

## FRAGMENTATION OF MATURE DICTYOSOME CISTERNAE

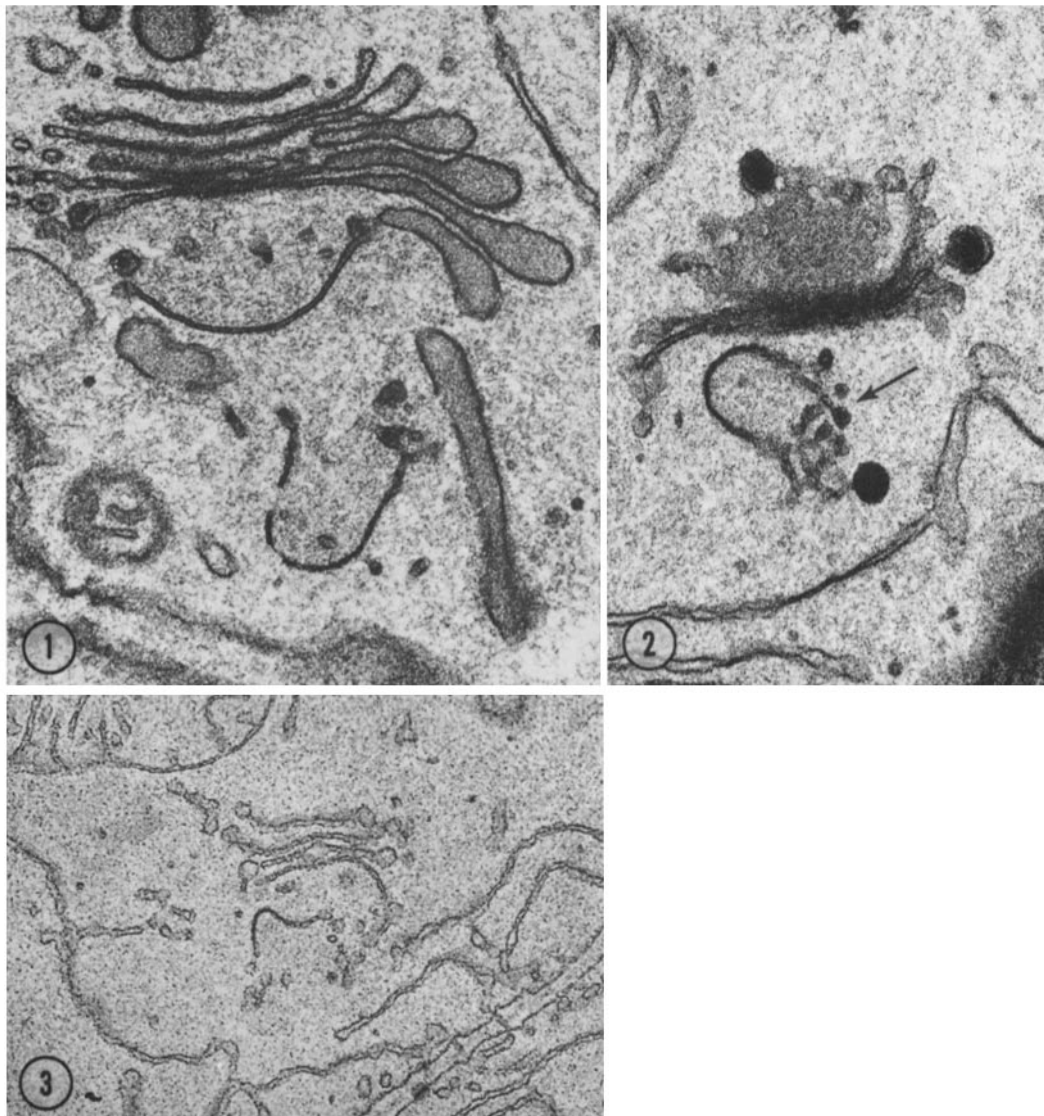
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The formation of secretory vesicles is progressive across the stack of dictyosome cisternae from one of its faces to the other. As a cisterna matures, the secretion vesicles increase in size, and their contents change in staining characteristics, suggesting the accumulation or transformation of product. Vesicles are ultimately released at the maturing face of the dictyosome, apparently by a pinching off of the tubules which connect the secretory vesicles to the flattened, nonsecretory portions of the cisternae. The secretory vesicles migrate to the cell surface where they discharge their product to the cell exterior. These steps are well documented, but there is no information on the fate of the cisterna or cisternal fragments left behind. From the concept of the maturing face and forming face, we know that entire cisternae must be lost from the maturing face as new cisternae are produced at the opposite or forming face. This is emphasized by information that the number of dictyosome cisternae remain relatively constant during periods of active cisternal formation at the immature face and active secretory vesicle production at the mature face; i.e., the processes of cisternal formation and fragmentation are balanced.

