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# STRUCTURE AND FUNCTION OF GOLGI APPARATUS

In the late nineteenth century, an Italian biologist, Camillo Golgi, was inventing new types of staining procedures that might reveal the organization of nerve cells within the central nervous system. In 1898, Golgi applied a metallic stain (the silver chromate method) to nerve cells from the cerebellum and discovered a darkly stained reticular network located near the cell nucleus. This network, which was later identified in other cell types and named the Golgi complex, helped earn its discoverer the Nobel Prize in 1906. The Golgi complex remained a center of controversy for decades between those who believed that the organelle existed in living cells and those who believed it was an artifact, that is, an artificial structure formed during preparation for microscopy. It wasn't until the Golgi complex was clearly identified in unfixed, freeze-fractured cells that its existence was verified beyond reasonable doubt.

OCCURANCE:

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.

NUMBERS:

- Their number per plant cell can vary from several hundred 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.



STRUCTURE AND ORGANISATION:

- LOCATION: 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.
- STRUCTURE:
  - In most cells, the Golgi is composed of flattened membrane-enclosed sacs (cisternae) and associated vesicles. A striking feature of the Golgi apparatus is its distinct polarity in both structure and function. Proteins from the ER enter at its cis face (entry face), which is convex and usually oriented toward the nucleus.
  - Typically, a Golgi stack contains fewer than eight cisternae called DICTYOSOME. An individual cell may contain from a few to several thousand distinct stacks, depending on the cell type. The Golgi stacks in mammalian cells are interconnected to form a single, large ribbon-like complex situated adjacent to the cell's nucleus.
  - The detailed structure of three basic components of the Golgi apparatus can be studied as follows:
    A. **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 (Sheeler and Bianchi, 1987)

B. **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.

C. **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 coalesce 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 GERL region and the endosomal and lysosomal compartments.

- The Golgi complex is divided into several functionally distinct compartments arranged along an axis from the cis or entry face closest to the ER to the trans or exit face at the opposite end of the stack. The Golgi is most commonly viewed as consisting of four functionally distinct regions:
  - ✓ **The cis Golgi network (CGN**)-is composed of an interconnected network of tubules. The CGN is thought to function primarily as a sorting station that distinguishes between proteins to be shipped back to the ER and those that are allowed to proceed to the next Golgi station.
  - ✓ **The Golgi stack** which is divided into the medial and trans sub-compartments- This constitutes the bulk of the Golgi complex made up of a series of large, flattened cisternae.
  - ✓ **The trans Golgi network (TGN)-** The trans-most face of the organelle contains a distinct network of tubules and vesicles called the trans Golgi network (TGN). The TGN is a sorting station where proteins are segregated into different types of vesicles heading either to the plasma membrane or to various intracellular destinations.

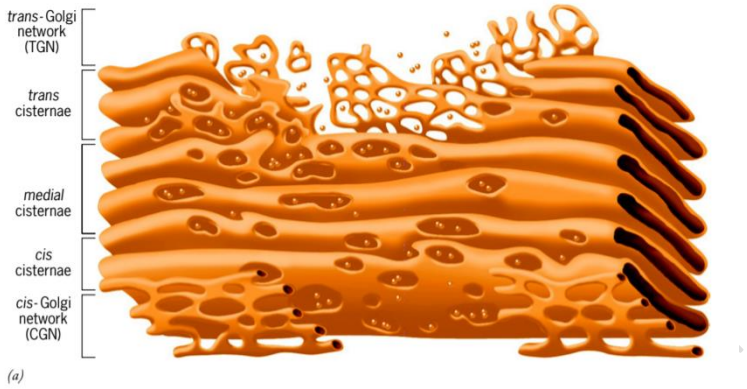
**The GERL Region**

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).




Schematic model of a portion of a Golgi complex from an epithelial cell of the male rat reproductive tract.

**FUNCTIONS:**

1. **Glycosylation of proteins:** Protein processing within the Golgi involves the modification of the N-linked oligosaccharides (14 sugar residues) that were added to proteins in the ER. Three glucose residues are removed while the polypeptides are still in the ER. Following transport to the Golgi apparatus, the N-linked oligosaccharides of these glycoproteins are subject to extensive further modifications.
   As newly synthesized soluble and membrane glycoproteins pass through the cis and medial cisternae of the Golgi stack, most of the mannose residues are also removed from the core oligosaccharides, and other sugars are added sequentially by various glycosyltransferases. In the Golgi complex, as in the RER, the sequence in which sugars are incorporated into oligosaccharides is determined by the spatial arrangement of the specific glycosyltransferases that come into contact with the newly synthesized protein as it moves through the Golgi stack.
   **N-linked glycosylation**:
   Two broad classes of N-linked oligosaccharides, the complex oligosaccharides and the high-mannose oligosaccharides, are attached to mammalian glycoproteins. Sometimes, both types are attached (in different places) to the same polypeptide chain.
   - Complex oligosaccharides are generated when the original N-linked oligosaccharide added in the ER is trimmed and further sugars are added. The sialic acids in the complex oligosaccharides are of special importance because they bear a negative charge. If the oligosaccharide is accessible to the processing enzymes in the Golgi apparatus, it is likely to be converted to a complex form;

