A Compact and a Dispersed Form of the Golgi Apparatus of Fish Liver[1]

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Abstract

A large, complex Golgi apparatus consisting of many closely aligned dictyosomes (stacks of Golgi apparatus cisternae) is characteristic or normal hepatocytes of the green sunfish *(Lepomis cyanellus)*. In contrast, livers from fish exposed for 24 hours to 10^{-4} Molar technical picloram (91% 4-amino-3,5,6-trichloropicolinic acid) contained Golgi apparatus consisting of distinct, often widely separated, dictyosomes. These results, plus other examples of reversible coalesence and separation of dictyosomes to yield alternating compact and dispersed forms of the Golgi apparatus, support the concept that all Golgi apparatus share a common pattern of organization based on varying degrees of association among dictyosome subunits.

The Golgi apparatus has been defined as that part of the cell's endomembrane system consisting of interassociated dictyosomes (3, 5). This definition of the Golgi apparatus is based on morphological concepts not yet universally accepted due to differences of opinion and terminology that exist among investigators. However, a definition based on the organization of dictyosome subunits into Golgi apparatus facilitates the recognition that all Golgi apparatus, both plant and animal, may share a common pattern of organization.

By the above definition, the form and extent of Golgi apparatus will vary from cell to cell depending on how the dictyosomes are arranged (Fig. 1). In the Golgi apparatus of plants, invertebrates and some animal germ cells, the dictyosomes are concentrated in certain regions of the cytoplasm but appear as discrete organelles. This arrangement we refer to as the "dispersed" form of the Golgi apparatus (Fig. 1A). In most somatic cells of higher animals, the dictyosomes are arranged end to end, close together, in a localized, often curved, array. This we refer to as the "compact" form of the Golgi apparatus (Fig. 1B).

Evidence presented in this paper demonstrates that under appropriate conditions, both the dispersed and compact form of Golgi apparatus exist in the same cell type. The results support our contention that all Golgi apparatus share a common pattern of organization based on varying degrees of association among dictyosomes.

[1] Supported in part by a grant from the NSF GB 23183. Journal Paper 4258. Purdue University Agricultural Experiment Station.

