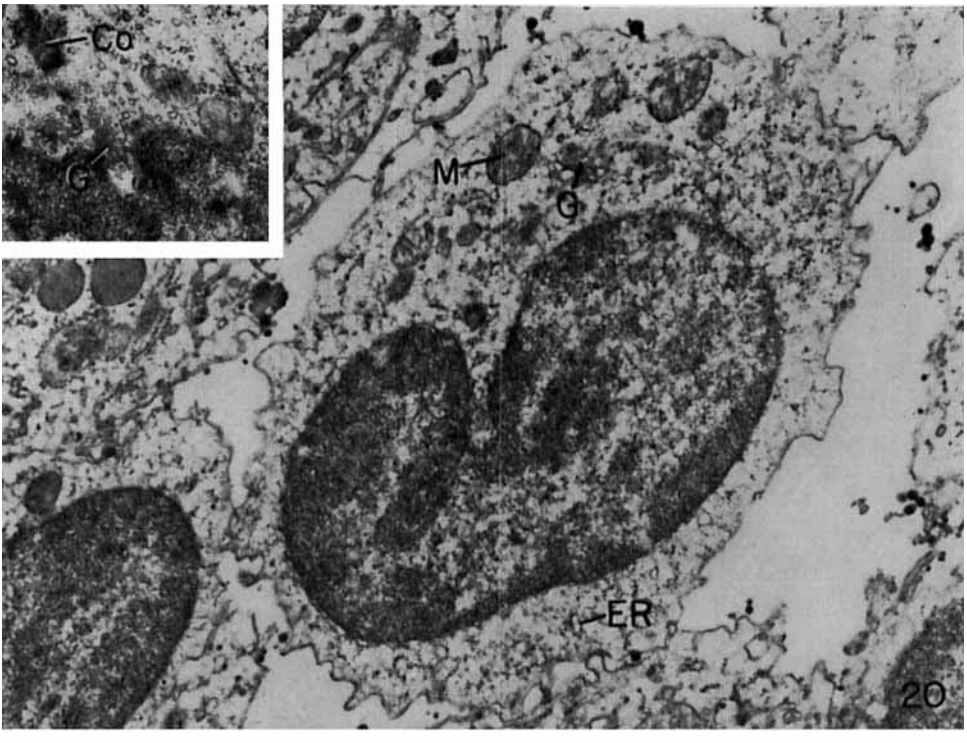
PLATE 9

EXPLANATION OF FIGURES

20 A medium-sized lymphocyte. The cell membrane is jagged. The endoplasmic reticulum is sparse. The nuclear membrane is indented deeply. In the cytoplasm opposing the indentation are mitochondria and the Golgi apparatus. × 11,200. The insert illustrates the close proximity of Golgi profiles to the nuclear indentation. At the upper left is an obliquely sectioned centriole. × 16,200.

21 The cell center of a medium-sized lymphocyte. Ovoid mitochondria with extremely well-developed cristae are clustered in this region. Some of the cristae extend across the entire width of the dense mitochondrial matrix. In addition to the stacks of paired membranes in the Golgi apparatus, many thick-walled vesicles are also present and are probably a component of this organelle. Fine granules compose the centrosome, in which no other structures are found except for a few ribosomes. The surrounding cytoplasm contains free ribosomes and a few small flattened cisternae. × 22,000.

22 A region of the cytoplasm from a medium-sized lymphocyte shows several vesicles of varied sizes with a double electron-dense membrane and secondary vesicles inside. × 66,000.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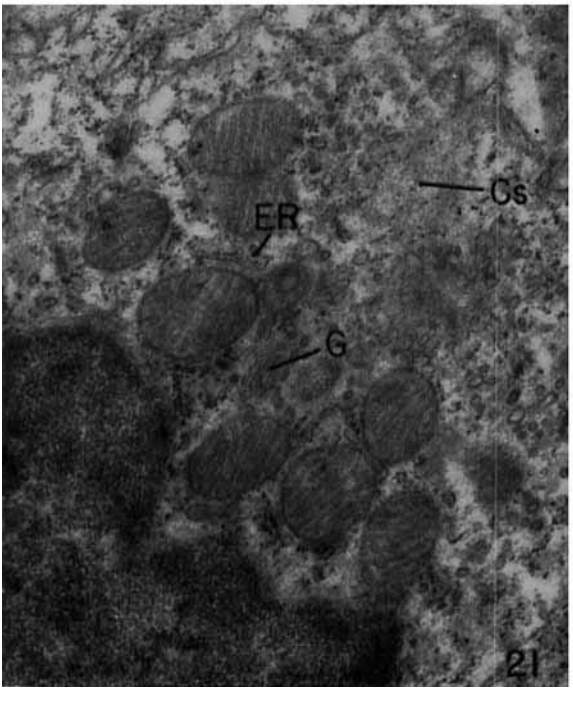
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PLATE 10

