Contents

CHAPTER

7

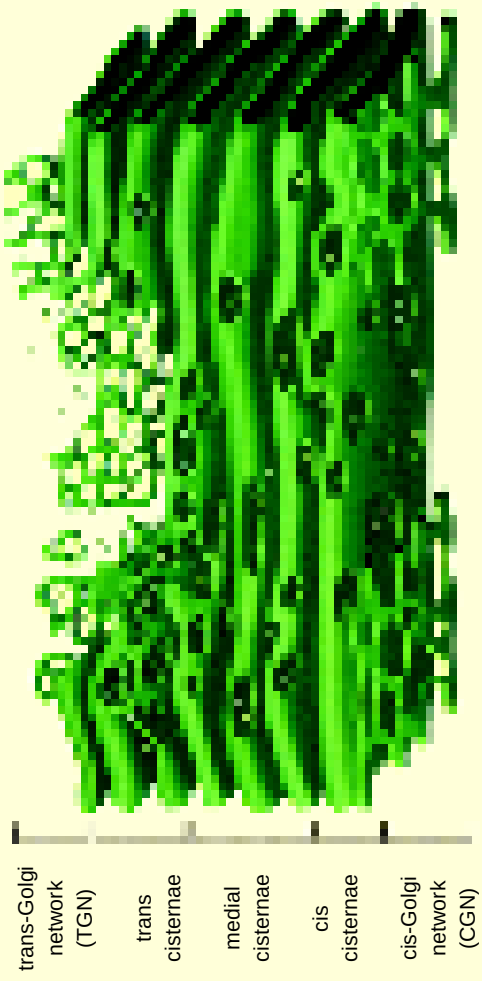
Golgi Apparatus

For the performance of certain important cellular functions such as biosynthesis of polysaccharides, packaging (compartmentalizing) of cellular synthetic products (proteins), production of exocytotic (secretory) vesicles and differentiation of cellular membranes, there occurs a complex organelle called **Golgi** complex or **Golgi** apparatus in the cytoplasm of animal and plant cells. The Golgi apparatus, like the endoplasmic reticulum, is a canalicular system with sacs, but unlike the endoplasmic reticulum it has parallely arranged, flattened, membrane-bounded vesicles which lack ribosomes and stainable by osmium tetraoxide and silver salts.

HISTORICAL

An Italian neurologist (*i.e.*, physician) **Camillo Golgi** in 1873 discovered and developed the **silver chromate method** (termed *la reazione nera*) for studying histological details of nerve cells. He, thus, opened a new field of scientific inquiry, called **neuromorphology**. In 1898, Golgi found that Purkinje cells (*i.e.*, nerve cells of cerebral cortex of brain) of barn owl contained an internal reticular network which stains black with the silver stain. He called this structure *apparato reticolare interno* (= internal reticular apparatus). By reporting the existence of such an organelle inside cell, he inadvertently raised a storm of controversy in the scientific world, which is commonly known as the Golgi controversy.

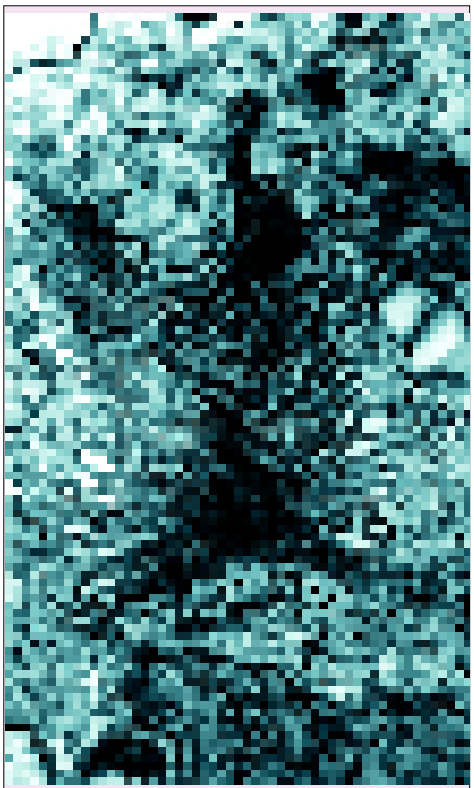
Camillo Golgi
(1844 - 1926)



