STRUCTURAL DIFFERENCES CONTRAST HIGHER PLANT AND ANIMAL GOLGI APPARATUS

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SUMMARY

The intercisternal spacings between cisternae of dictyosomes of higher plants differ from those of mammalian dictyosomes. In plants, the spacings increase from an average of about 8·0 nm at the forming face to about 14·0 nm at the maturing face. The increase in spacing coincides with the appearance within the intercisternal space of parallel filaments called intercisternal elements. In mammals, the intercisternal spacings are more nearly constant, and intercisternal elements have not been observed. Plant and animal dictyosomes may differ as well in the relative widths of the cisternal lumina, the widths of the intercisternal spacings, and in more subtle ways involving the appearance of the membranes. These structural differences may be indicative of some functional differences that contrast higher plant and animal Golgi apparatus.

INTRODUCTION

This study was undertaken to determine whether fundamental structural differences exist within the intercisternal regions of plant and animal Golgi apparatus. Specifically, we were concerned because (1) higher plant dictyosomes typically had intercisternal elements whereas similar structures have not been reported for animal dictyosomes (Mollenhauer, 1965; Turner & Whaley, 1965; Cunningham, Morré & Mollenhauer, 1966; Mollenhauer, Morré & Totten, 1973) and (2) dictyosomes of higher plants, but not those of animals, could be unstacked by exposure to monovalent salts (Mollenhauer *et al.* 1973). These observations indicated that structural differences might exist between the intercisternal regions of plant and animal dictyosomes.

MATERIALS AND METHODS

All tissues were prefixed in phosphate- or cacodylate-buffered glutaraldehyde or glutaraldehyde–paraformaldehyde, postfixed in osmium tetroxide, block-stained in uranyl acetate, and embedded in epoxy resin as described previously (Mollenhauer, 1963; Mollenhauer & Morré, 1975). Photographs of dictyosomes were from transverse sections through the midplane of the dictyosomes. All dictyosomes were photographed at an initial magnification of 33000 × or greater and subsequently enlarged to a print magnification of 150000 × or 240000 × . Measurements were from these prints using a Bausch and Lomb compound loupe (8 ×) with a 0·1-mm scale. Three measurements were obtained at parts of the cisternae where contiguous membranes were approximately parallel. Mean values of each cell type were used in the statistical analysis.
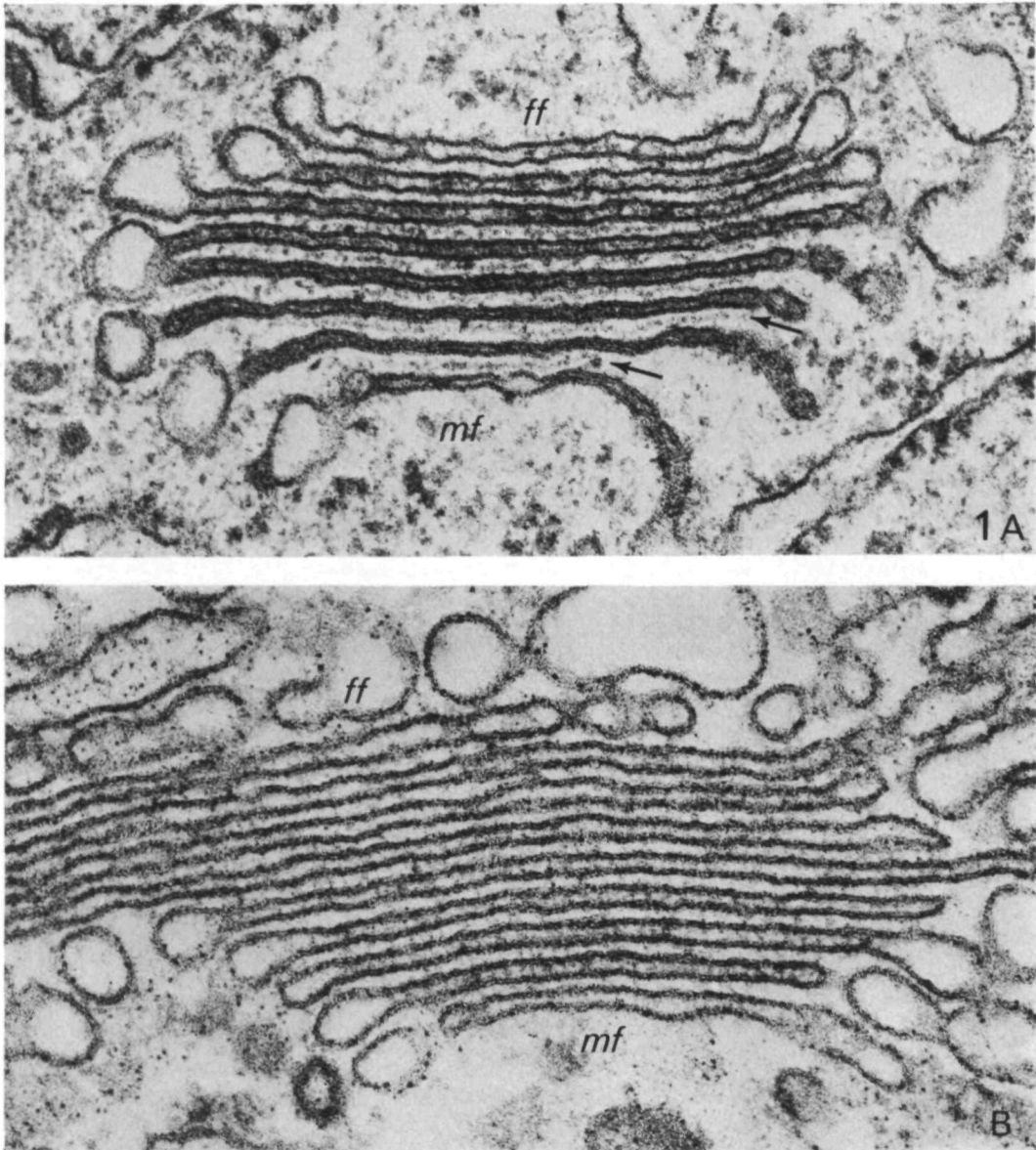
Fig. 1. Comparison of plant and animal dictyosomes.

