The Golgi-apparatus

Historical data

In 1898, GOLGI described an «Apparato reticulare interno» in nerve-cells, which was discovered also in other cells of the body in the following years. Lamellary, filamentous structures, granules and vesicles were ascribed to this creation named after him «Golgi-apparatus» (PAPPENHEIMER, 1916). Owing to the variability of the structures depending on the kind of cells and functions, this system as an independent cellular organelle was controversial for decades. PARAT (1928) referred to the netlike structure, represented by impregnation with silver and osmium, as an artifact. HIRSCH (1939) was the first to state that the form depended on the function and mentioned the connection with secretions (pancreas, intestine, salivary glands). In spite of the better morphological differentiation by electron-microscopy opened by DALTON (1952–1956), SIÖSTRAND and HANZON (1954), many controversial interpretations were given later on. However, the independence of this system as cell organelle with synthetic and transporting functions is no longer doubted.

Morphology

The Golgi-apparatus occurs, with few exceptions (erythrocytes, keratinized epidermic cells), in all cells of the vertebrates, and is most conspicuous in se-

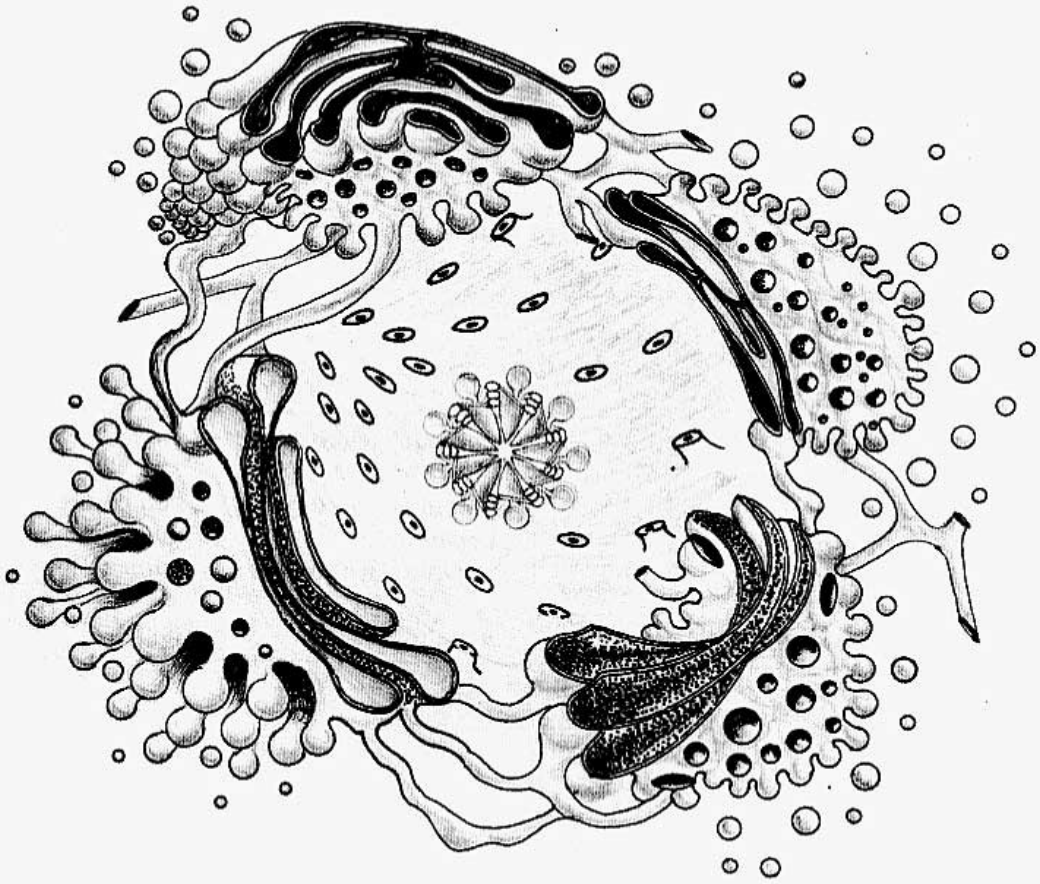

Fig. 15:
Three-dimensional representation of the *Golgi-apparatus* in its structural elements (lamellae and vesiculae) and interrelations to the nucleus and endoplasmatic reticulum.