- High-mannose oligosaccharides are trimmed but have no new sugars added to them in the Golgi apparatus. If the oligosaccharides are inaccessible because its sugars are tightly held to the protein's surface, it is likely to remain in a high-mannose form.

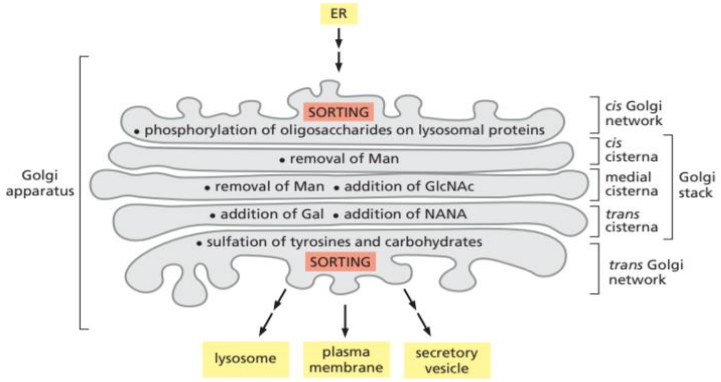



**Figure 13–29 Oligosaccharide processing in Golgi compartments.** The localization of each processing step shown was determined by a combination of techniques, including biochemical subfractionation of the Golgi apparatus membranes and electron microscopy after staining with antibodies specific for some of the processing enzymes. Processing enzymes are not restricted to a particular cisterna; instead, their distribution is graded across the stack, such that early-acting enzymes are present mostly in the *cis* Golgi cisternae and later-acting enzymes are mostly in the *trans* Golgi cisternae. Man, mannose; GlcNAc, *N*-acetylglucosamine; Gal, galactose; NANA, *N*-acetylneuraminic acid (sialic acid).

- N-linked oligosaccharides of secreted and plasma membrane proteins are processed within the Golgi apparatus in an ordered sequence of reactions. In most cases, the first modification of proteins destined for secretion or for the plasma membrane is the removal of four mannose residues. This is followed by the sequential addition of an N-acetylglucosamine, the removal of two more mannoses, and the addition of a fucose and two more N-acetyl-glucosamines. Finally, three galactose and three sialic acid residues are added. The proteins can emerge from the Golgi with a variety of different N-linked oligosaccharides. The enzymes that carry out the addition of sugar residues, glycosyltransferases, and those that remove them, glycosidases, are well-characterized.