Schematic model of a portion of a Golgi complex from an epithelial cell

The Golgi controversy. Since the refractive index of the Golgi apparatus is similar to that of cytosol (cytoplasmic matrix), the Golgi apparatus in the living cell was difficult to observe with the light microscopy, and this led to many controversies regarding its true nature. For years, it was thought to be an artifact of various fixation and staining procedures. In other words, many scientists believed that structure observed during numerous microscopy procedures and termed the Golgi, did not actually exist in the living cells (see **Berns**, 1983). For instance, **Holmgren** (1900) described a clear system of clear canals, which he called **trophospongium**. Though this structure was earlier described as being homologous with internal reticular apparatus, this comparison was later dropped. **Parat** and **Painleve** (1924) suggested **vacuome theory** : they believed that all plant and animal cells have only two fundamental but morphologically independent cytoplasmic components, *i.e.*, **vacuome** (watery vacuoles) or canals stainable with neutral red, and the **chodriome**, consisting of lipoidal mitochondria. They mixed up with Golgi apparatus and Holmgren's canalicular system and thought these were formed by the deposition of metallic silver or osmium on the vacuoles (see **Purohit**, 1980). **S.R. Cajal**, a contemporary of Golgi and Spanish histologist, was a solid supporter of Golgi during the years of controversy. Cajal referred to Golgi nets as the **Golgi-Holmgren canals**. He refined the Golgi's method of staining and became a pioneer student of the nervous system. Cajal verified Golgi's finding of a special internal cell complex and observed its morphology and behaviour under a variety of metabolic states. In the year 1906, **Camillo Golgi** and **S. R. Cajal** were jointly awarded the Nobel Prize. **Nath** (1930) using fresh eggs of the frog and later on, **Nath** and **Nangia** (1931) using telostean fish eggs, demonstrated that the vacuome and the Golgi apparatus were independent cytoplasmic organelles as were the mitochondria. Thus, not until electron microscopic studies were performed in the 1950's was the Golgi recognized and accepted as a legitimate cell organelle.

Due to their presumed high lipid contents, Golgi apparatuses were called **lipochondria (Baker**, 1951, 1953). Since originally these were known to be networks, they were also called "**dictyosomes**" (Gr., *dictyes*=net). Currently, the term **Golgi apparatus** is more prevalent one, than many other names such as **Golgi complex**, **Golgiosome**, **Golgi bodies**, **Golgi material**, **Golgi membrane**, etc. The Golgi apparatus of the cells of plants and lower invertebrates is usually referred to as **Golgi body** or **dictyosome**.



The various functions of the Golgi complex are summarised in this diagram.

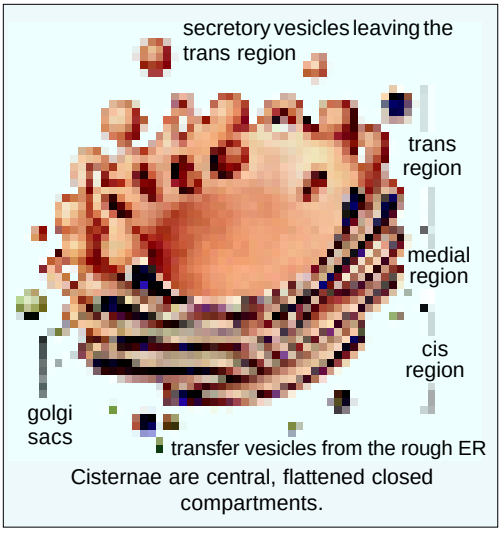
OCCURRENCE

The Golgi apparatus occurs in all cells except the prokaryotic cells (*viz.*, mycoplasmas, bacteria and blue green algae) and eukaryotic cells of certain fungi, sperm cells of bryophytes and pteridiophytes, cells of mature sieve tubes of plants and mature sperm and red blood cells of animals. Their number per plant cell can vary from several hundred as in tissues of corn root and algal rhizoids (*i.e.*, more than 25,000 in algal rhizoids, **Sievers**, 1965), to a single organelle in some algae. Certain algal cells such as *Pinularia* and *Microsterias*, contain largest and most complicated Golgi apparatuses. In higher plants, Golgi apparatuses are particularly common in secretory cells and in young rapidly growing cells.

In animal cells, there usually occurs a single Golgi apparatus, however, its number may vary from animal to animal and from cell to cell. Thus, *Paramoeba*

species has two Golgi apparatuses and nerve cells, liver cells and chordate oocytes have multiple Golgi apparatuses, there being about 50 of them in the liver cells.

