Electron Microscopy of Formed Elements of Normal Human Blood

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The high resolving power of the electron microscope has greatly increased the "visual" range for studying cell structures. Internal cellular detail at more than 100,000 magnifications has been demonstrated with current thin section technics. This advance in ability to "see" detail of cell morphology has greatly extended the realm of cytology and cytochemistry. At the same time it has imposed more strict disciplines upon the investigator. Greater care must be taken in preparing material and a new range of artifacts must be considered. Some factors that have bearing on the production or elimination of these artifacts have been studied. They include the fixing agent, the time, temperature, pH, ion concentration and penetration rate of fixation. The rate and agent for dehydration, as well as the nature of the embedding material and manner of hardening the impregnated specimen, have been the subject of investigations. The cutting technics have required modification of the existing microtomes and development of several new instruments. The need for better "cutting" edges has resulted in the development of the reinforced safety razor blade and the glass knife. These and other new methods developed in the last 10 years have resulted in thin section technics that make it possible for one to consider cytologic research at these new levels of magnification.

There are, however, still other facets that must be considered. The recent work of Rhodin has pointed to cytologic changes that take place in cells after their metabolism has stopped. His work on the mitochondria of the kidney tubule showed that autolytic changes were discernible at high magnification within one-half hour after the kidney blood supply was interrupted. The extent of similar changes in other cell structures and tissues has not been as carefully determined. Electron microscopists are well aware of the fundamental instrument limitation that forces the investigator to look at "fixed" or dead material. This means that the dynamics of cellular physiology and of cellular metabolism that have been seen with the phase microscope can only be inferred and are not subject to direct observation.

The development of this "new anatomy" at such high magnifications also means the redefinition of "normal" cells with a probable narrowing of the limits in normal conditions. The examination of the effects of innumerable agents and metabolic states upon "normal" cells will also need to be re-examined.

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The evidence of rapid autolytic changes and the complexities of obtaining "normal" specimens from humans reduces the range of cell types that are available from human sources. Surgical specimens could supply most pathologic material. However, availability of normal tissue in some cell types would be difficult to obtain, particularly before autolytic changes may have taken place. Circulating human blood cells are a type of tissue that is especially suited for availability of both normal and pathologic cells.

Electron microscopic studies of ultra thin sections of human blood cells have been reported by several investigators. Braunsteiner and Bessis have described some of the fine structures of blood cells that can be seen with the high resolving power of the electron microscope. Kautz and DeMarsh have reported more in detail on their methods of preparation and have shown good pictures. This was followed by Rinehart's description giving still more detail and improved photographs.

Grey and Biselle had also published a preliminary report on details of leukocyte structure. These reports have been supplemented by the bone marrow work of Pease. In the latter publication, Pease has delineated the development of the various cell types in the rat and guinea pig. This work has the inherent limitation of all heterologous species observations.

With each of these reports the variations in method of approach and details that were shown by the photographs attest to improvements in technic and an increased understanding of cell morphology.

**MATERIALS AND METHODS**

This laboratory has prepared thin sections of blood cells for electron microscopic study by the following method. Blood specimens were obtained by venipuncture from normal healthy adults (unless otherwise indicated) using heparin (and without siliconized glassware). The blood was centrifuged at 800 r.p.m. for 10 min. in an International Centrifuge. At this speed the leukocytes and platelets were not packed into a sticky layer and could be dispersed easily into a free cell suspension. One-quarter to one-half cc. of plasma containing leukocytes, platelets and a few red cells was added to about 5 cc. of 1 per cent veronal buffered isotonic osmium tetroxide (pH 7.4) (Palade). After shaking and standing 5 min. the cells were sedimented in a centrifuge. The supernatant was discarded and 2 cc. of fresh osmium added. The second osmium solution was also removed by centrifugation after standing 5 min. The cells were then resuspended and sedimented more rapidly through the following fluids: 65 per cent alcohol once, absolute alcohol 3 times, 50 per cent absolute alcohol-50 per cent n butyl methacrylate (monomer) mixture 3 times, and in uncatalyzed n-butyl methacrylate (monomer) 2 times. The cells were exposed to each of these fluids a total of about 2-3 minutes including the time for centrifugation. The centrifuge was accelerated rapidly and slowed with the brake. After the last plastic wash was decanted the cells were resuspended in 3 or 4 drops of catalyzed plastic and placed in a gelatin capsule (3), then heated at 68-70 C. for several hours. The total time from venipuncture to the heating of the plastic was usually less than one hour.

