

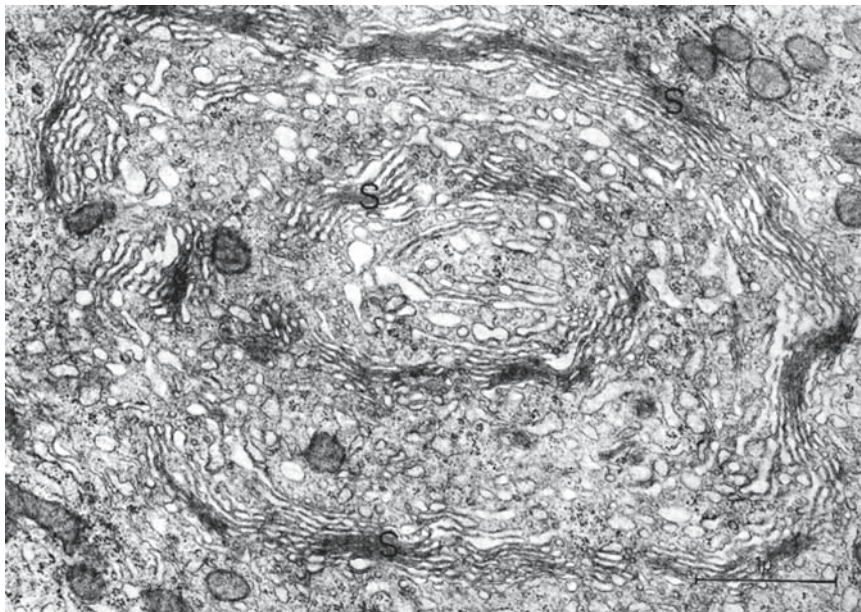
## Structure

With no cell compartment or organelle has morphology served such a pivotal role in its discovery and investigation as with the apparatus of Golgi. The original description of the “apparato reticulo interno” (internal reticular apparatus) now known as the apparatus of Golgi or Golgi apparatus was based on light microscopy (Chapter 1). Both classical Golgi apparatus study prior to 1953 and the modern rediscovery due to the advent of the electron microscope all were based on morphology. An understanding of Golgi apparatus architecture was one of the more important early developments resulting from electron microscopy.

Morphology was the sole basis to guide early attempts at Golgi apparatus isolation and, until its isolation in the mid to late 1960s and early 1970s, and the introduction of autoradiography (Peterson and LeBlond, 1964), morphology was the only basis for investigation of this complex cellular component. Even today, morphology remains as a major criterion by which Golgi apparatus are defined.

Biochemical definitions of Golgi apparatus are complicated by the fact that Golgi apparatus (either singular or plural) are transitional cell components sharing many biochemical characteristics with either the endoplasmic reticulum or the plasma membrane or both. Unlike the situation with true organelles such as chloroplasts or mitochondria, there have been virtually no biochemical markers common to all cell types and not shared with either endoplasmic reticulum or plasma membranes. Additionally, the functioning of Golgi apparatus in secretion and other activities is highly dependent upon the co-participation of endoplasmic reticulum, secretory vesicles, and other structures. Thus, the Golgi apparatus exists in the cell as a component within a highly integrated endomembrane system (Morré and Mollenhauer, 1974) often with biochemical characteristics intermediate between those of the endoplasmic reticulum and those of the plasma membrane, but with a characteristic and easily recognized pattern or morphology that unambiguously distinguishes the Golgi apparatus from all other cell components.

The most common form of the Golgi apparatus, exemplified by most mammalian cells, consists of side by side piles or stacks of smooth membrane cisternae lacking ribosomes (Fig. 2.1). The stacks are seen to be distributed and located within a special region of cytoplasm called the Golgi apparatus zone or Golgi apparatus matrix (Fig. 2.2). In plants, and in many animal cells as well, individual stacks of cisternae may be spread more or less evenly, through the entire cytoplasm. These stacks, even though dispersed, function synchronously indicating that they are functionally and perhaps structurally interconnected.