DISTRIBUTION



In the cells of higher plants, the Golgi bodies or dictyosomes are usually found scattered throughout the cytoplasm and their distribution does not seem to be ordered or localized in any particular manner (**Hall** *et al.*, 1974). However, in animal cells the Golgi apparatus is a localized organelle. For example, in the cells of ectodermal or endodermal origin, the Golgi apparatus remains polar and occurs in between the nucleus and the periphery (*e.g.*, thyroid cells, exocrine pancreatic cells and mucus-producing goblet cells of intestinal epithelium) and in the nerve cells it occupies a circum-nuclear position.

MORPHOLOGY

The Golgi apparatus is morphologically very similar in both plant and animal cells. However, it is extremely **pleomorphic** : in some cell types it appears compact and limited, in others spread out and reticular (net-like). Its shape and form may vary depending on cell type. Typically, however, Golgi apparatus appears as a complex array of interconnecting *tubules*, *vesicles* and *cisternae*. There has been much debate concerning the terminology of the Golgi's parts. The classification given by **D.J. Morre** (1977) is most widely used. In this scheme, the simplest unit of the Golgi apparatus is the **cisterna**. This is a membrane-bound space in which various materials and secretions may accumulate. Numerous cisternae are associated with each other and appear in a stack-like (lamellar) aggregation. A group of these cisternae is called the **dictyosome**, and a group of dictyosomes makes up the cell's Golgi apparatus. All dictyosomes of a cell have a common function (see **Berns**, 1983).

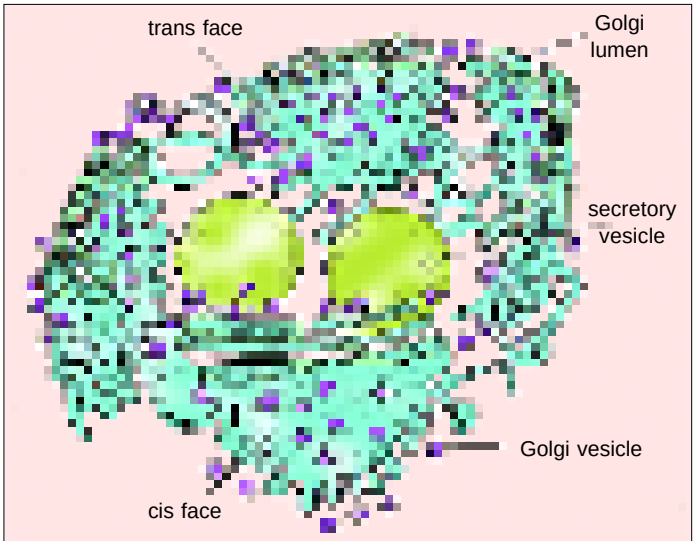


Fig. 7.1. Three-dimensional drawing of a Golgi apparatus ; it is drawn from electron micrographs of a secretory animal cell (after Alberts *et al.*, 1989).

The detailed structure of three basic components of the Golgi apparatus can be studied as follows (Fig.7.1) :

1. Flattened Sac or Cisternae

Cisternae (about 1 µm in diameter) are central, flattened, plate-like or saucer-like closed compartments which are held in parallel bundles or stacks one above the other. In each stack, cisternae are separated by a space of 20 to 30 nm which may contain rod-like elements or fibres. Each stack of

cisternae forms a dictyosome which may contain 5 to 6 Golgi cisternae in animal cells or 20 or more cisternae in plant cells. Each cisterna is bounded by a smooth unit membrane (7.5 nm thick), having a lumen varying in width from about 500 to 1000 nm (see **Sheeler** and **Bianchi**, 1987).

Polarity. The margins of each cisterna are gently curved so that the entire dictyosome of Golgi apparatus takes on a bow-like appearance. The cisternae at the convex end of the dictyosome comprise **proximal, forming** or **cis-face** and the cisternae at the concave end of the dictyosome comprise the **distal, maturing** or **trans-face.** The forming or cis face of Golgi is located next to either the nucleus or a specialized portion of rough ER that lacks bound ribosomes and is called **"transitional" ER**. Trans face of Golgi is located near the plasma membrane. This polarization is called **cis-trans axis** of the Golgi apparatus.

2. Tubules

A complex array of associated **vesicles** and anastomosing **tubules** (30 to 50 nm diameter) surround the dictyosome and radiate from it. In fact, the peripheral area of dictyosome is fenestrated (lace-like) in structure.