The capsules had a previously hardened button of plastic in the bottom so that the cells settled into a narrow ring on the hardened plastic rather than being deposited on the curvature of the capsule bottom. After the plastic hardened, portions of the ring of cells were excised and mounted for sectioning by a glass knife on a Porter-Blum type9 microtome. The sections were floated on 20 per cent acetone and picked up on copper screens covered with a very thin film of collodion reinforced with a film of vaporized carbon.

The sections were examined with an RCA EMU-2 electron microscope. This instrument was equipped with externally adjustable 10 mil and 25 mil apertures in the condenser lens,
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a 2 mil objective aperture and an additional intermediate projector lens. When the 10 mil aperture was in place it was possible to support the sections on copper screens coated with a single film of formvar producing pictures with better contrast.

Discussion

A complete dispersion of the free cells in each solvent transfer was essential in this procedure. This was attained by allowing the residual fluid from the decantation to flow down onto the sedimented cells. The tube was joggled to break up the packed cells before adding the next fluid. This technic gave a good dispersion and the potential penetration distance for each solvent was reduced to the radius of the largest cell.

The steps as outlined may not be the optimal procedure; however, several variations were tried in developing this method. Some of these are described. All fluids except the osmium were maintained either at room (circa 25 C.) or icebox temperature (4 C.) until used. The difference in temperature of fluids made no apparent difference in the cell detail. Shortening of the exposure time for each solvent step to two or three minutes, in dehydrating and embedding, and omission of the washing of osmium-fixed cells in water or buffer were definitely beneficial. This is in keeping with Porter’s observation that excessive standing resulted in leaching which tended to leave more of a “cytoplasmic skeleton” with the loss of fine detailed structures. Cells left in osmium for 20 hours before dehydration and embedding were thoroughly vacuolated and only the strongly stained granules remained.

The osmium fixation time was also varied from one solution for 2 min. to 2 solutions for a total of 50 min. The best results were from fixations ranging from one solution for 5 min. to two solutions for a total of 35 min. From this we chose two solutions for 5 min. each for routine fixation.

Different concentrations of alcohol were tried for the first alcohol wash, including either gradual increases in per cent alcohol or going directly from the second osmium solution into absolute alcohol. The one step, 65 per cent alcohol gave the most consistent results producing fine detailed structure. An initial alcohol wash of 80 per cent was not as consistent as the 65 per cent. When 70 per cent alcohol was used there was a great tendency for the cells to clump and cell detail was inferior. The concentration of the osmium solution may be altered and still produce good cell pictures. This variable has not been systematically explored; however, osmium concentrations as low as 0.05 per cent have given adequate fixation. Excellent preparations were also made by substituting corresponding concentrations of acetone in place of alcohol for the first wash, the absolute alcohol and 50-50 alcohol-plastic washes. Electron micrographs prepared from alcohol dehydration and acetone dehydration were equally good and apparently these dehydrating agents are interchangeable. More care must be taken in decanting fluids when acetone is used.

Observations

Leukocytes. Most sections through leukocytes are elliptical to circular in general outline. This was consistent in most preparations. A notable exception was the frequent appearance of pseudopods of neutrophils observed in a study on phagocytosis. Cells in these preparations were often elongated and distorted with
pseudopods producing rather bizarre outlines. Most normal cells in a resting state showed a tendency for serrated or scalloped edges with no apparent regularity in either the shape, spacing or size of these variegations. Due to the random nature of cutting, the size, shape and relative area of nucleus to cytoplasm was not always a reliable criterion for cell identification.

The outer cell membrane was a single boundary 80–110 Å thick. This measurement was obtainable when two cells were in close contact and sharply defined edges were present (fig. 3). When a cell surface was not in close apposition to another surface the cell wall measured about 150–250 Å and was not as sharply delineated. This increase in thickness may represent a fixing or cutting artifact. On the other hand it is reasonable that the thinner and more finite structure seen in cells in contact may truly represent the physiologic response to the physical or chemical presence of another surface. The phenomenon of a more sharply defined cell wall was also seen in the area of contact between leukocytes and bacteria. When free cell surfaces were cut at oblique angles the definition of the cell membrane diminished markedly. Strongly tangential cuts gave the impression that there was not a definitive dense cell membrane but an undulating surface only slightly more dense than the cytoplasm of the cell. Those sections that were more nearly at right angles to the cell surface distinctly showed a more dense nature to the outer cell membrane compared to cell cytoplasm.