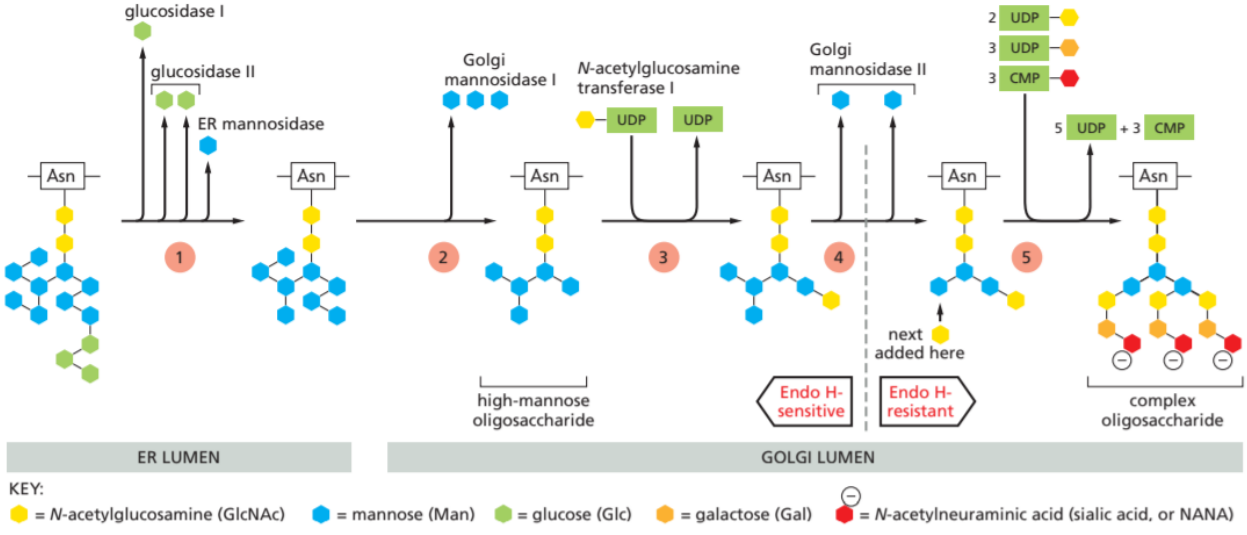



Fig: oligosaccharide processing in ER and Golgi apparatus

- The processing of the N-linked oligosaccharide of lysosomal proteins destined for incorporation into lysosomes are modified by mannose phosphorylation. ln the first step of this reaction, N-acetylglucosamine phosphates are added to specific mannose residues, probably while the protein is still in the cis Golgi network. This is followed by removal of the N-acetylglucosamine group, leaving mannose-6-phosphate residues

on the N-linked oligosaccharide. Because of this modification these residues are not removed during further processing. Instead, these phosphorylated mannose residues are specifically recognized by a mannose-6-phosphate receptor in the trans Golgi network, which directs the transport of these proteins to endosomes and on to lysosomes. The phosphorylation of mannose residues is thus a critical step in sorting lysosomal proteins to their correct intracellular destinations.

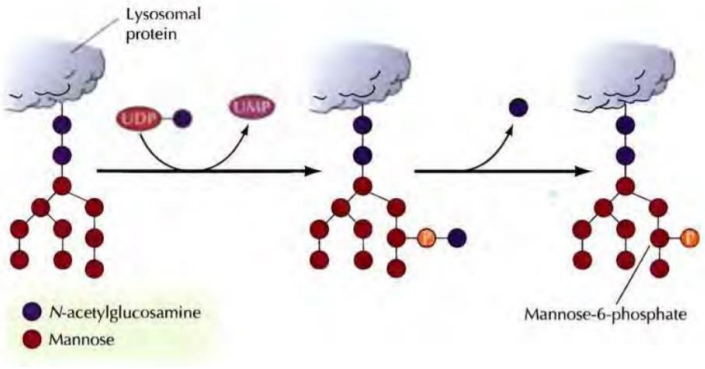



**FIGURE 10.29 Targeting of lysosomal proteins by phosphorylation of mannose residues** Proteins destined for incorporation into lysosomes are specifically recognized and modified by the addition of phosphate groups to the number 6 position of mannose residues. In the first step of the reaction, *N*-acetylglucosamine phosphates are transferred to mannose residues from UDP*N*-acetylglucosamine. The *N*-acetylglucosamine groups are then removed, leaving mannose-6-phosphates.

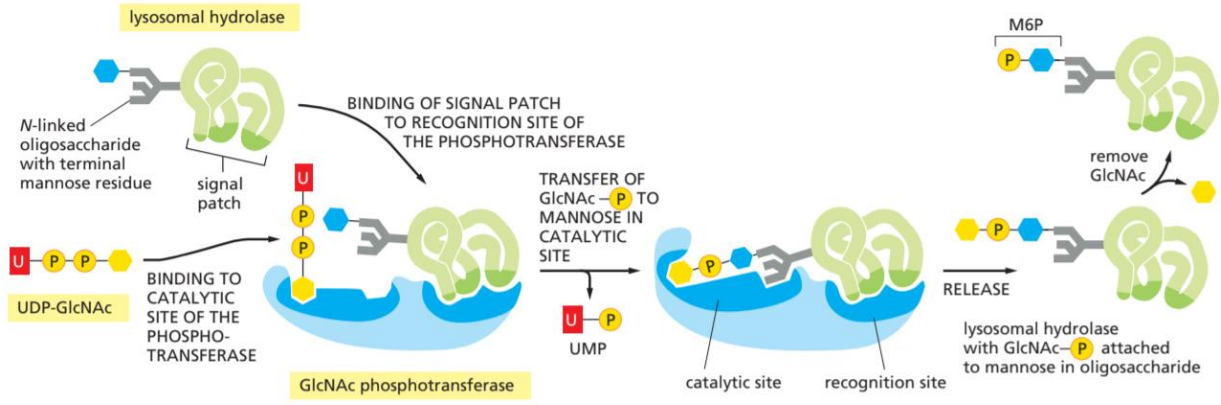



Fig: **The recognition of a lysosomal hydrolase. A GlcNAc phosphotransferase recognizes lysosomal hydrolases in the Golgi apparatus. The enzyme has separate catalytic and recognition sites. The catalytic site binds both high-mannose N-linked oligosaccharides and UDP-GlcNAc. The recognition site binds to a signal patch that is present only on the surface of lysosomal hydrolases. A second enzyme cleaves off the GlcNAc, leaving the mannose 6-phosphate exposed.**

**O-linked glycosylation:** Some proteins have sugars added to the hydroxyl groups of selected serines or threonines, or, in some cases—such as collagens—to hydroxylated proline and lysine side chains. This O-linked glycosylation is catalyzed by a series of glycosyl transferase enzymes that use the sugar nucleotides in the lumen of the Golgi apparatus to add sugars to a protein one at a time. Usually, N-acetyl-galactosamine is added first, followed by a variable number of additional sugars, ranging from just a few to 10 or more. The Golgi apparatus confers the heaviest O-linked glycosylation of all on mucins, the glycoproteins in mucus secretions, and on proteoglycan core proteins, which it modifies to produce proteoglycans.