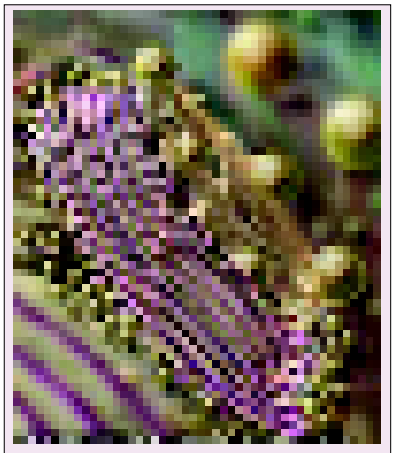
3. Vesicles

The vesicles (60 nm in diameter) are of three types :

(i) Transitional vesicles are small membrane limited vesicles which are thought to form as blebs from the transitional ER to migrate and converge to cis face of Golgi, where they coalasce to form new cisternae.

(ii) Secretory vesicles are varied-sized membrane-limited vesicles which discharge from margins of cisternae of Golgi. They, often, occur between the maturing face of Golgi and the plasma membrane.

(iii) Clathrin-coated vesicles are spherical protuberances, about 50 μm in diameter and with a rough surface. They are found at the periphery of the organelle, usually at the ends of single tubules, and are morphologically quite distinct from the secretory vesicles. The clathrin-coated vesicles are known to play a role in intra-cellular traffic of membranes and of secretory products, *i.e.*, between ER and Golgi, as well as, between GELR region and the endosomal and lysosomal compartments.



Secetory vesicles leaving the trans region.

The GERL Region

Golgi apparatus is a differentiated portion of the endomembrane system found in both animal and plant cells. This membranous component is spatially and temporally related to the endoplasmic reticulum (ER) on one side and by way of secretory vesicles, may fuse with specific portions of the plasma membrane. To the trans face of Golgi is associated the **trans-reticular Golgi**, **TGN** (=trans-Golgi-network ; **Alberts** *et al.*, 1989) or **GERL** (=Golgi + smooth ER + lysosomal), in which acid phosphatase enzyme (a characteristic lysosomal enzyme) makes its first appearance. GERL is found to be involved in the origin of **primary lysosomes** and of **melanin granules** ; in the processing, condensing and packaging of secretory material in endocrine and exocrine cells; and in lipid metabolism (**Novikoff**, 1976). GERL is also a region of sorting of cellular secretory proteins.

Zones of Exclusion

A Golgi body or Golgi apparatus is surrounded by a differentiated region of cytoplasm where ribosomes, glycogen, and organelles such as mitochondria and chloroplasts are scarce or absent. This is called **zone of exclusion** (**Morre** *et al.*, 1971) or **Golgi ground substance** (**Sjostrand** and **Hanzon**, 1954). Endoplasmic reticulum within the zone of exclusion has a smooth surface (lacking ribosomes),

and coated vesicles of the Golgi apparatus are restricted to this region. Similar zones of exclusion are associated with microtubules (**Porter**, 1966), centrioles (**Bainton** and **Farquhar**, 1966), and regions of centriole formation (**Sorokin**, 1968).

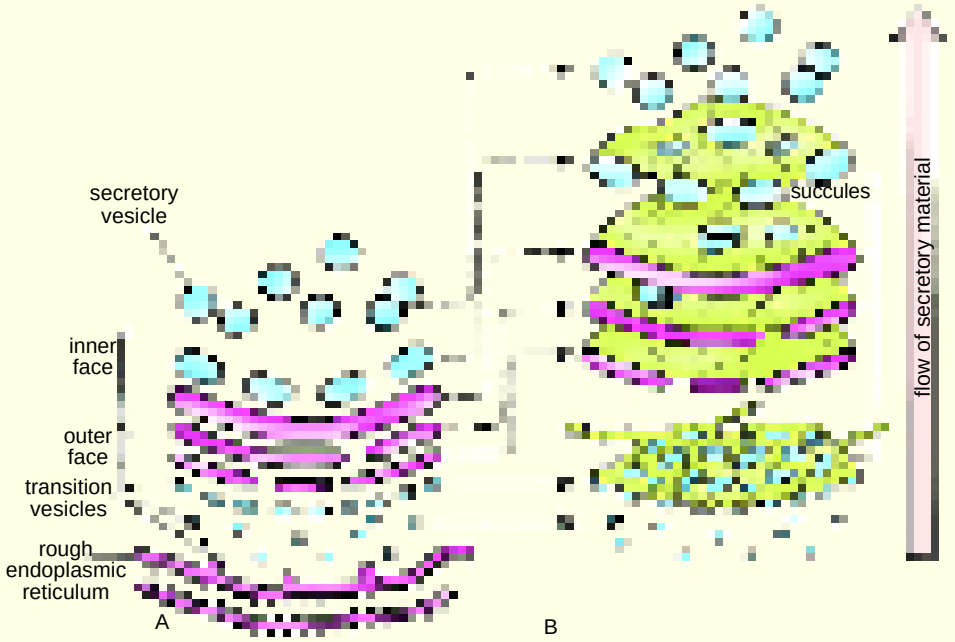


Fig. 7.2. The position and orientation of the Golgi apparatus in the secretory pathway. A—The components as they might be seen by electron microscopy of thin sections ; B—A three-dimensional reconstruction of Golgi apparatus (after Thorpe, 1984).