**Neutrophilic leukocytes:** The cytoplasm of the neutrophil was well-filled with granules that varied in size from 0.5 μ down to fine particles of 0.02 μ (figs. 1 and 2). Some of the granules stained heavily with osmium and were generally thought to have fairly high lipid content. Some of the less dense granules had a thick wall which had a fairly high affinity for osmium and were considered to be the endoplasm reticulum of Palade's. Other granules of similar density had a single dense membrane and were more vesicular in appearance. There was a fine textured cytoplasmic protein matrix surrounding all the granular structures.

Mitochondria when seen were characterized by the presence of cristae or cross plates, segmenting the interior of the mitochondria. In the neutrophil the mitochondria were usually the long rod type although these were not present in every section. The cristae of the mitochondrion were not as prominent in neutrophils as those of other cell types such as lymphocytes, monocytes, kidney tubules, etc. Rinehart described a degeneration of mitochondria into granules and postulates this mechanism as a source of granule formation. This may be true. However, we have not seen evidence for this. He also identified the Golgi apparatus and referred to A. J. Dalton's work on the comparison of electron micrographs and phase contrast studies of the Golgi substance of mouse epididymus. Dalton described the Golgi substance of these cells as having three parts: vacuoles, lamellae and granules that were approximately 400 Å in diameter and intimately associated with the lamellae. The lamellae themselves were arranged concentrically around the vacuoles.

Numerous light staining cytoplasmic vesicles such as Rinehart indicated were present in our photographs of neutrophils; however, we have not seen the vacuoles, lamellae and granule in combination in normal neutrophils that would characterize the Golgi apparatus. Palade considered these small vesicles with heavy osmium staining in the periphery as endoplasm reticulum that was not as fully developed as the endoplasm reticulum in other cell types.
Fig. 1.—This normal neutrophil shows three lobes of the nucleus (N) and many cytoplasmic granules. A long rod like mitochondrion at M has indistinct cristae. Light granules with a more dense periphery are the endoplasm reticulum of Palade (ER). The larger pale areas are more truly vesicular in nature (V). There are also many smaller granules of varying density. The whole is embedded in a matrix of very fine grained cytoplasmic protein. A portion of a platelet is in the lower left corner and a 1 micron mark is in the lower right.

A report on the apparent lack of function of the larger granules in phagocytosis and digestion of bacteria has recently been made by the authors. If the granules played a role in these physiologic functions they did so at some distance from the bacterium within the cell, for there was no specific grouping of the larger granules about the bacteria during the digestive process.

The digestion of non-virulent bacteria by a neutrophil produced an aggregation of very fine grained material around the degrading bacterium. This did not
FIG. 2.—This is another normal neutrophil with two nuclear lobes (N) and a fairly extensive distribution of endoplasm reticulum (ER), a few vesicles and smaller granules, but apparently no mitochondrion. The double wall of the nucleus is apparent on the larger lobe in the original print. The mark in the lower right corner is one micron.

FIG. 3.—A portion of a normal neutrophil on the right is in close apposition to a lymphocyte on the upper left. This shows clearly the sharpening of the outer cell wall at point of contact with another cell. The thickness of the membrane at “A” was measured with an ocular micrometer and found to be 80 Å. A portion of the nucleus of each cell is present (N). A portion of a mitochondrion (M) is present in the neutrophil. The black mark in the lower left is one micron.

FIG. 4.—This is a portion of the strand (S) connecting two lobes of the nucleus (N). The double walled nature of the nuclear membrane can be seen and at higher magnifications it is apparent that the dense nuclear material is continuous the full length of the strand. The scalloped nature of the cell surface is also evident. The micron calibration is in the lower left.
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Appear to be a membrane and frequently increases in thickness as the destruction of the bacterium continued. The nature and origin of this dense (electron absorbing) material has not been determined. It was apparently developed from the cytoplasmic protein of the leukocyte or the interaction of this material with the degraded products of the bacteria. The cytoplasmic protein material appeared to be the portion of the neutrophil that was most directly involved in the degradation of ingested bacteria.