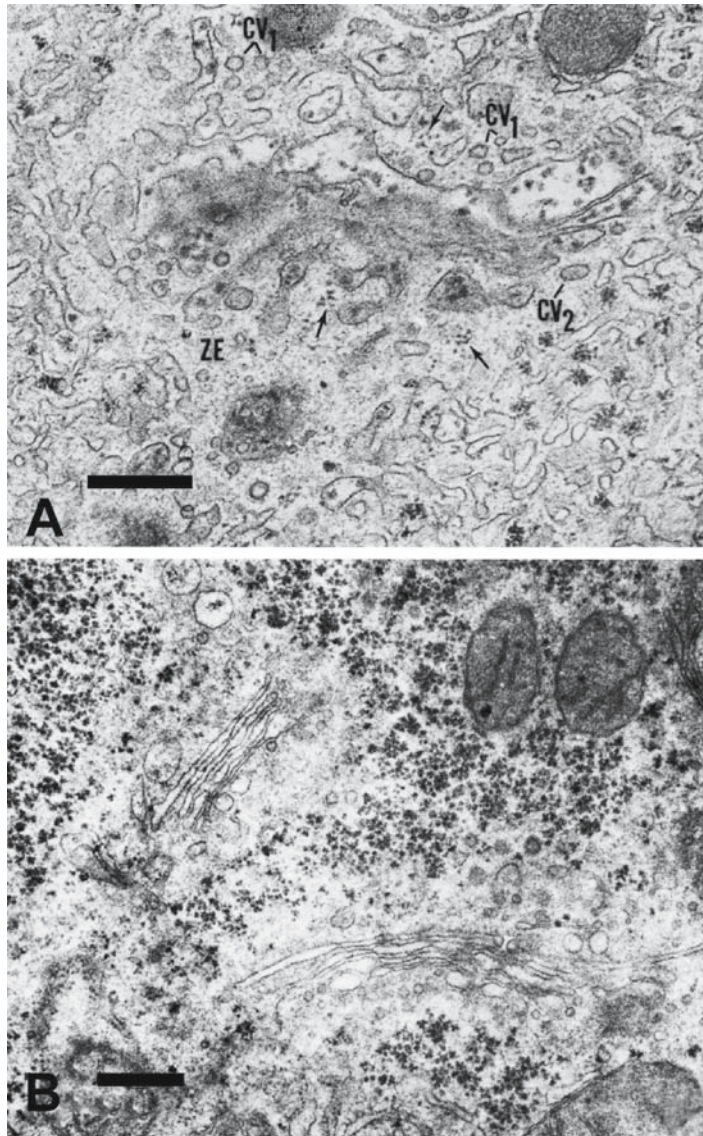


**Fig. 2.1.** Portion of the Golgi apparatus of rat epididymis showing numerous closely-spaced stacks (S). Karnovsky's fixative. From Flickinger (1969b). Electron micrograph courtesy of Dr. C. J. Flickinger, University of Virginia Medical School, Charlottesville. Reprinted by permission of Academic Press, Inc., New York.

Vesicles and tubules either may be attached to or associated with various parts of the Golgi apparatus. Structural features at each level of organization will vary depending on cell type, method of fixation, and of specimen preparation and the physiological state of the cell. However, those emphasized may be observed as consistent features of most electron microscope preparations.

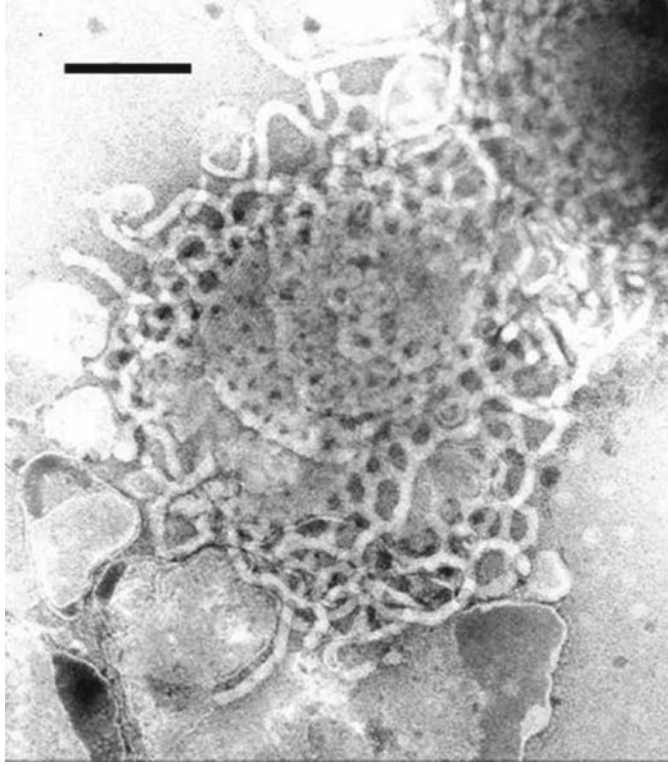
## 2.1. Cisternae

By definition, a cisterna (plural = cisternae) is a sac or cavity within a cell or organism, usually filled with fluid (i.e., a cistern). The term was used originally in electron microscope morphology to describe one of the interconnected vesicles, lamellae or tubules comprising the endoplasmic reticulum but has served the same purpose for the Golgi apparatus. Each cisterna of the Golgi apparatus consists of a lumen or central cavity surrounded by a membrane lacking ribosomes (one of the several so-called “smooth” membranes that frequently contribute to the smooth microsome fraction of cell homogenates). Cisternae will differ in architectural detail depending on cell type and their position in the stack (Figs. 2.3 to 2.7). Perhaps no two are exactly alike. Many cisternae especially from the mid-region of the stack (i.e., the intercalary cisternae) often have



**Fig. 2.2.** Golgi apparatus regions showing the zone of exclusion or Golgi matrix. Coated vesicles (CV) of the Golgi apparatus regions are restricted to this zone. Elements of endoplasmic reticulum entering the zone are smooth (lacking attached ribosomes). Free polyribosomes (Golgi apparatus polyribosomes) are frequently observed within the zone. (A). Normal rat liver. (B). Rat hepatomas induced by N-2-fluorenylacetamide (FAA). The hepatoma cells contain a Golgi apparatus with dispersed stacks but still each stack is surrounded by a zone of exclusion. Reproduced from Mollenhauer and Morr , 1978b with permission from Plenum Publishers. Scale bar = 5  $\mu$ m.