2. **Transport of materials through the Golgi complex:**
   It is still uncertain how the Golgi apparatus achieves and maintains its polarized structure and how molecules move from one cisterna to another, and it is likely that more than one mechanism is involved in each case.
   - **The cisternal maturation model**: Up until the mid-1980s, it was generally accepted that Golgi cisternae were transient dynamic structures. It was supposed that Golgi cisternae formed at the cis face of the stack by fusion of membranous carriers from the ER and ERGIC and that each cisterna physically moved from the cis to the trans end of the stack, changing in composition as it progressed. This is known as the cisternal maturation model because, according to the model, each cisterna "matures" into the next cisterna along the stack.
   - **The vesicle transport model**: From the mid-1980s to the mid-1990s, the maturation model of Golgi movement was largely abandoned and replaced by an alternate model, which proposed that the cisternae of a Golgi stack remain in place as stable compartments. In this latter model, which is known as the vesicular transport model, cargo (i.e., secretory, lysosomal, and membrane proteins) is shuttled through the Golgi stack, from the CGN to the TGN, in vesicles that bud from one membrane compartment and fuse with a neighboring compartment farther along the stack. Directional flow could be achieved because forward-moving cargo molecules are selectively packaged into forward-moving vesicles. Although both forward- and backward-moving vesicles would likely be COPI-coated, the coats may contain different adaptor proteins that confer selectivity on the packaging of cargo molecules. Alternatively, transport vesicles shuttling between Golgi cisternae might not be directional at all, transporting cargo randomly back and forth; directional flow would then occur because of the continual input to the cis cisterna and output from the trans cisterna.

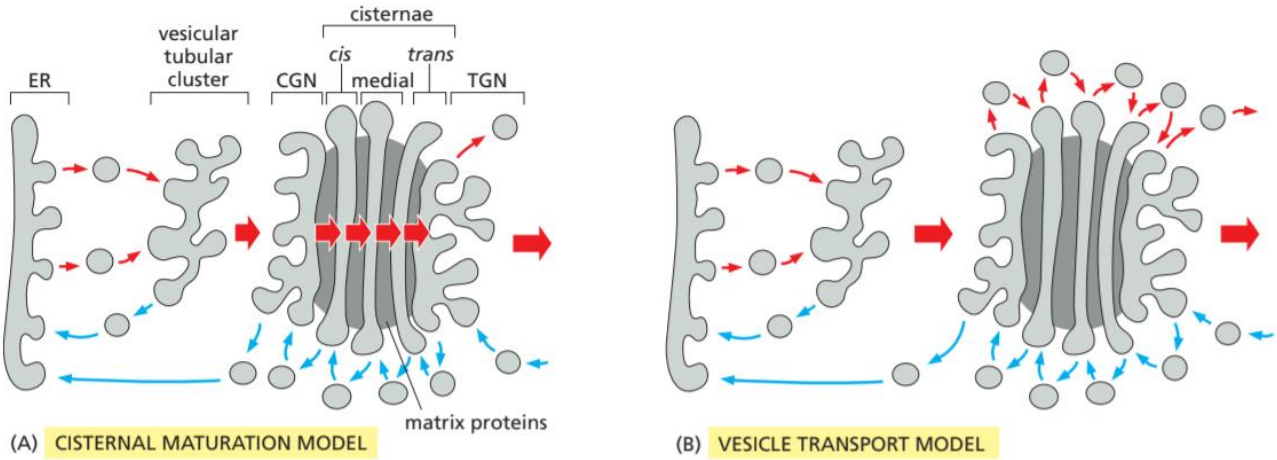



fig: Two possible models explaining the organization of the Golgi apparatus and how proteins move through it.