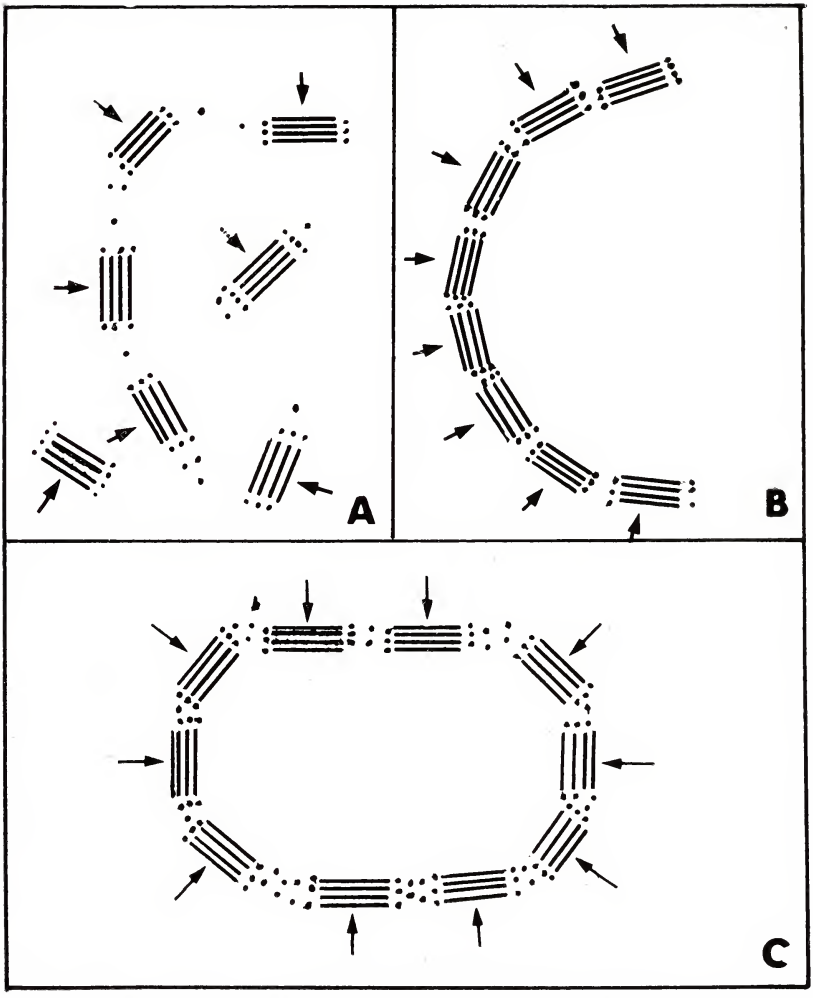

FIGURE 1. *Diagram illustrating principal forms of the Golgi apparatus. Arrows indicate individual dictyosomes (stacks of plate-like regions of Golgi apparatus cisternae, the "saccules", interrupted by discontinuous tubular or fenestrated regions).* A. *The dictyosomes are dispersed as is characteristic of plants, invertebrates and some animal germ cells.* B. *The dictyosomes are compactly arranged to form a localized, curved array as is characteristic of most somatic animal cells.* C. *A variation of the compact form of the Golgi apparatus in which the dictyosomes are arranged in a cylindrical array.*

Materials and Methods

Green sunfish *(Lepomis cyanellus)*, 50-150 g, were maintained in pond water at 24°C with continuous aeration in the presence or absence of 10^{-4} M technical picloram (91% 4-amino-3,5,6-trichloropicolinic acid). After 24 hours, the livers were excised and portions fixed at 0-4° C in 2.5% glutaraldehyde (Fisher, Biological Grade) in 0.1 M

sodium phosphate at pH 7.2 followed by a buffer rinse and post fixation in 1% osmium tetroxide in the same buffer. Specimens were dehydrated in a graded acetone series and embedded in Epon (9). Thin sections were post-stained with lead citrate (7) after being mounted on carbon-coated, parlodion-covered grids and were viewed with a Philips EM-200. Magnifications are approximate.

Results

In normal fish livers, the cells contain Golgi apparatus of considerable complexity (Fig. 2). The numerous, closely spaced dictyosomes are compactly arranged into a distinct Golgi apparatus zone with secretory vesicles at one or both faces. The Golgi apparatus may appear straight, curved or cylindrical. In Figure 2, the Golgi apparatus is in the form of a hollow cylinder with the system of interassociated dictyosomes forming the wall of the cylinder (*cf.* Fig. 1C).

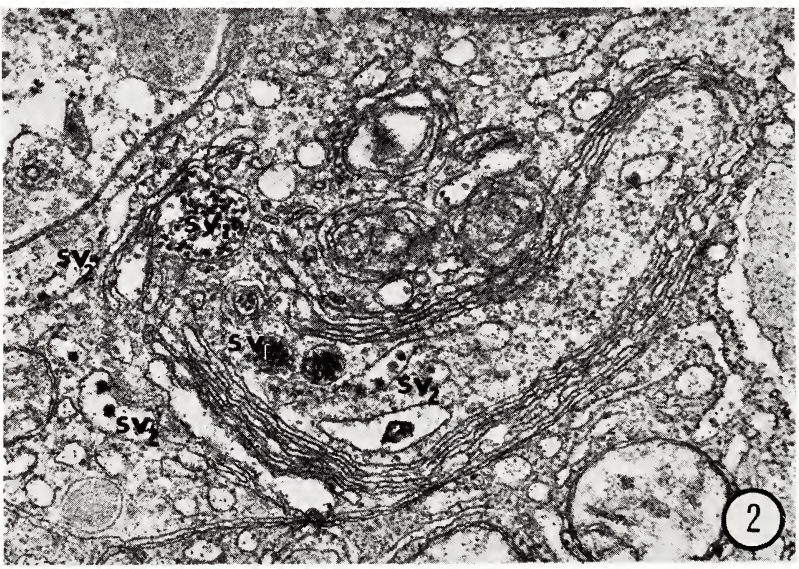

FIGURE 2. *Electron micrograph of a portion of the Golgi apparatus from the liver of a control fish showing the compact arrangement of dictyosomes in cylindrical array (compare with Figure 1C). Two types of secretory vesicles are illustrated. One has a compact appearance with many small, dark-staining particles and often a dark-staining matrix* (SV_1). *The other has a swollen appearance with scattered dark-staining particles of larger diameter and a non-staining matrix* (SV_2). *Compare with Figure 4. X 32,300.*

