Endoplasmatic reticulum

Definition: The endoplasmatic reticulum is a three-dimensional intracytoplasmatic system of membranes, which is found in various forms in every animal cell, except the ripe erythrocytes. The main functions are regulations of transportation and protein synthesis.

Historical data

The knowledge of structure and function is closely connected with the evolution of electron microscopy and with the names of PALADE and PORTER. The most important recognition was won in the years 1953–1960. In 1952/53, PALADE discovered in the electron-optical slide of chicken-embryo cultures a filigrane-like cytoplasmatic ground structure in the form of a «reticulum of filamentous or canalicular structures». The existence of this system was proved by PALADE and PORTER (1954). The membrane system is also called ergastoplasm, but the term «endoplasmatic reticulum» is more common though the membrane system is neither restricted to the «endoplasm» nor is found always in a reticular formation.

The membranes studded with granules (= «Palade granules» = ribosomes) correspond to the basophile regions of the cell; GARNIER (1899) called «ergastoplasm» these regions occurring on secreting glands. The formal distinction of the form studded with ribosomes from the «smooth» form (= smooth-walled membranes) termed «sarcoplasmatic reticulum», «sarcotubular system» or «annulatae lamellae» is probably not justified as here morphological variants of the same principle, dependent on the functional condition, are in question.

Morphology

The endoplasmatic reticulum is a system of membranes originating from the outer nuclear membrane and communicating through nucleopores with the perinuclear space. The framework is constituted by cytomembranes, which, as «unit membranes», are 60–70 Å thick. The inside diameter of these membranes imposing as tubes, varies from 50–300 mμ as long as they run parallel but grows wider in the secreting stage of the synthe sis products to form «little bags» or «cisterns» with larger diameters of round, oval or garland-like shape.

The membranes are «windowed» in the form of rounded or oval openings (fig. 27) probably intended to facilitate changes of space and form. The interior

of the endoplasmatic reticulum communicates with the nucleus direct: the outer layer of the nuclear membrane blends into the first lamellae of the membranes of the ergastoplasm. The outer space communicates through the nucleopores direct with the interior of the nucleus and is separated form it only by a «diaphragm» with a central ball of threads.

The outer surface of the lamellae o ergastoplasm is more or less studdec with ribosomes: consequently, there is a rough-walled granular form (PALADE 1955) and a smooth-walled form lacking these granules. Ribosomes can gather in groups and are then called polysomes or polyribosomes (see fig. 31–35).

Function

The formation and compactness of the endoplasmatic reticulum indicate the functional condition. The more intense the rate of protein synthesis, the compacter the ergastoplasm. Compact formations can be found in protein-secreting glands, the «Nissl's bodies» of the neurons correspond to formations of ergastoplasm thickly studded with ribosomes and with free ribosomes. Cells of fatty tissue contain sometimes membranes arranged in concentric layers with granules 250 Å large « phospholipid bodies» (MÖLBERT, 1968). The intensity of these basophilous consolidations has created the term « accessory nucleus».

The changes of form and functions of the ergastoplasm can be observed best when the monocytes turn into immunocytes (plasma cells). A stimulation with antigens provokes first in the perinuclear space a «basophilous» consolidation, which spreads centrifugally in the ripening stage of the immunocytes till the entire cytoplasmatic space is deeply basophilous. These optico-microscopic changes have their electron-microscopic equivalent in a growing compactness of the tubes of ergastoplasm and of the coat of ribosomes. The multiplying structures of ergastoplasm increase the space of cytoplasm, change the relation between the nucleus and cytoplasm at the expense of the nucleus, the nucleus is forced toward the periphery. When the stage of synthesis of the immunocytes changes into the secretory phase, first the spaces between the lamellae extend, the parallel formation of the lamellae is lost, cistern-like extensions to receive the products of synthesis (immunoglobulins) arise. Cytochemical analyses have proved that besides the main function of synthesis and secretion of proteins also the by-products of the metabolic processes are extruded through these systems. After excreting the synthetised proteins, the immunocytes grow poor in lamellae of ergastoplasm and appear dispersed like vacuoles in the optic microscope (fig. 173–192).