EXPLANATION OF FIGURES

23 A small lymphocyte. The cell center has a large centrosome of dense cytoplasm, but fewer mitochondria than the larger lymphocytes. The cristae mitochondriales are less concentrated and the Golgi apparatus appears to be composed primarily of vesicular components. A few large vacuoles often appear in the cell center. Endoplasmic reticulum and free ribosomes are sparse, the latter generally being freely disposed. Nucleoplasm is exceedingly dense. × 17,600. The insert shows the position of mitochondria in the nuclear indentation. The structure of the deeper mitochondrion, and of the lower end of the outer one, is obscure. × 15,800.

24 The cell center of a mature lymphocyte shows the centrosome and its contained centriole. In addition to some vesicular Golgi components a few triple-layered vesicles are seen (arrows). Mitochondrial contact with the nucleus is well shown. Membranes are blurred at points of contact. × 24,000.

25 A small lymphocyte illustrates the sparsity of ribosomes and endoplasmic reticulum, and the presence of clear nuclear channels (arrows). The outer nuclear membrane is almost completely devoid of ribosomes. × 10,200.

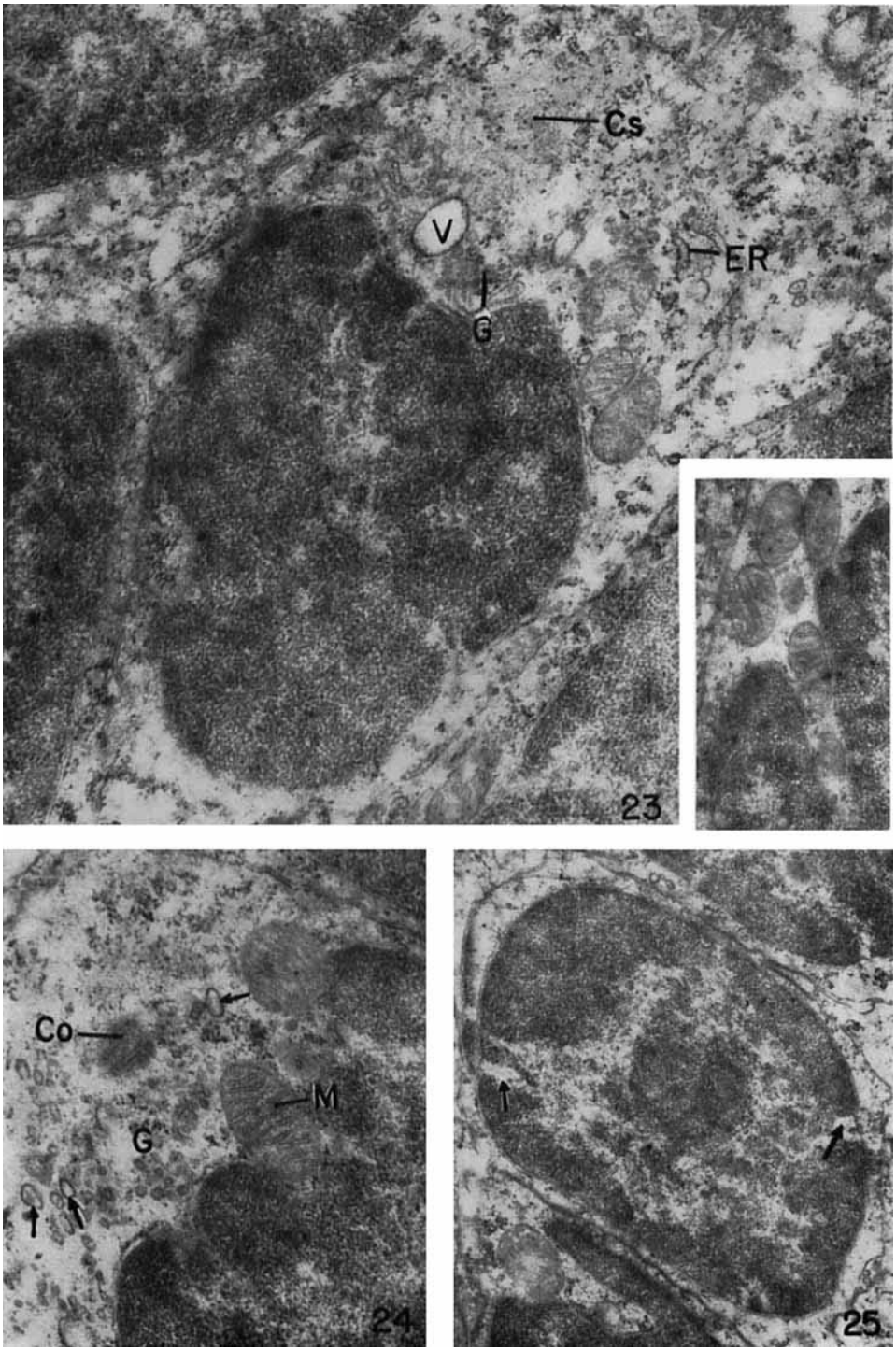
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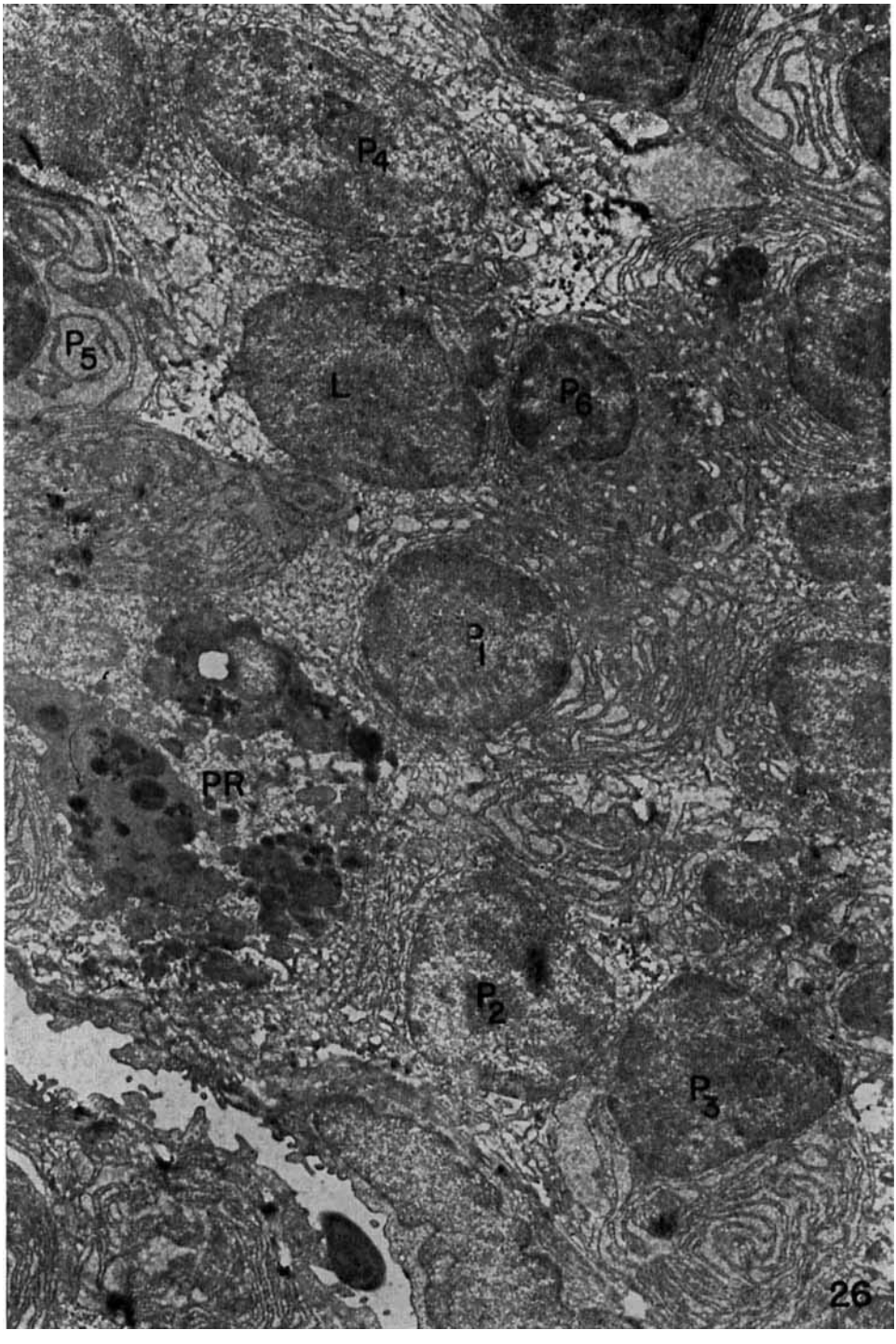
PLATE 11