Livers of fish treated for 24 hours with 5×10^{-4} M picloram were characterized by Golgi apparatus consisting of discrete dictyosomes, frequently widely separated, within the Golgi apparatus zone (Fig. 3). Frequently the dictyosome cisternae were curled or in the form of rings.

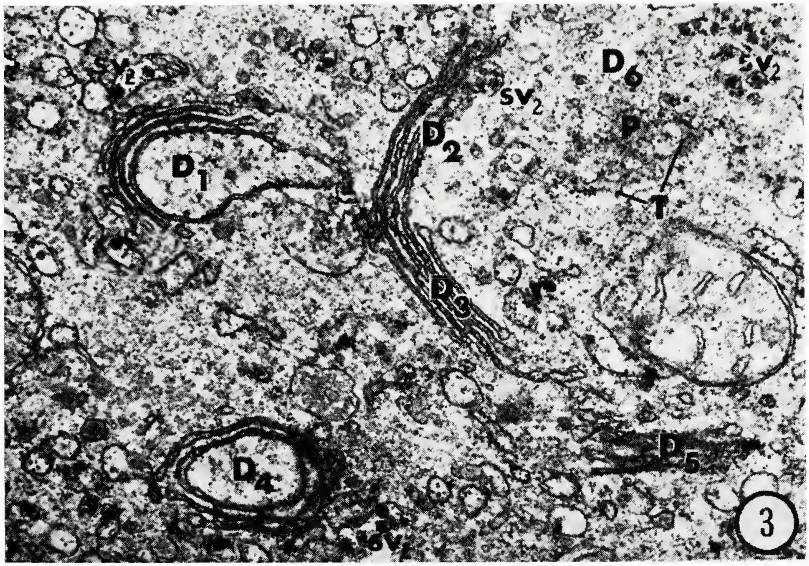

FIGURE 3. *Electron micrograph of a portion of the Golgi apparatus from the liver of a fish exposed for 24 hours to 10^{-4} M technical picloram (91% 4-amino-3,5,6-trichloropicolinic acid) showing the dispersed arrangement of dictyosomes* (D_1 - D_6). D_6 *is sectioned tangentially and reveals a portion of a cisterna in face view with a central plate-like region* (P) *and tubules* (T) *at the periphery of the plate or "saccule". Lipoprotein particles are restricted to elements of the smooth reticulum and the swollen vesicles* (SV_2) *which contain the large lipoprotein particles. X 33,500.*

In normal fish livers, secretory vesicles of the Golgi apparatus contain darkly osmiophilic particles 250-600 Å in diameter corresponding to lipoprotein particles of mammalian hepatocytes (Figs. 2 and 4). Similar staining particles, but frequently of larger diameter (500-650 Å), are found within the cavities of the smooth endoplasmic reticulum and in the sinusoidal space suggestive of secretory activity. Additionally, lipoprotein-containing secretory vesicles of the Golgi apparatus appear to be of two types. One type has a compact appearance with many small, dark-staining particles and a dark-staining matrix. The other has a swollen appearance with scattered dark-staining particles of larger diameter and a non-staining matrix (Fig. 4). In livers of fish treated for 24 hours with 5×10^{-4} M picloram, conspicuous lipoprotein-containing secretory vesicles were absent from the Golgi apparatus although lipoprotein particles were still present in the smooth endoplasmic reticulum. The type of secretory vesicle characterized by a dark matrix was completely absent from livers of treated fish but a few of the swollen vesicles containing larger lipoprotein particles remained associated with the dictyosomes. (Fig. 3).