ISOLATION AND CHEMICAL COMPOSITION

Initially, Golgi apparatus was isolated only from cells of the epididymis, however, in recent years, it has been isolated from number of plant and animal cells. The isolation of Golgi apparatus is brought about mainly by gentle homogenization followed by differential and gradient homogenization. Gentle homogenization is preferred to preserve the stacks of cisternae. Due to its low density, Golgi apparatuses tend to form a distinct band in gradient centrifugation. The isolated Golgi apparatus is washed with distilled water for purifying it, though, its secretory components are lost (see **Thorpe**, 1984).

Chemically, Golgi apparatus of rat liver contains about 60 per cent lipid material. The Golgi apparatus of animal cells contains phospholipids in the form of **phosphatidyl choline**, whereas, that of plant cells contains **phosphatidic acid** and **phosphatidyl glycerol**. The Golgi apparatus also contains a variety of enzyme (Table 7-1), some of which have been used as cytochemical markers.

Cytochemical Properties of Golgi Apparatus

Different parts of Golgi apparatus have been histochemically identified by specific staining properties (**Thorpe**,1984 ; **Alberts** *et al.*, 1989) :

1. Osmium tetroxide (O_sO_4) selectively impregnates the outer face (cis face) of the Golgi apparatus. This stain adheres well to lipids, especially phospholipids and unsaturated fats.

2. Phosphotungstic acid ($H_3PO_4.12\,WO_3.24\,H_2O$) selectively stain the maturing or trans face of Golgi stack. This stain is an anionic stain having special affinity for polysaccharides and proteins.

3. Glycosyl transferase and **thiamine pyrophosphatase** can be localized cytochemically in

the trans cisternae of Golgi apparatus. Transferase enzymes are found to be located in the membranes of Golgi, not in the lumen of cisternae (**Thorpe**, 1984).

4. Acid phosphatase enzyme is cytochemically marked in the GERL region.

Table 7.1. **Some important enzymes of the Golgi apparatus of animal cells (Source: Thorpe, 1984; Rastogi, 1988).**

Enzymes : class and types	Function
A. Glycosyl transferases : Glycoprotein biosynthesis	
1. Sialyl transferases	Transfers sialic acid from CMP-sialic acid
2. Galactosyl transferases	Transfer galactose to lipids or proteins
B. Sulpho-and glycotransferases : Glycolipid biosynthesis	
3. Sulphotransferase	Transfer of sulphate from activated donor
4. Lysolecithin acetyltransferase	Transfer of acyl groups to phospholipid
5. Glycero-phosphate phosphatidyl transferase	Transfer of phosphatidyl group
C. Oxireductases : Oxidation and reduction	
6. NADH- cytochrome c-reductase	Removal or addition of hydrogen
7. NADPH- cytochrome c-reductase	Removal or addition of hydrogen
D. Phosphatases : Hydrolysis of phospholipids	
8. Glucose-6-phosphatase	Removal of phosphate
9. Thiamine pyrophosphatase (Nucleoside diphosphatase)	Hydrolysis of inorganic pyrophosphate
10. ATPase	Removal or addition of phosphate
11. Acid phosphatase	Removal of phosphate
E. Phospholipases : Hydrolysis of lipids	
12. Phospholipase A_1	Removal of non-specific fatty acid chains from phospholipids
13. Phospholipase A_2	Removal of fatty acid chains
F. Kinases : Phosphorylation	
14. Casein phosphokinases	Phosphorylation of casein
G. Mannosidases : Removal of mannose	
15. Mannosidase I and II	Removal of mannose residue from oligosaccharide

ORIGIN

Origin of Golgi apparatus involves the formation of new cisternae and there is great variation in shape, number and size of cisternae in each stack (dictyosome). The process of formation of new cisternae may be performed by any of the following methods: 1.Individual stacks of cisternae may arise from the pre-existing stacks by division or fragmentation. 2.The alternative method of origin of Golgi is based on *de novo* formation. In fact, various cytological and biochemical evidences have established that the membranes of the Golgi apparatus are originated from the membranes of the smooth ER which in turn have originated from the rough ER. The proximal Golgi saccules are formed by fusion of ER-derived vesicles, while distal saccules "give their all" to vesicle formation and disappear. Thus, Golgi saccules are constantly and rapidly renewed.

