Structure of Golgi apparatus

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Summary. Golgi apparatus (GA) of eukaryotic cells consist of one or more stacks of flattened saccules (cisternae) and an array of fenestrae and tubules continuous with the peripheral edges of the saccules. Golgi apparatus also are characterized by zones of exclusion that surround each stack and by an assortment of vesicles (or vesicle buds) associated with both the stacks and the peripheral tubules of the stack cisternae. Each stack (sometimes referred to as Golgi apparatus, Golgi complex, or dictyosome) is structurally and functionally polarized, reflecting its role as an intermediate between the endoplasmic reticulum, the cell surface, and the lysosomal system of the cell. There is probably only one GA per cell, and all stacks of the GA appear to function synchronously. All Golgi apparatus are involved in the generation and movement of product and membrane within the cell or to the cell exterior, and these functions are often reflected as structural changes across the stacks. For example, in plants, both product and membrane appear to mature from the cis to the trans poles of the stacks in a sequential, or serial, manner. However, there is also strong ultrastructural evidence in plants for a parallel input to the stack saccules, probably through the peripheral tubules. The same modes of functioning probably also occur in animal GA; although here, the parallel mode of functioning almost surely predominates. In some cells at least, GA stacks give rise to tubular-vesicular structures that resemble the trans Golgi network.

Rudimentary GA, consisting of tubular-vesicular networks, have been identified in fungi and may represent an early stage of GA evolution.

Keywords: Golgi apparatus; Dictyosome; Ultrastructure.

Introduction

The purpose of this report is to review the structure of Golgi apparatus, primarily through the ultrastructural studies of the authors (e.g., Mollenhauer and Morré 1966a, 1980, 1991; Morré 1977). Many aspects of this very complicated structure remain obscure even today; and some aspects of Golgi apparatus structure, which were recognized and documented in the 1960s, are only now being rediscovered. Although the emphasis is on plants, most of the concepts developed here are applicable to animal Golgi apparatus as well.

Historically, the Golgi apparatus was defined at the light microscope level as a cellular component made visible through the application of a specific cytochemical procedure; i.e., the black reaction devised by Camillo Golgi, and discussed in various publications dating from the late 1890s (e.g., Golgi 1898, Perroncito 1910, Bowen 1926, Beams and Kessel 1968, Inferrea and Carrozza 1975, Whaley 1975). The black reaction left a residue of silver at specific, and fairly reproducible, sites within a cell to reveal, in some cells, a rather elaborate reticulum that often coursed through the cytoplasm. However, the pattern of silver deposition was not always consistent either in its application or in respect to the distribution of precipitated silver between cells of different types. Moreover, the organelle could not be verified without staining, even with phase contrast, because its density was approximately the same as that of the cytoplasmic ground substance. These results led many to believe that Golgi's reticulum was an artifact, a belief that was not resolved until the 1950s with the advent of ultrastructural data from electron microscopy (see Bourne 1964, Whaley 1975 for historical accounts).

The application of electron microscopy beginning in the early 1950s to the study of Golgi apparatus revealed a structure of flattened saccules stacked one upon another, but with a distinct space between each saccule (see Dalton and Felix 1956). Each saccule of the stack had an assortment of vesicular profiles associated with
its periphery (Fig. 1A, B). This structure became known as the Golgi apparatus or Golgi complex. The extensive reticulum originally visualized by Golgi’s black reaction of precipitated silver was not identified as a part of the Golgi apparatus in these early studies. Numerous studies soon revealed that Golgi apparatus (still defined as stacks of flattened saccules) were present in most eukaryotic cells, were generally uniform in structure except for variations in the number and size of the saccules, and were often associated with cellular secretion. Variations in form and intracellular distribution were also verified and related to the functional requirements of the cell (Beams and Kessel 1968). The interrelationship of the Golgi apparatus with other cellular constituents was appreciated very early (Hirsch 1961; also see Bourne 1964, Whaley 1975 for succinct accounts of the early history of Golgi’s reticulum).

**Definition**

What Camillo Golgi saw was a reticulum and, if the structure we call Golgi’s apparatus is to bear his name, it should reflect this fact. The reticulum that Golgi described may have been discovered many years earlier by La Valette St. George (1865, 1867; see Whaley 1975 for historical perspective). What Golgi did, however, was to devise a histochemical procedure which contrasted the reticulum so vividly that he and his students could effectively study the structure in a variety of eukaryotic cells (Whaley 1975). Current studies of Golgi apparatus confirm it as a reticular structure, with repeating non-reticular units (i.e., the Golgi stacks) that are dispersed (albeit not randomly) within the reticulum. Golgi’s reticulum with its repeating units may be compacted within a confined cellular region as in most mammalian cells, or distributed (but again not randomly) throughout much of the cell as in most plants. What is significant is that all of the repeating units of Golgi’s reticulum appear to function synchronously; i.e., there seems to be but a single Golgi apparatus within each cell. It is this composite structure that we have called the Golgi apparatus (Mollenhauer and Morrè 1965, 1966a). The punctate units, or stacks of saccules (i.e., stacks of cisternae), were called dictyosomes or, more recently, stacks (a more universal and descriptive term). However, the term dictyosome (Perroncito 1910) should not be abandoned because it literally means “net-body” which is a most apt description. The terms dictyosome and stack can be applied to the non-reticular units of both plant and animal Golgi apparatus.