Discussion

Dictyosomes of the Golgi apparatus, or simply dictyosomes, are the individual stacks of plate-like cisternae and associated tubules which

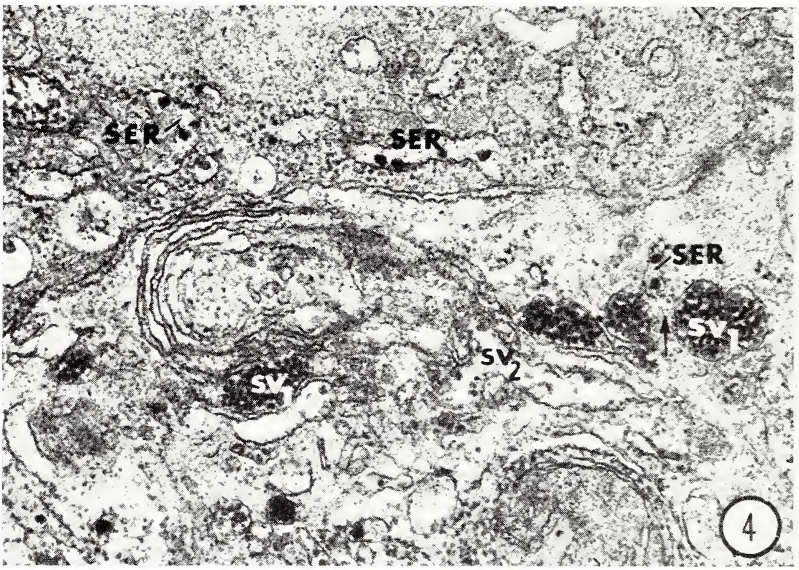

FIGURE 4. *As in Figure 2 but showing the two types of secretory vesicles more clearly. Segments of smooth endoplasmic reticulum (SER) containing large lipoprotein particles are located at the Golgi apparatus periphery and at the top of the micrograph. Continuity between smooth endoplasmic reticulum (SER) and a secretory vesicle* (SV1) *is shown at the arrow. X 39,000.*

form the Golgi apparatus of plant and animal cells (3, 5). The individual dictyosomes of a Golgi apparatus may be compactly arranged into distinct Golgi apparatus zones as in normal fish livers and most mammalian cells, or dispersed in the form of distinct subunits within the Golgi apparatus zone as in picloram-treated fish, plants, invertebrates and germ cells (*cf.* Fig. 1). As discussed in an accompanying report (8), we do not know what material contained in the 91% technical picloram is responsible for the ultrastructural changes. Picloram itself is relatively non-toxic to fish but an impurity, 2-(3,4,5,6-tetrachloro-2-pyridyl) guanidine, is highly toxic (8) and may be the active material.

As discussed by Morré *et al.* (5), the formation of large, complex Golgi apparatus consisting of many closely aligned dictyosomes could result from either the aggregation of widely spaced dictyosomes or from multiplication of dictyosomes without extensive separation. The first of these interpretations is favored in spermatids where rapid fusion of dictyosomes forms the large, aggregate Golgi apparatus of the acroblast (2, 6). The second interpretation is favored in studies of the fungus *Pythium aphanidermatum* where closely spaced dictyosomes are observed during cell division when dictyosome multiplication occurs (C. E. Bracker, S. N. Grove and D. J. Morré, unpublished data).

Reversible fusion and separation of dictyosomes to yield alternating compact and dispersed Golgi apparatus was reported by Pollister (6)

during early stages of spermatogenesis in *Gerris*, in maize roots subjected to cold treatment (4) and by Heintz and Bracker (C. Heintz and C. E. Bracker, unpublished data). In the study by Heintz and Bracker, Golgi apparatus in sporangia of the fungus *Pythium middletonii* shortly before cell cleavage to form zoospores appear as clusters of closely associated dictyosomes. Subsequently, and at other stages of the life cycle, these specialized formations of dictyosomes are lacking, and the Golgi apparatus consists of separated dictyosomes.

The results show that both the dispersed and compact forms of the Golgi apparatus can exist within the same cell type and that the Golgi apparatus of plant and animal cells are homologous structures. Except to insure synchronous function (3), there is little evidence to explain how the degree of association might affect dictyosome function.

Acknowledgments

We wish to thank Mr. Michael Sergeant, Mr. John H. Elder and Miss Denise Blazek for assistance in conducting these experiments and Dorothy Wederitsh for technical assistance.

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