The nucleus had a double membrane wall. These membranes were about 70–90 Å in thickness with a space of 100–200 Å between. Figures 8 and 9 show this most clearly of the prints in this article. Very thin sections that transect the nuclear membrane at right angles occasionally showed regions of the membrane that appear to become a single layer for distances of about 200–300 Å. These gave a “link sausage” effect with regions lacking the middle layer allowing the two dense layers to collapse into an apparent single membrane. This may possibly have been an artifact. If they were real they could represent chemical windows that would allow for the passage of hydrophilic molecules in one area and lipophilic molecules in another.

Watson has examined the nuclear envelope in other cell types and has reported areas of single and double membranes. He has also described areas without membrane and apparent free access from the interior of the nucleus to the cell cytoplasm. Cells that have a well-developed endoplasmic reticulum were seen to have a nuclear envelope that appeared to be a special adaptation or position of that structure. Such a relationship was not apparent in the blood cells that we have observed.

The interior of the nucleus had zones of osmophilic dense material of various depths. Some cell nuclei showed a greater contrast of osmic staining than others. There was no boundary between the lighter and more dense regions, nor was there a definite shape to either of the areas. In general the more dense areas were about the nuclear membrane with the less dense region being primarily confined to the interior of the nucleus. However, occasionally regions with less dense material were observed adjacent to the nuclear membrane. Also islands or masses of more dense material were seen deep within the nucleus surrounded by the less dense regions. Frequently, cross sections showed three or four lobes of the nucleus and only on rare occasions the connecting structure between lobes was seen. These strands showed continuous strings of the dense nuclear material connecting the main nuclear masses (fig. 4). No regions were observed with the two double nuclear membranes in direct contact without a layer of nuclear material separating the two membranes.

Eosinophils. There is a general agreement among electron microscopists that eosinophils have distinct and characteristic granules (fig. 5). These were large in size (0.7–1.3 μ) and had a strongly osmophilic substance either present as an angular or rectangular shaped body in the granule. These structures suggested a crystal occupying a large portion of a definitively outlined granule; the rest of the granule had material of low density. These angular bodies in the human eosinophil granules were seen to take many shapes, from simple rods or rectangles to trapezoids, triangles and irregular masses showing straight sides and in some instances long needle-like inclusions within the eosinophil granule. The larger
masses were as much as 1.3 μ in their greatest dimension. The needles were as small as 0.2 μ in diameter. Pease\textsuperscript{7} has reported disc like inclusion in the eosinophils of rat and guinea pig marrow. We have also seen this more limited rod or disc shaped granular inclusion in monkey eosinophils. Sheldon and Zetterquist\textsuperscript{15} described cytoplasmic granules in the white cells of the rat. They were not

![Fig. 5](image)

**Fig. 5.**—This is a normal eosinophil with its nucleus in the upper left portion (N). The many cytoplasmic granules with the dense inclusions are the eosinophilic structures that characterize this cell type. Some granules have multiple inclusion and show greater variability of form than published pictures of rat and guinea pig (Pease\textsuperscript{7}). Unpublished monkey eosinophils (from this laboratory) also have granules with the simple bar or rod type of inclusion very similar to the rat and guinea pig. No mitochondria are present in this cut; however, they have been seen in other human cells and resemble those seen in the neutrophil. The micron calibration is in the lower right corner.
certain as to the nature of the cell type to which these structures belonged although eosinophils were suggested. Since similar granules have been found in eosinophils it may be presumed that their cells were eosinophils. Their excellent photographs showed the angular structures to be made up of layers of dense material that in cross section were 6–7 layers deep. One section cutting the dense angular body perpendicular to its long axis shows the laminations to be more nearly a roll similar in structure to a cinnamon pastry roll. We have not been able, as yet, to demonstrate similar laminar or rolled structures within the angular inclusion of the human eosinophil granule.