**Vesicle transport in golgi**

The biosynthetic pathway of a eukaryotic cell consists of a series of distinct membrane-bound organelles that function in the synthesis, modification, and delivery of soluble and membrane proteins to their appropriate destination in the cell. The cargo that are carried between compartments by vesicles (or other types of membrane-bound carriers) that bud from donor membranes and fuse with acceptor membranes consists of a protein coat. Protein coats have at least two distinct functions: (1)

they act as a mechanical device that causes the membrane to curve and form a budding vesicle, and (2) they provide a mechanism for selecting the components to be carried by the vesicle. Several distinct classes of coated vesicles have been identified; they are distinguished by the proteins that make up their coat, their appearance in the electron microscope, and their role in cell trafficking. The three best studied coated vesicles are the following:

**a) COPII-coated vesicles move materials from the ER "forward" to the ERGIC and Golgi complex.**

COPII-coated vesicles mediate the first leg of the journey through the biosynthetic pathway—from the ER to the ERGIC and Golgi complex. COPII coats select and concentrate certain components for transport in vesicles. Certain integral membrane proteins of the ER are selectively captured because they contain **"ER export"** signals as part of their cytosolic tail. These signals interact specifically with COPII proteins of the vesicle coat. Proteins selected by COPII-coated vesicles include

(1) enzymes that act at later stages in the biosynthetic pathway, such as the glycosyltransferases of the Golgi complex,

(2) membrane proteins involved in the docking and fusion of the vesicle with the target compartment, and

(3) membrane proteins that are able to bind soluble cargo.

Cells lacking a specific cargo receptor typically fail to transport a specific subset of proteins from the ER to the Golgi complex.

**b) COPI-Coated Vesicles: Transporting Escaped Proteins Back to the ER**

COPI coated vesicles have been most clearly implicated in the retrograde transport of proteins, including the movement of

(1) Golgi resident enzymes in a trans-to-cis direction and

(2) ER resident enzymes from the ERGIC and the Golgi complex back to the ER.

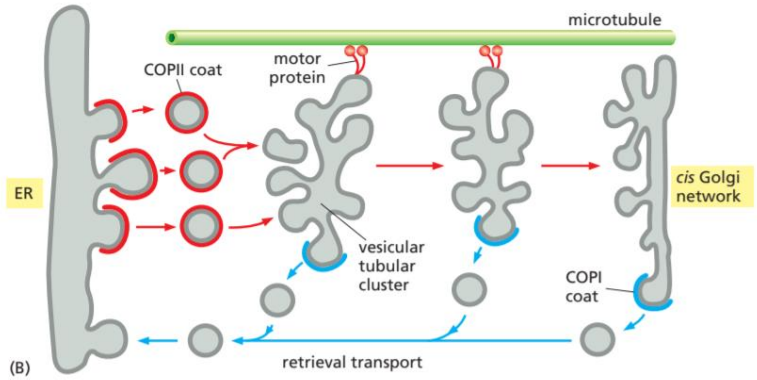



Figure 13–24 **Vesicular tubular clusters.** (A) An electron micrograph of vesicular tubular clusters forming around an exit site. Many of the vesicle-like structures seen in the micrograph are cross sections of tubules that extend above and below the plane of this thin section and are interconnected. (B) Vesicular tubular clusters move along microtubules to carry proteins from the ER to the Golgi apparatus. COPI-coated vesicles mediate the budding of vesicles that return to the ER from these clusters (and from the Golgi apparatus). (A, courtesy of William Balch.)

from Bruce Albert

**Retaining and Retrieving Resident ER Proteins**: Vesicles continually bud from membrane compartments, but still retain its unique composition. Whether a particular protein in the membrane of the ER remains in the ER or proceeds on to the Golgi complex are maintained in an organelle by a combination of two mechanisms:

i. **Retention of resident molecules** that are excluded from transport vesicles. Retention may be based primarily on the physical properties of the protein. For example, soluble proteins that

are part of large complexes or membrane proteins with short transmembrane domains are not likely to enter a transport vesicle.

ii. **Retrieval of "escaped" molecules** back to the compartment in which they normally reside. Proteins that normally reside in the ER, those both in the lumen and in the membrane, contain short amino acid sequences at their C-terminus that serve as retrieval signals, ensuring their return to the ER if they should be accidentally carried forward to the ERGIC or Golgi complex.

- The signal sequence of the ER transmembrane proteins is best-characterized by KKXX sequence as a retrieval signal which contains two lysines, followed by any two other amino acids, at the extreme C-terminal end of the ER membrane protein. It is called a KKXX sequence, based on the single-letter amino acid code. The retrieval signals on ER membrane proteins, can interact directly with the COPI coat.
- The signal sequence of the ER luminal soluble proteins is characterized by KDEL sequence as a retrieval signal which typically possess the retrieval signal "lys-asp-glu-leu".