The cells of dormant seeds of higher plants generally lack Golgi apparatuses but they do display zone of exclusion having aggregation of small transition vesicles. Photomicrographs of cells in early stages of germination suggest progressive development of Golgi bodies in these zones of exclusion; and the development of Golgi apparatuses coincides with the disappearance of the aggregation of vesicles (see **Sheeler** and **Bianchi**, 1987).

FUNCTIONS

Golgi vesicles are often, referred to as the "**traffic police**" of the cell (**Darnell** *et al*., 1986). They play a key role in **sorting** many of cell's proteins and membrane constituents, and in **directing** them

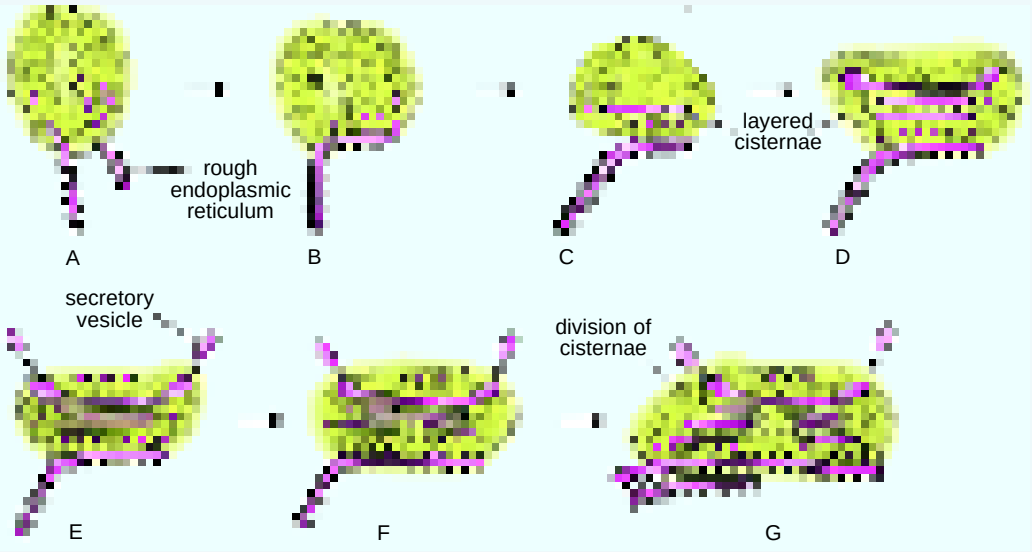


Fig. 7.3. A model of formation of Golgi apparatus from endoplasmic reticulum (A—C) and subsequent developmental stages : formation of stack of cisternae (C and D), formation of secretory vesicles (E) division (F,G) (after Sheeler and Bianchi, 1987).

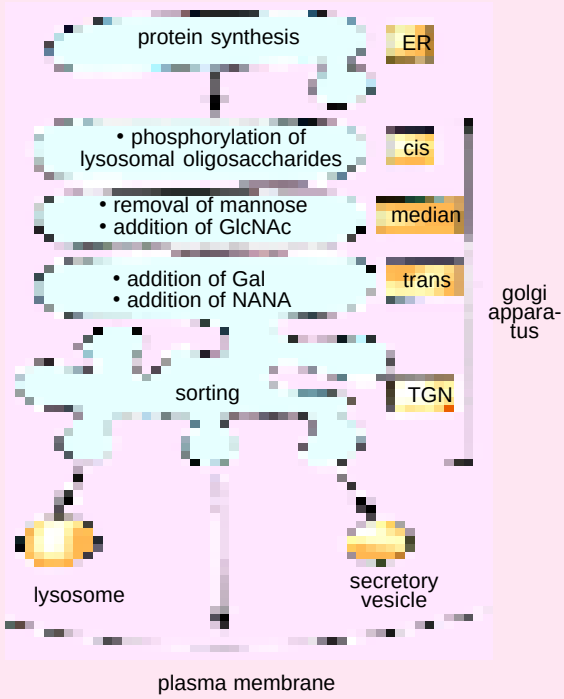
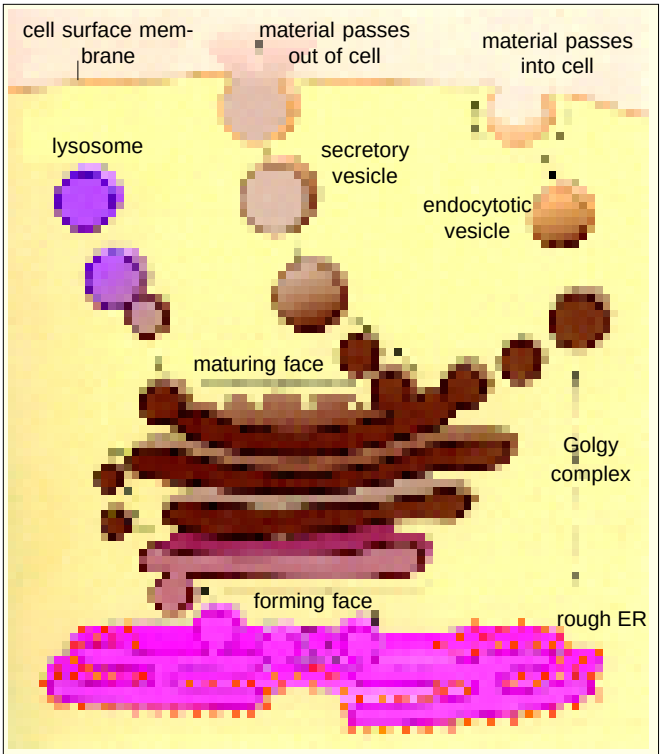