creting cells i. e. in those which make and eliminate products of synthesis. The Golgi-apparatus, therefore, can be recognized well in cells of the pituitary gland, the Langerhans' islets, the tubular epithelium of the kidneys, the fundic glands of the stomach, adrenal-cortex cells and marrow cells, the neurons of the ganglious cells, the thalamus, the chemoreceptors of Glomus caroticus, the cerebral cortex (MÖLBERT). Several Golgifields connected with each other are found specially in the cells of the thalamus. Less developed are Golgi-apparatuses in skeleton muscles, myocardium, lung, epidermis.

Observations of ovocytes and spermatocytes, moreover of cells of the oral mucosa have shown how much the morphological formation depends on the functional condition. In the stage of activation e. g. in the stages of incubation and exanthema of viral infectious diseases, the system can clearly be recognized by tubes and granules through cytochemical staining even in the light microscope (fig. 16) whereas these structures cannot be seen in cells at rest and with little metabolic activity.

The Golgi-apparatus consists of the following structural elements: double lamellae called sacculi (fig. 15, 18) for their bilateral club-shaped inflations; cistern-like, rounded, oval or irregular

extensions (fig. 18) called vacuoles as they are «optically empty» but actually constitute spaces surrounded by membranes containing fluids and products of synthesis. Further, there are smaller or larger vesicles and granules (fig. 15, 16, 17). As the synthetic functions require high amounts of energy (in our examples synthesis of immunoglobulin) the Golgifield is interspersed with plenty of mitochondria and related intimately to the endoplasmatic reticulum (fig. 18). The orientation round the nucleus is rather conspicuous; if the latter, however, becomes peripherical when a compact, endoplasmatic reticulum is built up (e.g. in immunocytes, plasma cells), the probably more important orientation toward the centrosome (fig. 20) becomes visible (fig. 191).

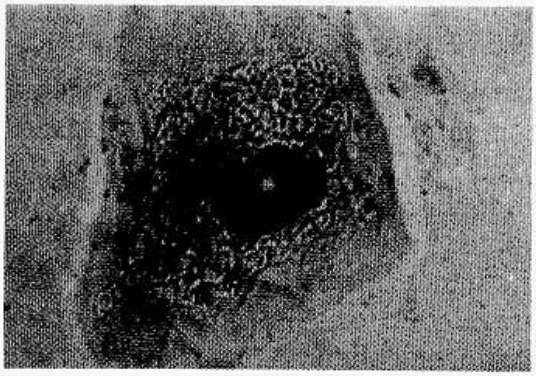

Fig. 16:
Cell of the pharyngeal epithelium in the stage of the measles exanthema, first day. Paranuclear consolidation, surrounded by a close-meshed network of tubes. Best-carmin coloration 1:1500.

Fig. 17:
Lamellär structures of the Golgi-apparatus (G) in a monocyte-peritoneal exudate guinea-pig, 1:20,000. N = nucleus.

are 3–4 (up to 8) smooth double lamellae, which, layered roughly parallel, show a concave and a convex side (fig. 1, 18); these are cytochemically different (KRSTIĆ, 1976). The membranes have a diameter of cytomembranes – 60–80 Å –, the interval of a couple of membranes comes to 50–200 Å (POLLISTER and POLLISTER, 1957); intervals of about 200 Å are more frequent than minor figures. The membrane layers constitute the chromophile part of the Golgi system. The smooth membranes have often terminal club-shaped inflations, which gives the impression of dumbbell-like, parallel layered structures (fig. 15, 17). The membranes are interspersed with pores through which they communicate with the ground substance (fig. 15). The double membranes of the endoplasmatic reticulum (fig. 18) are guided by a flow of the double lamellae; the smooth elements near the Golgifield are referred to as Golgi-bound endoplasmatic reticulum. A connection of the Golgi-apparatus with the nuclear pores (indicated in fig. 15) is probable.