EXPLANATION OF FIGURE

26 A portion of a medullary cord, which is rich in plasma cells, shows various stages in their life history. Near the capillary at the lower left is a phagocytic reticular cell with many inclusion bodies. × 6800.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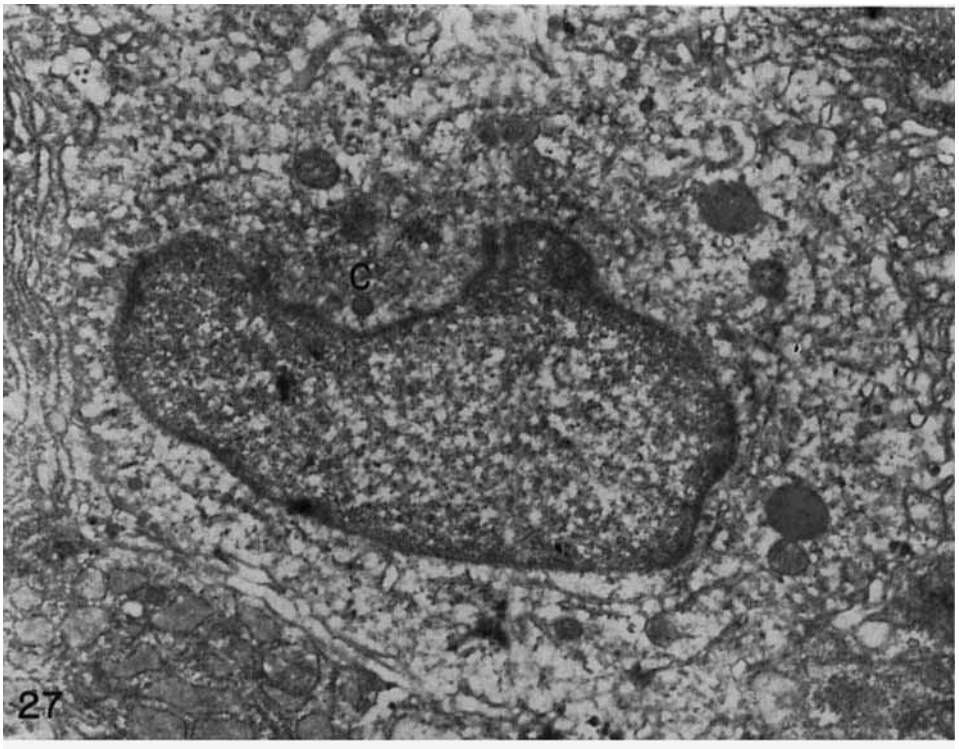
26

PLATE 12

EXPLANATION OF FIGURES

27 A very immature plasma cell which still shows many of the characteristics of non-differentiated reticular cells. Flat profiles of endoplasmic reticulum are arranged parallel to the nuclear membrane. Many ribosomes are located freely in the cytoplasm. Although cytoplasmic condensation above the central nucleus indicates early maturation of the cell center, the Golgi apparatus is only vaguely defined and mitochondria are small. × 10,800.