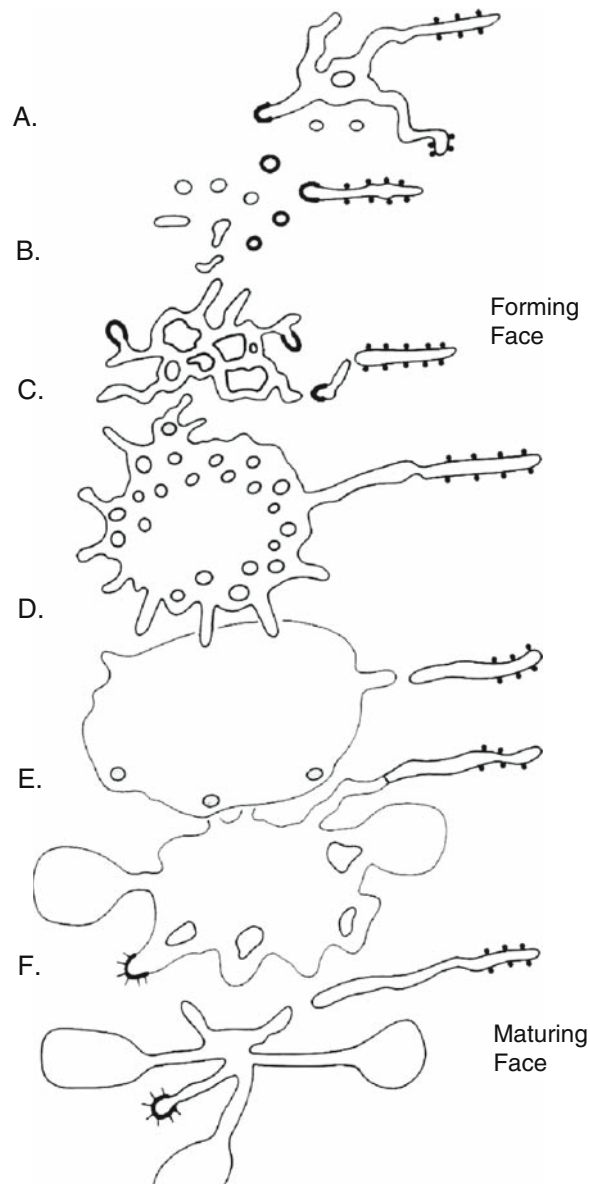




**Fig. 2.3.** A Golgi apparatus stack from radish root isolated and viewed in negative contrast directly on an electron microscope grid. The stack has been partially unstacked to reveal a progression change diagrammed in Figure 2-4 from the cis (top) to trans (bottom) face of the stack. Reproduced from Mollenhauer and Morré (1966) from the *Journal of Cell Biology*, 1966, 29:373-376. Copyright 1966b The Rockefeller University Press. Scale bar = 0.2 μm.

small perforations or fenestrae at the margins. This central portion of the cisternal stack is referred to also as the central *saccule* or simply as the saccule. Normally, 4 to 6 such saccules are arranged one on top of the other, in parallel array, to yield the characteristic “stack” or dictyosome as one of the more obvious features used to identify Golgi apparatus both in situ and isolated in cell fractions (Chapter 3). The plate-like regions, up to the fenestrated margins, are typically 0.5 to 1 μm in diameter (Fig. 2.5).

Continuous with the central plate like region is a complex system of tubules and secretory or coated vesicles (Fig. 2.9). Secretory vesicles lack coats or are partially coated over their surfaces with spiny clathrin coats. Vesicles of the Golgi apparatus zone coated either with clathrin or coatomer proteins (COP) may be either free or attached to tubule ends (Mollenhauer and Morré, 1966b). The connecting tubules that attach secretory vesicles to saccules are short (Fig. 2.7) and begin as narrow partitions extending beyond the fenestrated peripheries of the central plates. Longer tubules may continue for several microns and follow



**Fig. 2.4.** Diagrammatic representation of successive cisternae within a single stack as partially revealed in Figure 2-3. (A). Part rough (with ribosomes) -part smooth (lacking ribosomes) transitional endoplasmic reticulum with (B). COPII-coated buds and vesicles which (C). coalesce to form the largely tubular first Golgi apparatus cisternae of the forming face. (D). Continued delivery of ER-derived material results in fenestrated cisternae with a central plate-like region and tubular peripheries. (E). As cisternal maturation proceeds, plate-like regions dominate. (F). Secretory vesicles connected to plate-like regions by tubules characterize the maturing face. (G). The post Golgi structures or trans Golgi network = cisternal remnants with clathrin-coated membrane and vesicles represent the final stage of cisternal maturation and utilization in secretory vesicle formation.

The Golgi Apparatus

The First 100 Years

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