The retrieval of "escaped" ER soluble proteins from these compartments is accomplished by specific receptors that capture the molecules and return them to the ER in COPI-coated vesicles. Soluble resident proteins of the ER lumen are recognized and returned to the ER by the KDEL receptor, a multipass transmembrane protein that binds to the KDEL sequence and packages any protein displaying it into COPI-coated retrograde transport vesicles. To accomplish this task, the KDEL receptor itself must cycle between the ER and the Golgi apparatus, and its affinity for the KDEL sequence must differ in these two compartments. The receptor must have a high affinity for the KDEL sequence in vesicular tubular clusters and the Golgi apparatus, so as to capture escaped, soluble ER resident proteins that are present there at low concentration. It must have a low affinity for the KDEL sequence in the ER, however, to unload its cargo in spite of the very high concentration of KDEL-containing soluble resident proteins in the ER. The affinity of the KDEL receptors for the KDEL sequences is dependent on the pH of each organelle. While the KDEL receptors has a high affinity for the KDEL sequences at the more low or acidic pH of the Golgi lumen, the neutral pH of the ER lumen decreases the affinity of the receptor for the proteins prompting its release. Thus, the **Retrieval pathway is pH dependent.**

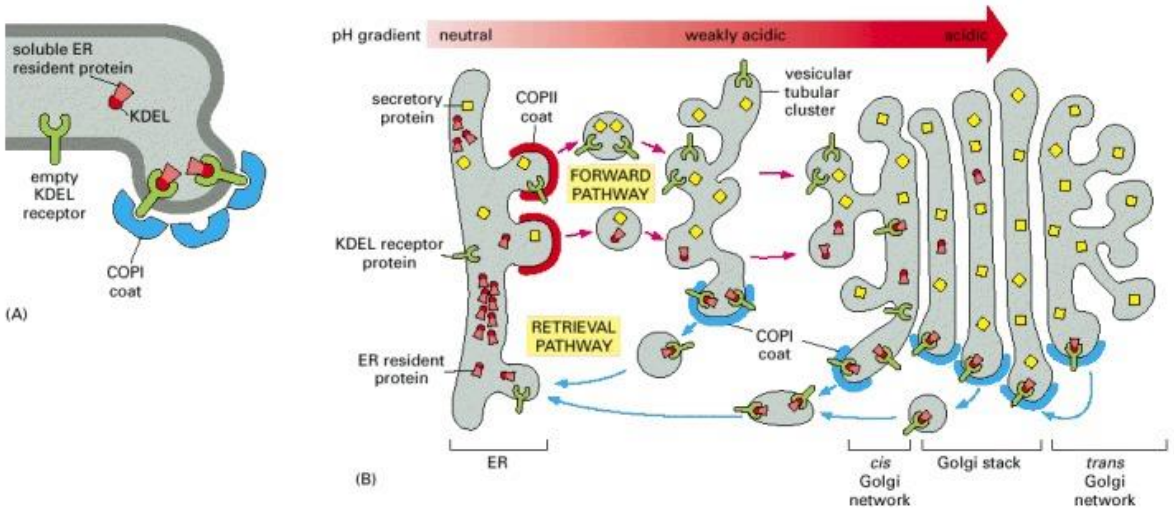



**Fig:** A model for the retrieval of ER resident proteins

c) **Clathrin-coated vesicles** move materials from the TGN to endosomes, lysosomes, and plant vacuoles. They also move materials from the plasma membrane to cytoplasmic compartments along the endocytic pathway. They have also been implicated in trafficking from endosomes and lysosomes.

**Targeting lysosomal enzymes to lysosomes**.

(a) Lysosomal enzymes are recognized by an enzyme in the cis cisternae that transfers a phosphorylated N-acetylglucosamine from a nucleotide sugar donor to one or more mannose residues of N-linked oligosaccharides. The glucosamine moiety is then removed in a second step by a second enzyme, leaving mannose 6-phosphate residues as part of the oligosaccharide chain.

(b) The mannose residues of the lysosomal enzyme are phosphorylated in the Golgi cisternae

(c) In animal cells they carry a unique marker in the form of mannose 6-phosphate (M6P) groups,

(d) The transmembrane mannose 6-phosphate receptors which are present in the TGN are thought to have a dual role: they interact specifically with the lysosomal enzymes on the luminal side of the vesicle, and they interact specifically with adaptors on the cytosolic surface of the vesicle.

(e) In this way, the receptors help package the hydrolases into clathrin-coated vesicles that bud from the TGN and deliver their contents to early endosomes.

(f) Thus, after the receptor is delivered, the lysosomal hydrolases dissociate from the M6P receptors, which are retrieved into transport vesicles that bud from endosomes. These vesicles are coated with retromer, a coat protein complex specialized for endosome-to-TGN transport, which returns the receptors to the TGN for reuse

(g) The lysosomal enzymes are delivered to an endosome and eventually to a lysosome.