Fig. 7.4. The compartmentalization of the Golgi apparatus. GlcNAc = N-actyl-glucosamine galactose; NANA = N-acetyl neuraminic acid (sialic acid) (after Alberts *et al.*, 1989).

to their proper destinations. To perform this function, the Golgi vesicles contain different sets of enzymes in different types of vesicles—**cis, middle** and **trans cisternae**—that react with and modify secretory proteins passing through the Golgi lumen or membrane proteins and glycoproteins that are transiently in the Golgi membranes as they are *en route* to their final destinations (Fig.7.4). For example, a Golgi enzyme may add a "signal" or "tag" such as a carbohydrate or phosphate residues to certain proteins to direct them to their proper sites in the cell. Or, a proteolytic Golgi enzyme may cut a secretory or membrane protein into two or more specific segments (*e.g.*, molecular processing involved in the formation of pancreatic hormone insulin : preproinsulin→ proinsulin→ insulin).

Recently, in the function of Golgi apparatus, subcompartmentalization with a division of labour has been proposed between the *cis* region (in which proteins of RER are sorted and some of them are returned back possibly by coated vesicles), and the trans region in which the most refined proteins are further separated for their delivery to the various cell compartments (*e.g.*, plasma membrane, secretory granules and lysosomes)



The EM of the Golgi complex with a very large number of vesicles.

(Fig.7.5; **Rothman** 1981; **Rothman** and **Leonard**, 1984).

Thus, Golgi apparatus is a centre of *reception*, *finishing*, *packaging*, and *dispatch* for a variety of materials in animal and plant cells:

1. Golgi Functions in Plants

In plants, Golgi apparatus is mainly involved in the secretion of materials of primary and secondary cell walls (*e.g.*, formation and export of glycoproteins, lipids, pectins and monomers for hemicellulose, cellulose, lignin, etc.). During cytokinesis of mitosis or meiosis, the vesicles originating from the periphery of Golgi apparatus, coalesce in the phragmoplast area to form a semi-solid layer, called **cell plate**. The unit membrane of Golgi vesicles fuses during cell plate formation and becomes part of plasma membrane of daughter cells (For details see Chapter 5).