28 An immature plasma cell is further advanced than the one shown in figure 27. The extensive cisternae of the endoplasmic reticulum are often confluent, and most of the ribosomes are associated with the endoplasmic reticulum. The nucleus is still centrally located, but the peripheral aggregation of electron-dense material is apparent. The nucleolus is very large. × 11,200.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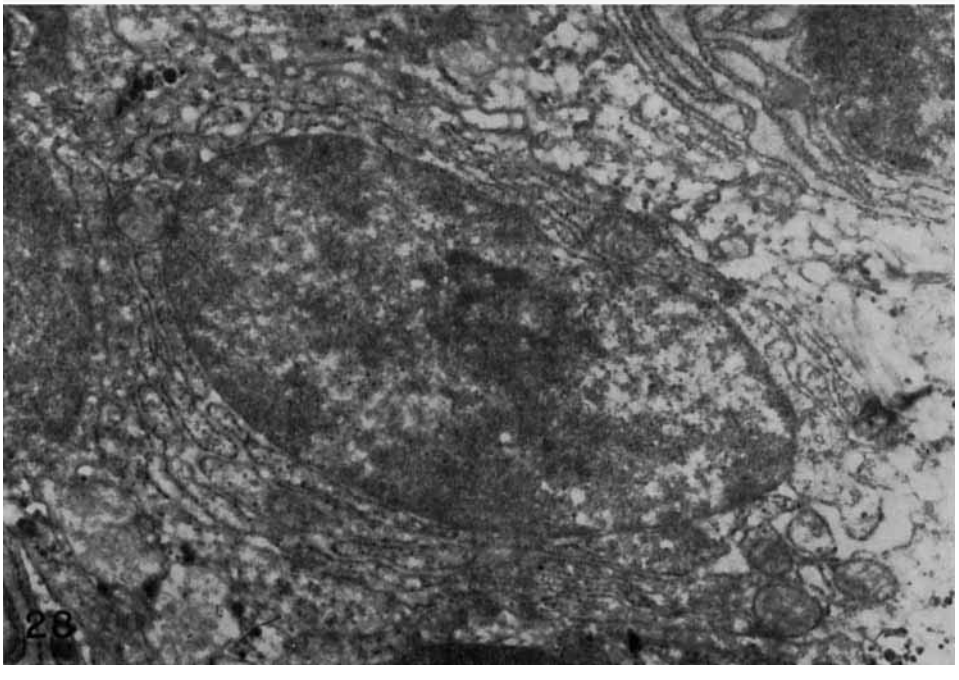
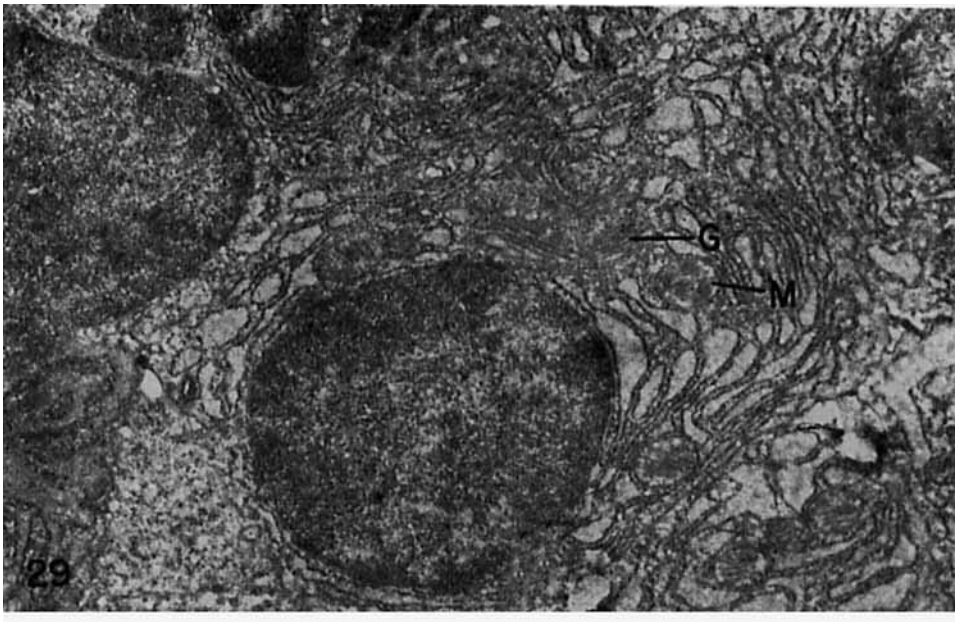

28

PLATE 13

EXPLANATION OF FIGURES

29 A mature plasma cell shows an extensive endoplasmic reticulum with somewhat dilated cisternae which contain a cloudy material. Mitochondria are large and well-organized. The Golgi apparatus is large. The nucleus contains dense nucleoplasm and is eccentrically located. × 11,200.