() Mannose 6-phosphate receptors are also present in the plasma membrane, where they capture lysosomal enzymes that are secreted into the extracellular space and return the enzymes to a pathway that directs them to a lysosome.

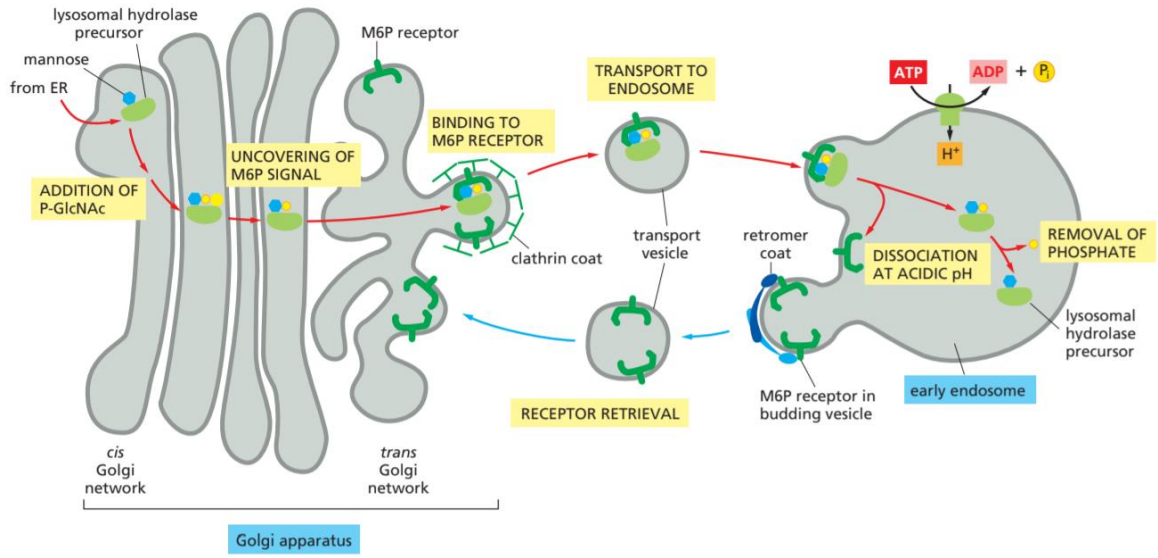


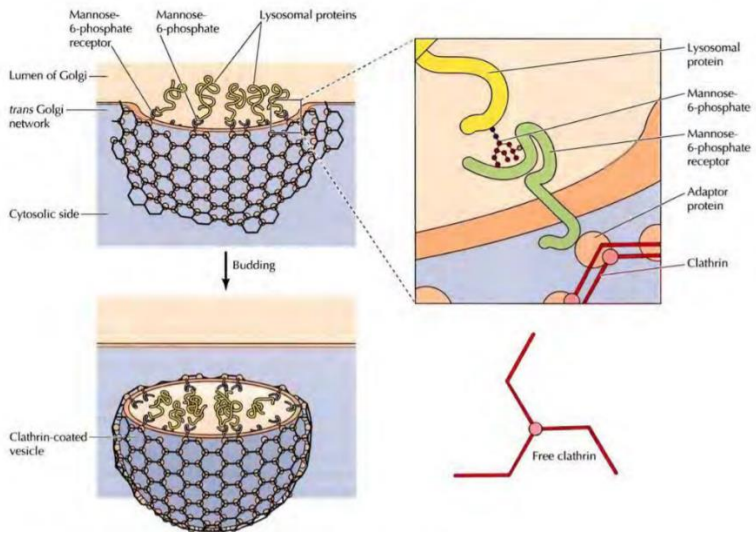

Fig: **The transport of newly synthesized lysosomal hydrolases to endosomes. The sequential action of two enzymes in the cis and trans Golgi network adds mannose 6-phosphate (M6P) groups to the precursors of lysosomal enzymes. The M6P-tagged hydrolases then segregate from all other types of proteins in the TGN because adaptor proteins (not shown) in the clathrin coat bind the M6P receptors, which, in turn, bind the M6P-modified lysosomal hydrolases. The clathrin-coated vesicles bud off from the TGN, shed their coat, and fuse with early endosomes.**

**At the lower pH of the endosome, the hydrolases dissociate from the M6P receptors, and the empty receptors are retrieved in retromercoated vesicles to the TGN for further rounds of transport. In the endosomes, the phosphate is removed from the M6P attached to the hydrolases, which may further ensure that the hydrolases do not return to the TGN with the receptor.**

**RECEPTOR MEDIATED ENDOCYTOSIS (applicable for pinching off of vesicles from TGN carrying the lysosomal enzymes)**

**1. The Assembly of a Clathrin Coat Drives Vesicle**

Formation Clathrin-coated vesicles, the first coated vesicles to be identified, transport material from the plasma membrane and between endosomal and Golgi compartments. The major protein component of clathrin-coated vesicles is clathrin itself, which forms the outer layer of the coat. Each clathrin subunit consists of three large and three small polypeptide chains that together form a three-legged structure called a triskelion. Clathrin triskelions assemble into a basketlike framework of hexagons and pentagons to form coated pits (buds) on the cytosolic surface of membranes. Under appropriate conditions, isolated triskelions spontaneously self-assemble into typical polyhedral cages in a test tube, even in the absence of the membrane vesicles that these baskets normally enclose. Thus, the clathrin triskelions determine the geometry of the clathrin cage.