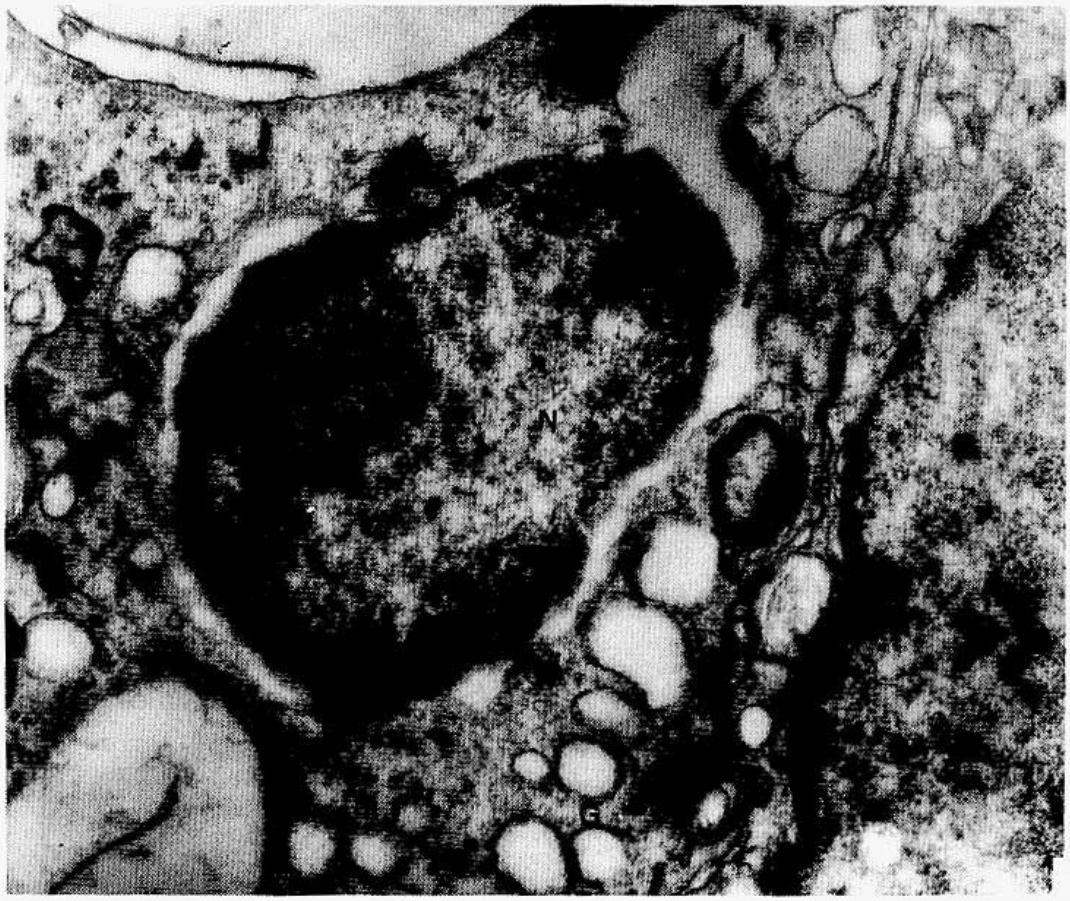

Fig. 18:
Golgi-apparatus (G) with large *vesicles* and *cisterns* in the secretory stage of an immunocyte (plasma cell), 1:18,000.