A. Dictyosome from a leaf of *Vicia faba* showing that the increase in intercisternal widths is gradual from the forming face (*ff*) to the maturing face (*mf*) of the dictyosome, that the increase in intercisternal width is related to the presence of intercisternal elements (see arrows for examples), and that cisternal differentiation across the dictyosome is clearly depicted in terms of cisternal widths and membrane characteristics.

B. Dictyosome from a rat epididymal cell showing that intercisternal widths are relatively constant across the dictyosome, that no intercisternal elements are visible, and that differentiation across the dictyosome is not pronounced. *ff*, forming face; *mf*, maturing face. Both × 120000.

RESULTS AND DISCUSSION

The intercisternal spacings of the plant dictyosomes increased toward the mature pole of each dictyosome (Fig. 1A, Table 1). The mean spacing between cisternae was in the range of 6·6–9·7 nm at the forming face and 9·7–18·0 nm at the maturing face. Within a given dictyosome, the increase in spacing was progressive with each succeeding cisterna toward the maturing face (Fig. 1). Preliminary observations indicated that there was also a decrease in cisternal width concomitant with the increase in intercisternal spacing (Fig. 1). Thus, the overall distance between comparable parts of adjacent cisternae was approximately constant.

Table 1. *Plant cells: minimum mean intercisternal spacing between adjacent cisternae*

| | nm ± s.e. | | |
| | Forming face | Maturing face* | No. of determinations |
Tissue and cell type			
Bean leaf epidermis	9·7 ± 0·52	16·7 ± 1·59	10
Bean leaf parenchyma	8·1 ± 0·32	14·5 ± 1·07	8
Bean leaf phloem	8·5 ± 0·87	13·2 ± 0·95	4
Bean leaf stomate	8·0 ± 1·00	16·5 ± 0·50	2
Bean leaf trichome	8·9 ± 1·04	18·0 ± 1·37	6
Cauliflower inflorescence	7·4 ± 0·28	9·7 ± 0·65	15
Maize root epidermis	7·3 ± 0·24	12·8 ± 0·65	12
Maize root inner mantle	7·2 ± 0·34	11·3 ± 0·34	12
Maize root cap initial	8·0 ± 0·10	12·0 ± 0·30	2
Maize root cortex	7·1 ± 0·24	11·2 ± 1·07	5
Petunia stigma	7·0 ± 0·10	10·0 ± 0·21	2
Poppy pollen	6·6 ± 0·38	10·5 ± 0·65	4
Average of all cells	7·8 ± 0·24**	13·5 ± 0·84**	82