30 This is a typical Golgi apparatus of the mature plasma cell. Extensive bilaminated membranes encompass the cell center which contains dense ground cytoplasm. The membranes are associated with vacuoles. Numerous thick-walled vesicles (arrows) with an interior of variable density are found both inside and outside the paired membranes. Irregularly shaped dense bodies (D) with thick walls appear to have arisen by transformation from the smaller vesicles. A portion of the nucleus is visible below. × 46,000.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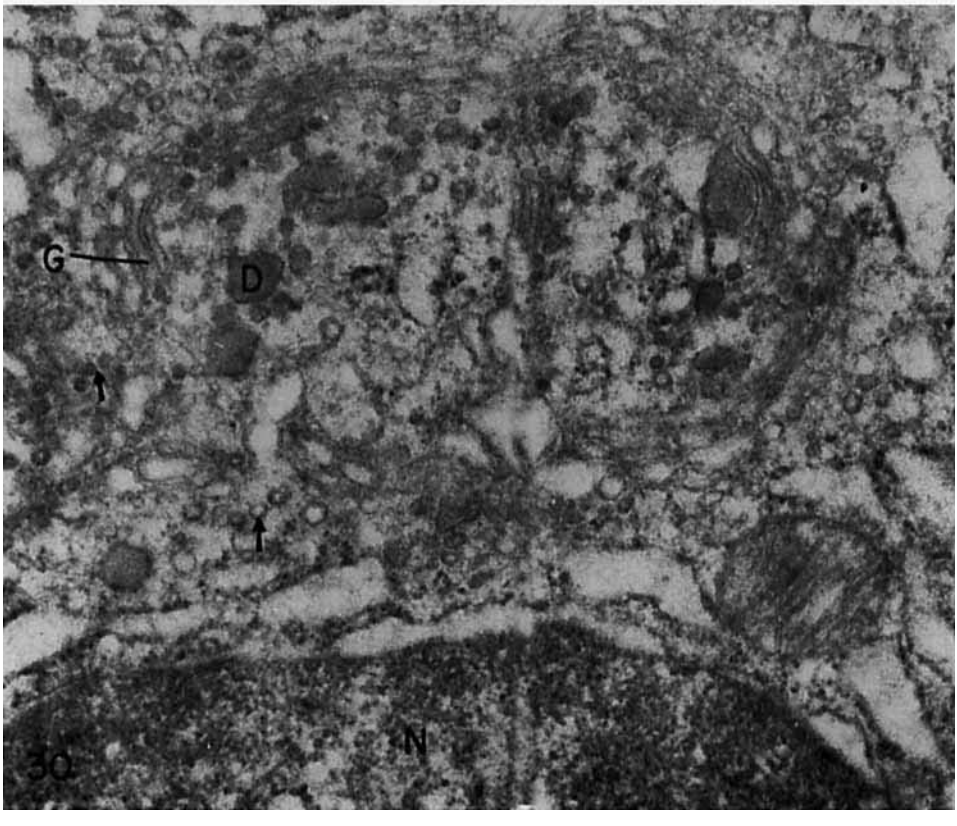
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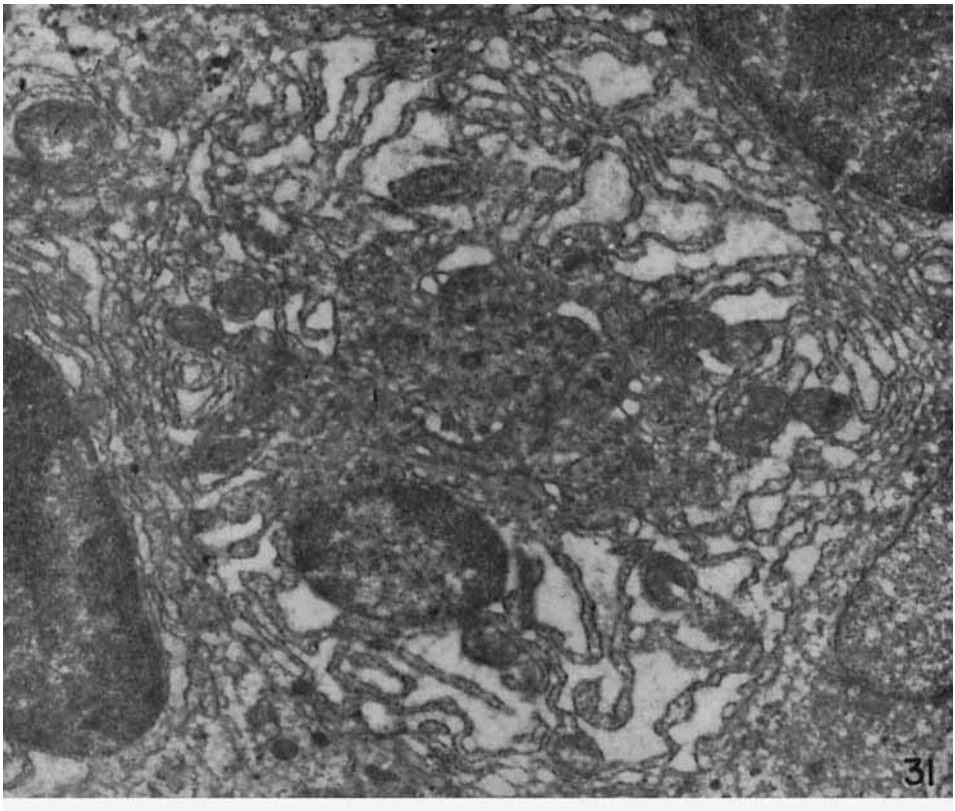
PLATE 14