The chemical nature of this material has been investigated by Vereauteren. The presence of an antihistamine substance has been attributed to the eosinophil by Kovacs and Juhasz. Vereauteren isolated granules from horse eosinophils by rupture and differential centrifugation. Cold trichloracetic acid, ether-ethanol and hot trichloracetic acid extracts were made and analyzed. A study of the behavior of the granules to osmotically varied solutions, solubility and chemical reactions of the fractions led Vereauteren to conclude that the granules had two parts. An outer relatively insoluble shell of phospholipids contained at least in part sphingosine. The internal portion of the granule contained an arginine rich protein. There was no cholesterol present in the ethanol-ether extracts that contained the sphingosine. The hot trichloracetic acid extract had some nucleic acids that gave a positive test for arabinose, although it tested negative for desoxyribonucleic acid. The concept of two distinct parts of the eosinophil granule has been substantiated by the electron micrographs. The mitochondria and other granules in the cytoplasm and the appearance of the nucleus were similar to the neutrophil.

Fig. 6.—This is a portion of a basophil’s cytoplasm from a myelogenous leukemic patient with 13 per cent basophils in peripheral blood. The tip of a nuclear lobe is seen at N. All large basophil granules are round or slightly ovoid. There are at least two or perhaps three types of these large granules. Those with the ring of dense material and a light central core are shown at arrow 1. The arrangement at arrow 2 is just a cut through one end of the hollow ball type (arrow 1). The mottled core type as shown at arrow 3 may be another version of the dense inclusion type granule. There are a group of granules that are more vesicular (arrow 4). These are apparently completely lacking in the more dense material and in general appear structureless. All of these large granules have a double walled peripheral membrane.
Basophils. Basophils were not found in the peripheral blood from a “normal specimen.” Their infrequent appearance and the chance nature of electron micrographic technic made it difficult to secure a good example of a “normal basophil cell.” Basophils have been found in several leukemic preparations and these have been used to characterize the cells, although they would not necessarily represent “normal” basophils (fig. 6). The cytoplasm of these cells contained large granules with a smooth outline and were evidently globular or slightly elongated spheres. These large granules (0.8-1 μ) apparently had a distinct double walled membrane (80-150 Å), a narrow band of low density material, then a zone
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Fig. 8.—This portion of a lymphocyte shows the large mitochondria (M) and the well developed cristae system. The cell nucleus is at the bottom (N). The black mark represents one micron.

of dense material a short distance in from the granular surface, and a core of pale or very low density material (.25–.35 μ diameter). Some granular sections seemed to be almost the reverse of this with a dense core and a wider, lighter zone around it. This arrangement could be accounted for as a section through the top quarter of the granule without transecting the light core of the structure. The round central light zone was occasionally seen to have other shapes. Also some granules have been observed that had a mottled appearance of dense material dispersed within the lighter less dense material. Still other large granules were present that had no dense internal structures. There were other small cytoplasmic granules present along with an occasional mitochondria. The nucleus had the same appearance as those seen in neutrophils.

Lymphocytes. The outline of lymphocytes was nearly always oval to circular in nature (fig. 7). True pseudopods as seen in the neutrophil were not present and consequently odd shapes or distortions of cell outline were rare. The outer cell membrane was very similar to the neutrophil membrane with a tendency for more prominent serrations, some of which look almost like spicules. The lymphocytes were characterized by a single large nucleus occupying a major portion of the cell section. The cytoplasm had large distinct mitochondria that were round or ovoid in shape as compared to the smaller rod type that were seen in the neutrophil. The mitochondria of the lymphocyte had well defined cristae in large number within these larger ovoid structures (fig. 8). Aside from the mitochondria, there were very few and in many sections no other large granules. The rest of the cytoplasm was mainly composed of very fine particles that make up the cytoplasmic protein.

The nucleus had a double membrane surface and the interior showed zones of varying osmophilia similar to the nucleus of the neutrophil. The zone contrast within the nucleus was most pronounced in the cells from a patient with chronic
Fig. 9.—This is a normal monocyte. The nuclear cytoplasmic ratio is lower than in the lymphocyte. This cell also has the large-ovoid type mitochondria (M) with distinct cristae. There are more small cytoplasmic granules than in the lymphocytes. There is also a distinct Golgi structure (G) in the “holf” of the nucleus (N). The double membrane of the nucleus is quite evident in this cell. The mark at the bottom represents one micron.

lymphatic leukemia of more than 20 years duration. This individual has not been subjected to medication and at the time the specimen was obtained had a W.B.C. of 250,000—99 per cent lymphocytes described as being all mature by light microscopic examination.