Structure of clathrin

**2. Adaptor protein**

Adaptor proteins, another major coat component in clathrin-coated vesicles, form a discrete inner layer of the coat, positioned between the clathrin cage and the membrane. They bind the clathrin coat to the membrane and trap various transmembrane proteins, including transmembrane receptors that capture soluble cargo molecules inside the vesicle—so-called cargo receptors. Clathrin-coated vesicles budding from different membranes use different adaptor proteins and thus package different receptors and cargo molecules. The assembly of adaptor proteins on the membrane is tightly controlled, in part by the cooperative interaction of the adaptor proteins with other components of the coat. For example the adaptor protein AP2 binds to a specific phosphorylated phosphatidylinositol lipid (a phosphoinositide), it alters its conformation, exposing binding sites for cargo receptors in the membrane. The simultaneous binding to the cargo receptors and lipid head groups greatly enhances the binding of AP2 to the membrane. The best characterized AP2 adaptor ptoteins have four different protein subunits that only assemble at the right time and place to stably bind AP2 proteins to the membrane.

Upon binding, they induce membrane curvature, which makes the binding of additional AP2 proteins in its proximity more likely. The cooperative assembly of the AP2 coat layer then is further amplified by clathrin binding, which leads to the formation and budding of a transport vesicle.

### 3. Role of dynamin

As a clathrin-coated bud grows, soluble cytoplasmic proteins, including dynamin, assemble at the neck of each bud. Dynamin contains a PI (4,5) P2-binding domain, which tethers the protein to the membrane, and a GTPase domain, which regulates the rate at which vesicles pinch off from the membrane. The pinching-off process brings the two noncytosolic leaflets of the membrane into close proximity and fuses them, sealing off the forming vesicle. The dynamin recruits other proteins to the neck of the bud. Together with dynamin, they help bend the patch of membrane by directly distorting the bilayer structure, or by changing its lipid composition through the recruitment of lipid-modifying enzymes, or by both mechanisms. Once released from the membrane, the vesicle rapidly loses its clathrin coat. A PIP phosphatase that is co-packaged into clathrin-coated vesicles depletes PI (4,5) P2 from the membrane, which weakens the binding of the adaptor proteins. In addition, an hsp70 chaperone protein functions as an uncoating ATPase, using the energy of ATP hydrolysis to peel off the clathrin coat.

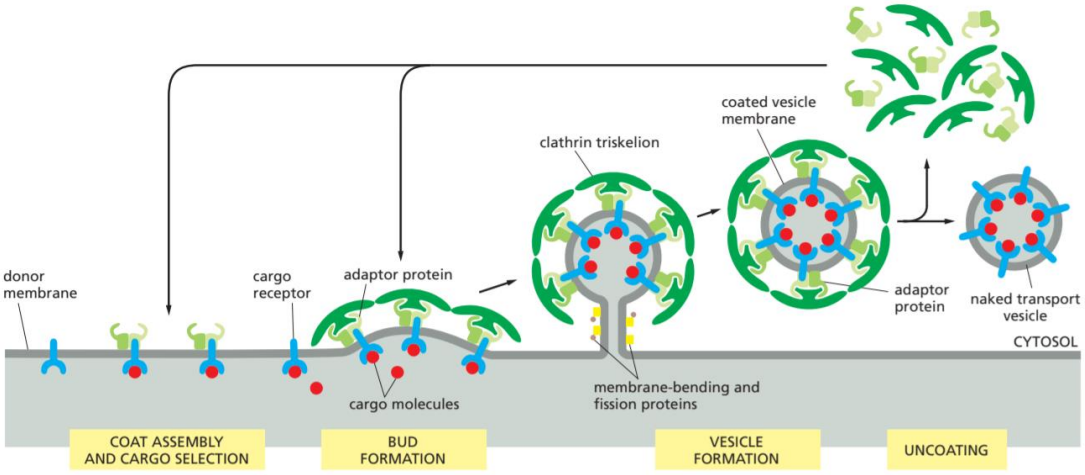



Fig: The assembly and disassembly of a clathrin coat.