EXPLANATION OF FIGURES

31 A plasma cell illustrates the type A modification. Greatly enlarged cisternae contain less dense flocculent material than that in the mature plasma cell. Mitochondria in the narrow strands of ground cytoplasm bulge toward the cisternae. The centrally located Golgi body is large and dense, and contains a centriole which is cut transversely. The nucleus is sectioned far from its equatorial plane. × 8000.

32 This plasma cell shows the type B modification. The cisternae are more rounded and contain denser material than is true of the mature plasma cell. Several mitochondria are packed in between the cisternae. × 7600.

33 Dense globular bodies in the cytoplasm of a cell somewhat similar to the one shown in figure 31. They are within the cisternae of rough-surfaced endoplasmic reticulum and are believed to be Russell bodies. × 48,000.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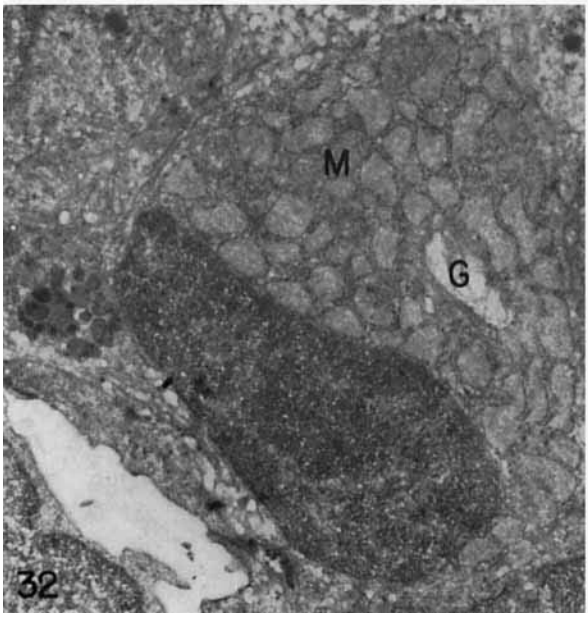
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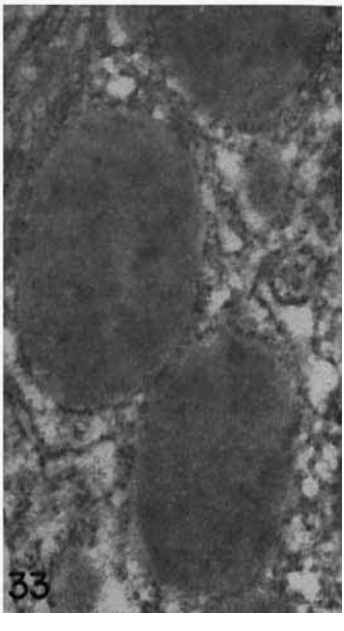
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