Monocytes. There were distinct large mitochondria of the round or oval type in the cytoplasm similar to the mitochondria seen in the lymphocyte. The cytoplasm of the monocyte contained small granules other than mitochondria, although there were not as many as were found in the neutrophil. The monocyte
shown in figure 9 contains the characteristics of the Golgi apparatus as described by Dalton. It was possible to discern here the vacuole, lamellae, and granules that together made up the Golgi substance of Dalton's. Monocytes have a large nucleus that usually occupied a smaller proportion of the sectioned area than was seen in the lymphocyte. Frequently a “hof” was seen, although the chance nature of the cutting did not always demonstrate this. In general, the nucleus was more uniformly stained with osmium and did not have the tendency of contrasting zones as seen in the mature lymphocyte, neutrophil and eosinophil.

Platelets. Platelets were well preserved and seen in excellent detail in nearly all preparations (fig. 10). They were intact and apparently in good condition, although no special care was taken to protect them with siliconized equipment. Spicules were frequently seen extending from the platelets (fig. 11). These spicules were extensions of the cytoplasm containing only the finest cytoplasmic protein and were not external structures attached to the surface of the platelet. The outer membrane of the platelets appeared to be identical with the outer cell membrane of the leukocytes. The cytoplasm contained granules that were 0.2–0.3 μ in diameter and closely resembled the microsomes in the cytoplasm of neutrophils. No distinct mitochondria were observed and no large granules like these seen in neutrophils were present. Numerous vacuoles or droplets of very low staining material were usually scattered among the denser granules. The consistency of granular size and density helped to differentiate between platelets and the tip of a neutrophil, although in instances it was difficult. The role of the spicules or of specific cytoplasmic granules of the platelet in the formation of fibrin clots has not been resolved.

Red blood cells in thin sections were remarkable for their great uniformity and lack of structure (fig. 12). They were more osmophilic or more dense from the standpoint of electron absorption than the leukocytes. The biconcave disk shape

![Fig. 10](image1.png)

**Fig. 10.**—This is a group of platelets showing fairly uniform dense granules. A few vesicles and spicules are also present.

![Fig. 11](image2.png)

**Fig. 11.**—This large single platelet shows clearly that the spicule is an extension of the cytoplasm and contains only the cytoplasmic protein. There are several vesicles present and several granules of differing density.
FIG 12

FIG. 12.—This normal red cell has a very uniform texture and little evidence of cell membrane.

and random cutting produced many odd forms. These usually showed little or no evidence of a cell membrane although occasional preparations had darker bands at the periphery. The most finite and distinct of these measured 200 Å in thickness. The dense homogenous interior obscured any matrix or stroma structures that may have been present. The consistency and homogeneity of the red cells were convenient criteria for observing defects in fixation or cutting. Imperfections were much more apparent in the uniform red cells than in the more heterogenous structures of the leukocytes. Occasionally small vesicles, inclusions or less dense areas were seen. These were thought to be the remnant of mitochondrion or nuclear structure that remained after nuclear dissolution or extrusion.

SUMMARY

The history of the development of practicable electron microscope technics for examination of the formed elements of the blood was reviewed. A method found to yield good reproductions of ultrathin sections of blood cells was presented in considerable detail. The various phases of the technic were critically evaluated.

The morphologic characteristics of the various formed elements of normal peripheral blood were defined in association with sample electron micrographs. Ultramicroscopic detail of neutrophils, eosinophils, basophils, lymphocytes, monocytes, platelets and erythrocytes was discussed.

SUMMARIO IN INTERLINGUA

Es presentate un revista historic del disveloppamento de practicable technicas de microscopia electronic in le examine de elementos formate del sanguine. Es desribite in grande detalio un metodo que ha provate su capactate de effectuar bon reproductiones de ultratenue sectiones de cellulas sanguine. Le varie phases de iste metodo es evalutate criticamente.

Le caracteristicas morphologic del varie elementos formate que occurre in normal sanguine peripheric es definite. Specimens de microphotographia electronic es presentate. Es discutite detalios ultramicroscopic de neutrophilos, eosinophilos, basophilos, lymphocytos, monocytos, plachettas, e erythrocytos.
REFERENCES


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