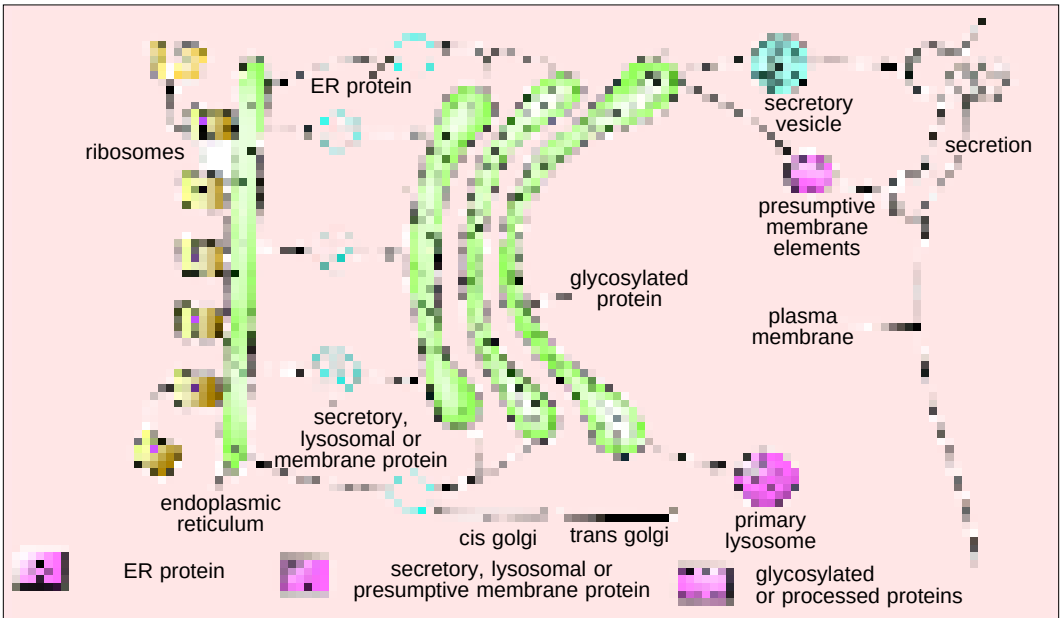


Fig. 7.5. Diagram illustrating the hypothetical dual function of cis and trans cisternae of the Golgi apparatus. The closed circles correspond to ER proteins that are removed from the rims of cis and middle Golgi cisternae ("refiners") and return to the ER (dashed arrow). The open circles represent secretory proteins which are destined for secretion or incorporation into organelles (lysosomes, plasma membrane) (after Sheelar and Bianchi, 1987).

2. Golgi Functions in Animals

In animals, Golgi apparatus is involved in the packaging and exocytosis of the following materials : 1. Zymogen of exocrine pancreatic cells; 2. Mucus (=a glycoprotein) secretion by goblet cells of intestine ; 3. Lactoprotein (casein) secretion by mammary gland cells (Merocrine secretion) ; 4. Secretion of compounds (thyroglobulins) of thyroxine hormone by thyroid cells; 5. Secretion of tropocollagen and collagen ; 6. Formation of melanin granules and other pigments; and 7. Formation of yolk and vitelline membrane of growing primary oocytes. It is also involved in the formation of certain cellular organelles such as plasma membrane, lysosomes, acrosome of spermatozoa and cortical granules of a variety of oocytes.

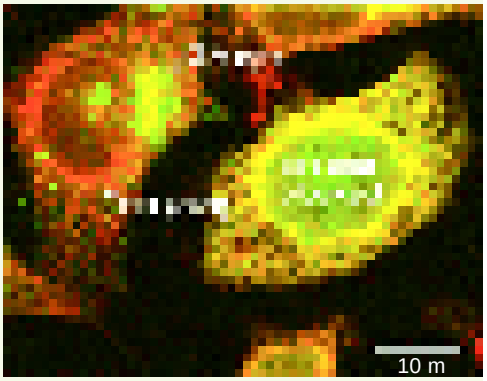
(a) Vesicular transport model (b) Cisternal maturation model (c) "Combined" model

Three models depicting the dynamics of transport through the Golgi complex. (a) In the vesicular transport model, cargo (dark dots) is carried in an anterograde direction by transport vesicles, while the cisternae themselves remain as stable elements. (b) In this model, the cisternae progress gradually from a *cis* to a *trans* position and then disperse at the TGN, (c) In this model, the cisternae progress from *cis* to *trans*, at the same time that cargo is carried forward at a more rapid pace in anterograde vesicles and Golgi resident enzymes are carried backward in retrograde vesicles.

REVISION QUESTIONS

1. Describe the Golgi apparatus. Which is the proximal and which is the distal face ? What types of vesicles arise from Golgi membranes ?
2. Write an essay on “Golgi apparatus and secretion”.
3. Describe various functions of Golgi apparatus in the cells.
4. There appears to be a regular turnover of Golgi membranes. According to the available evidence, where do the membranes come from, and what happens to them.
5. Write short notes on the following :

   (i) The Golgi controversy : (ii) Morre’s classification of Golgi ; (iii) GERL region ; (iv) Isolation of Golgi apparatus ; (v) Enzymes of Golgi apparatus ; (vi) Compartmentalization of Golgi apparatus.



Photograph showing how proteins are delivered to the cell’s Golgi apparatus for processing in vesicles that bud from the ER.