* Note. Intercisternal elements were visible in all of the dictyosomes examined.
** Significantly different at the 0·01 confidence interval.

The increase in intercisternal spacing could be correlated with the presence of intercisternal elements (Fig. 1A). These 3·0- to 5·0-nm-thick filaments characteristically occupied a part of the intercisternal space midway between the flattened parts of adjacent cisternae. They appeared in micrographs either as dense lines or as linear arrays of particles, depending upon orientation. All of the higher plant cell dictyosomes examined had intercisternal elements.

The intercisternal spacing of animal dictyosomes was relatively constant from the forming to the maturing face (Fig. 1B, Table 2). The mean intercisternal spacing for all animal dictyosomes was 8·5 ± 0·15 nm. Intercisternal elements were not visible in any of the animal cell dictyosomes examined.

Two of the cell types sampled proved to be exceptions in relation to the intercisternal spacings. These were the outer root cap cells of maize and cells of *Euglena gracilis*. In the outer root cap cells of maize, the intercisternal elements were associated with the secretory vesicles rather than with the central (or flattened) parts of the cisternae

(Mollenhauer & Morré, 1975). The intercisternal spacings were relatively constant across the dictyosome with mean values of 7.8 ± 0.16 and 7.6 ± 0.2 nm for the central (flattened) parts of the dictyosome cisternae at the forming and maturing faces respectively (Table 3). However, the spacings between immature and mature secretory vesicles were 13.8 ± 0.49 and 15.0 ± 0.44 nm, respectively (Table 3). These larger spacings between vesicles were associated with regions containing intercisternal

Table 2. *Animal cells: minimum mean intercisternal spacing between adjacent cisternae*

| | nm ± S.E. | | |
| | Forming face | Maturing face* | No. of determinations |
Tissue and cell type			
Chicken liver	8.1 ± 0.13	8.1 ± 0.13	15
Deer retinal rod	8.3 ± 0.33	8.3 ± 0.33	3
Guinea-pig sertoli cell	8.9 ± 0.26	9.2 ± 0.32	9
Guinea-pig spermatid cell	9.3 ± 0.33	9.7 ± 0.32	3
Rat alveolar macrophage	8.7 ± 0.37	8.7 ± 0.37	5
Rat epididymis principal cell	9.1 ± 0.25	8.9 ± 0.23	7
Rat kidney convoluted tubule	9.1 ± 0.90	8.6 ± 0.69	4
Rat liver	8.5 ± 0.32	8.6 ± 0.33	11
Rat pancreas acinar cell	9.2 ± 0.17	9.1 ± 0.25	15
Rat sertoli cell	7.9 ± 0.17	8.1 ± 0.19	13
Rat spermatogonium	7.8 ± 0.31	7.9 ± 0.27	6
Rat spermatid	7.9 ± 0.18	7.5 ± 0.17	9
Rat residual body	8.9 ± 0.18	8.9 ± 0.18	10
Rat leydig cell	7.9 ± 0.24	7.6 ± 0.24	4
Average of all cells	8.5 ± 0.15	8.5 ± 0.17	114

* Note. No intercisternal elements were visible in any of the dictyosomes examined.

Table 3. *Outer root cap cells of maize: minimum mean intercisternal spacings comparing cisternae and secretory vesicles*

| | nm ± S.E. | | |
	Forming face	Maturing face	No. of determinations
Cisternae	7.8 ± 0.16	7.6 ± 0.20	15
Secretory vesicles	13.8 ± 0.49	15.0 ± 0.44	13

Note. Intercisternal elements were visible only between the secretory vesicles.

elements. The intercisternal spacings of *Euglena* dictyosomes were also nearly constant across the dictyosome with mean values of 16.2 ± 0.61 and 16.6 ± 0.59 nm for the forming and maturing faces respectively. No intercisternal elements were found associated with dictyosomes of *Euglena*. *Euglena* dictyosomes sometimes have intercisternal microtubules (Mollenhauer, 1974), and this may account in part for the relatively large intercisternal spacing.