Vesiculae

arise by tying off bulges of membranes after club-shaped or dumb-bell-like extensions of the inner layers (LACY, 1956). POLICARD (1958) demonstrated on human leukocytes that the vesicles and granules split from the chromophobous part of the pairs of membranes so that they are on the convex side turned from the centrosome as shown in the three-dimensional representation of fig. 15; he therefore spoke of a polarity of the Golgifield determined by the centriole. The vesicles serve for the secretion of the products of synthesis as well as for their further chemical processing and their transportation through the cytoplasm. The so-called vacuoles are also constituents of this system of ecological spaces in the Golgi-apparatus dependent on the functional circumstances, filled with fluids and surrounded by membranes, somewhat more irregular as to their shape (fig. 18). There are various sizes from these cisterns and vesicles to the granules.

Granules

are found specially in secreting cells (fig. 15, 17). In particular, melanin granules were used to explain the interrelations.

Function

The functional interrelations result from the close relationship between the Golgi-apparatus, the endoplasmatic reticulum and mitochondria. The substances built up in the endoplasmatic reticulum are subject to final processing in the Golgi system before they are transported through the cytoplasm and excretion (secretion, clasmatosis). The products of synthesis «ripened» in the Golgi-membranes are tied off and eliminated through vesicles and granules. A condensation may take place in these ecological substructures surrounded by membranes; but its main function is probably the controlled transportation through the cell. The reduction of the endoplasmatic reticulum in the «starving condition» of the cell is followed by an inhibition of the protein synthesis, a gradual shrinking of the Golgi-membranes while the Golgi-products decrease (MÖLBERT).

Taggings with DL-leucin-4.5-3 H (CARO and PALADE, 1964) have shown that the contents of cisterns in the endoplasmatic reticulum are tagged already 5 minutes after the injection, and that the Golgifields are tagged after 20 minutes and the zymogen granules show compact concentrations after 1 hour. Zymogen granules, consequently, seem to originate by flowing together and condensating vesicles and cisterns of the Golgi-apparatus. The condensated cisterns, vesicles and granules migrate centrifugally out of the Golgifield.

This principle has been demonstrated in cells of the milk-secreting mamma (BARGMANN and KNOOP, 1959), chondrocytes (SHELDON and KIMBALL, 1962), the Langerhans' islets, follicular cells of the thyroid gland, active cells of the parathyroid gland, hypophysis, neurons and many other secreting cells (survey see MÖLBERT, 1968). The processes were worked out most impressively by the collagenous synthesis (REVEL and HAY,

1963). By means of collagenous prophases tagged with radio-elements it has been demonstrated that after the protein synthesis in the ergastoplasm the material is transported to the Golgi-apparatus via separate vesicles. The concentrated protein tagged with 3H-prolin can be identified as fine fibrils in Golgi-cisterns of 0.2–0.5 mi, migrates with the vesicles out of the Golgifield and is found later in the extracellular space as material tagged with radio-elements.

Apart from structural functions, the Golgi-apparatus effects a number of key-processes of the intermediary metabolism: the synthesis of the carbohydrates, specially the glycogen; formation of triglycerides; formation of myelin; formation of pigments. The following enzymes have been identified: alkaline phosphatase in epithelial cells of the small intestine and tubular cells; nucleoside-diphosphatase in duodenal cells; acid phosphatases in tubular epithelia and liver cells as well as thyroid cells activated with thyreotropin.

The Golgi-apparatus is extended as a result of great synthetic and secretory activity of the cells, after application of diamox (2-acetyl-amine-1.3.4-thiadiazol-5-sulphonamide), after doses of oestrogen at the epithelium of the uterus of mice, after stimulation with phytohaemagglutinine in lymphocytes. Intensified transportation of fluids receives expression in an increase of large cisterns (MÖLBERT, 1968).

Atrophies or degeneration of Golgi-fields are found in many tumour cells, especially in carcinoma of the bladder (OBERLING, 1959).

The origin of the Golgi membranes has not been explained. Divergent findings indicate causalities with the centrioles, the nuclear membrane and the endoplasmatic reticulum.