Endoplasmatic reticulum without ribosomes is found in the striated muscles (FAWCETT, 1965) and in steroid-producing cells, tubular systems in the striated muscles and myocardium of mammals and in insects (MÖLBERT).

The interior of the endoplasmatic reticulum is, for the most part, homogeneous and less electron-tight than the environment. Homogeneous compact particles up to 350 mμ in diameter were found in the endoplasmatic reticulum of osteoblasts (ZELANDER, 1959), chondroblasts (PALADE, 1956), exocrine pancreatic cells.

The speed of the metamorphoses de-

scribed above is considerable. DL-leucin tagged with 3H was identified electronmicroscopically in the autoradiogram already after 5 minutes in the ergastoplasm, after 20 minutes in the Golgifield and after 60 minutes in the zymogen granules (CARO and PALADE, 1964). This order is highly significant also in the synthesis of cartilage: 3H prolin – the most important element of the profibrils of tropocollagen – was found first in the endoplasmatic reticulum, then in the Golgifield, later in the extracellular fibrils (REVEL and HAY, 1963).

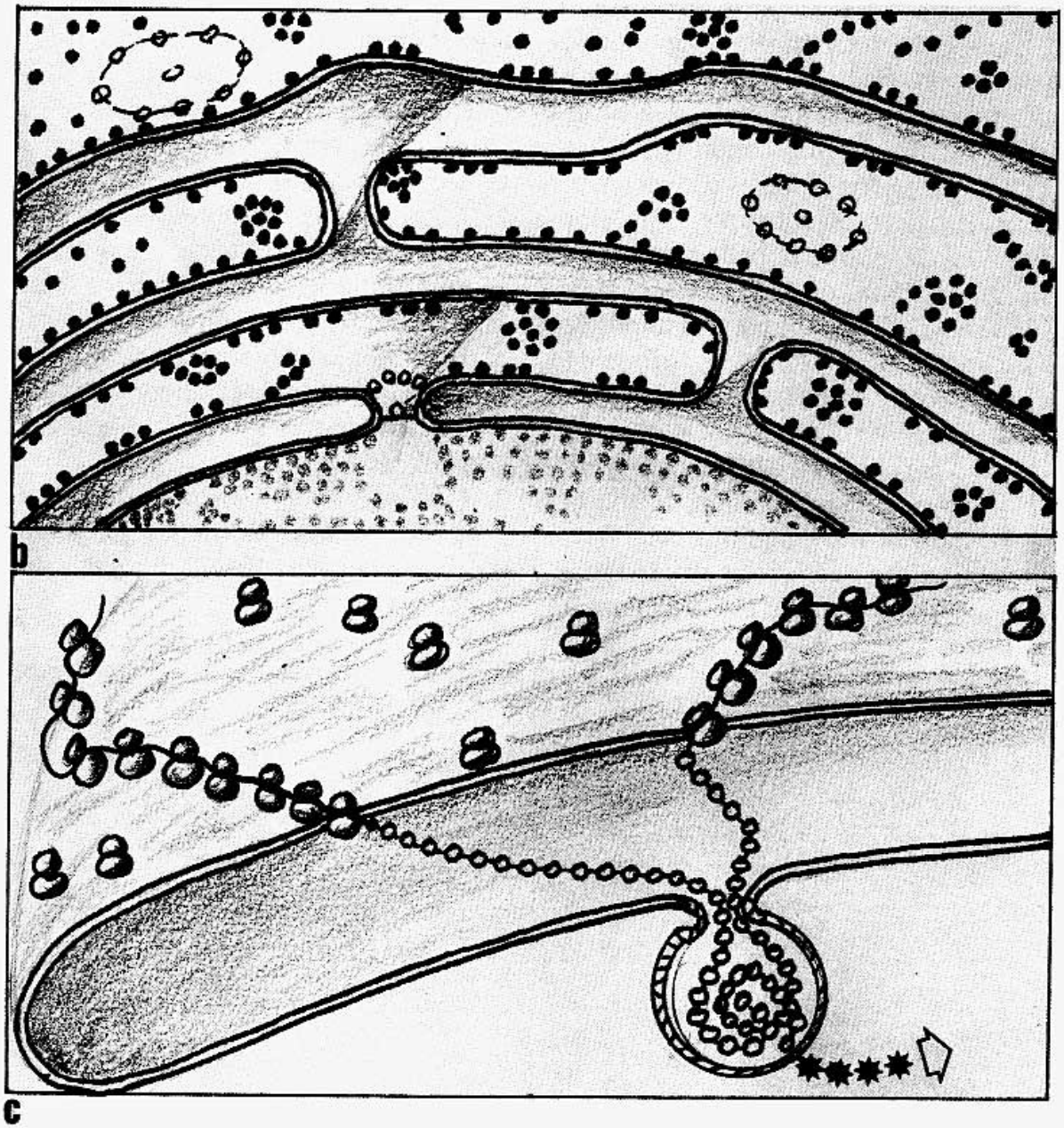

Fig. 27:
Endoplasmatic reticulum in various magnifications.
b) lamellae of ergastoplasm (from an electron-optical picture); membranes of the endoplasmatic reticulum studded with ribosomes and polysomes; below: cut nucleus with nucleopore; c) three-dimensional scheme of an ergastoplasmic lamella studded with polysomes, m-RNA cords between the ribosomes; protein synthesis (chains) and its secretion via cisterns (arrow).

The synthetic activity of the cell is characterized by the enlargement and consolidation of the endoplasmatic reticulum. Phases of secretion are distinguished by a dispersion in the form of extensions of the interlamellar spaces and the formation of cistern-like spaces. The lamellae of ergastoplasm disappear when the protein synthesis is terminated or prevented. A decrease to complete depletion was seen in