Preliminary evidence indicates that plant and animal dictyosomes may differ also in relation to the relative widths of the cisternal lumina (Figs. 1, 2). In plants, the luminal changes are represented by a gradually decreasing lumen width toward the mature face of the dictyosome. In animals, these changes are much more abrupt. The first, or forming, cisterna of a dictyosome may be distended, especially under conditions where lumina of endoplasmic reticulum also are distended, but a gradient of luminal change across the dictyosome is usually not observed. Additionally, there
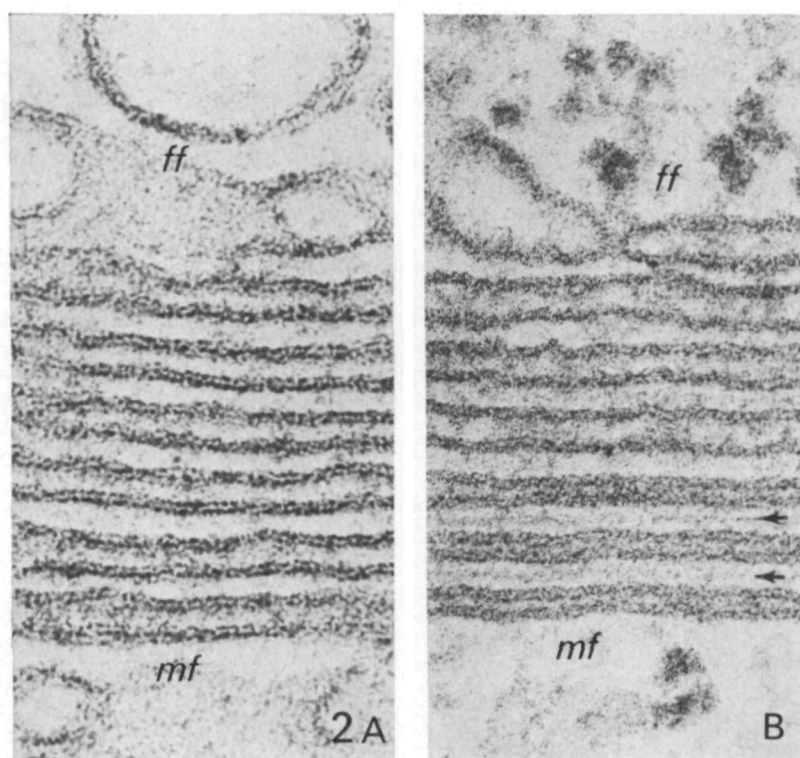

Fig. 2. Membrane changes are usually more pronounced in plant dictyosomes than in animal dictyosomes.

A. Cross-section through a dictyosome from a rat epididymal cell.

B. Cross-section through a dictyosome from a stigmatic cell of a red poppy. *ff*, forming face; *mf*, maturing face. Both × 350 000.

may be differences in the membranes comparing plant and animal dictyosomes (compare Figs. 2A and 2B). One result of these differences is that identification of the forming and maturing faces of plant dictyosomes is much easier than for animal dictyosomes.

The biochemical or functional bases of the above structural differences between plant and animal dictyosomes are unknown. However, the findings suggest that membrane maturation and dictyosome polarity in plant and animal dictyosomes are not identical. These variations may account for the seemingly more complex nature of

secretory vesicle or granule formation in certain nongrowing but secretory animal or plant cells (Morré & Ovtracht, 1977).

The intercisternal spaces of the Golgi apparatus now appear as complex regions capable of modification and change. That the intercisternal regions of plants and animals differ in form provides evidence for a fundamental difference between plant and animal dictyosomes. Thus, new impetus is added to the need to understand the nature of the components of the intercisternal regions and their roles in Golgi apparatus functioning.

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