starving animals (BERNHARD et al., 1952). But remainders of ergastoplasm can be traced even under extreme starving conditions (FAWCETT, 1955). The changes are reversible after supplies of substrate. The ribosomes settle on the lamellae first in the neighbourhood of the nuclear membrane and cell membrane. An important function in the activation is attributed to the nucleolus. Hypoxy causes a vacuolation in the liver-cells (MÖLBERT). This mechanism is ascribed to the pathogenesis of myocardial infarction, to the degeneration of the ganglious cells in asphyxia, to the necrosis of striated muscles in ischemia and to the degeneration of tubular epithelium in the case of engorged kidney. The strongest vacuolar degenerations are observed in poisonings (hydrocyanic acid, malonic acid, carbon tetrachloride), similar degenerative processes occur in phosphorous poisonings, overdoses of strophantin and L-tri-iodine-thyroxin.

Besides vacuolation, the following phenomena are regarded as degeneration of the endoplasmatic reticulum:

1. Consolidations into myelin figures – epinuclear formation (e.g. in cirrhosis of the liver, after administration of actinomycin-D).
2. Autophagous vacuoles (LANE and NOVIKOFF, 1965), observed after administrations of thiohydantoin, thioacedamide, aethionin, actinomycin D, aflatoxin B1, carbon tetrachloride, after intense UV-radiation and X-ray therapy, in cases of alcoholism and viral hepatitis.
3. Occurrence of lysosomes and cytosomes; this phenomenon is closely connected with the mitotic activity of the organs.

Fig. 28:
Incipient formation of the endoplasmatic reticulum in a maturing immunocyte of the peritoneal exudate in the upper part of the picture. Magn. 1:20,000.

Fig. 29:
Extension of the interlamellar spaces of the endoplasmatic reticulum of an immunocyte in the stage of secretion; secretion of the synthesis products (immunoglobulins) into cistern-like bulges of the interlamellar spaces by pressure filtration. Magn. 1:20,000.