The morphological observations on maize root tips reported here suggest that nonsecretory portions of mature cisternae are sloughed from the dictyosomes at or about the same time that secretory vesicles are released into the cytoplasm (Figs. 1 and 2). These sloughed cisternae are frequently found near the mature faces of dictyosomes and are observed in various stages of decomposition. Their lifetime in the cytoplasm is probably short since recognizable cisternal fragments never accumulate. Morphological stages in the release and breakdown of cisternae at the distal face of the

Golgi apparatus seem to involve a breakdown of the cementing substances between the distal cisterna and its nearest neighbor in the stack, release of the cisterna from the stack (Fig. 1), vesiculation of the released cisterna into small tubules and vesicles (Fig. 2), and degradation of the sloughed cisterna, the final breakdown products being below the limits of resolution of the electron microscope. It is conceivable that the breakdown products are reincorporated into the Golgi apparatus as a mechanism for conserving some of the membrane material, but we have no evidence on this point.

The central portions of maize root dictyosomes do not retain significant amounts of secretory product at the time of their release and are not involved directly with the transport of product to the cell surface. However, these cisternal remnants may represent a very significant amount of membranous material delivered to the cytoplasm. For example, externally supplied sugars are transported into and through the Golgi apparatus of root cap cells of wheat in 15–30 min, which suggests rapid secretory vesicle production and release (4). We do not have similar information on rate of turnover of cisternae in maize root cap cells, but estimates from other cell types are in the range of 15–30 min (1, 5). If similar values hold true for maize root cap dictyosomes, then with approximately 400–800 dictyosomes per cell and a cisternal diameter (central region) of about  $0.8 \mu$ , cisternal fragmentation would yield 14–26  $\mu^2$  of dictyosome-derived membrane per minute into the cytoplasm. This is approximately equivalent to the amount of membrane delivered by secretory vesicles to the plasma membrane and represents a considerable turnover of membranous material.



**FIGURE 1** Dictyosome in an outer root cap cell of maize, showing two mature cisternae that are presumably being sloughed from the dictyosome after release of the secretory vesicles. Tissue was fixed in 2% aqueous  $\text{KMnO}_4$ .  $\times 40,000$ .

**FIGURE 2** Dictyosome in an epidermal cell of the maize root tip, showing a mature cisterna separated from the dictyosome. The formation of small tubules and vesicles on sloughed cisternae (see arrow) is very characteristic and may be the result of cisternal degradation. Note the typical tubular connection to the secretory vesicle in the upper left portion of the micrograph. The appearance of a tangential and a transverse section through the dictyosome is due to the fact that some cisternae are sufficiently curved to present several aspects of structure in a single plane of section. Tissue was fixed in 2% aqueous  $\text{KMnO}_4$ .  $\times 35,000$ .

**FIGURE 3** Dictyosome from a cortical cell of the maize root tip, showing a mature cisterna which, we believe, has been sloughed from the dictyosome. Tissue was fixed in 2% aqueous  $\text{KMnO}_4$ .  $\times 30,000$ . (approx).

Whether these sloughed cisternae are associated with the endoplasmic reticulum, or whether they give rise to lysosomal particles, as similar structures do in animal tissues (see GERL, reference 3), is not yet clear. Acid phosphatase is a component of mature cisternae in these cells (2; Mollenhauer, unpublished data) but is not easily demonstrated in the same cisternae once they are separated from the dictyosomes. It is not clear, however, whether this loss in activity is due to the vagaries of the histochemical procedure or to a real deactivation or loss of the phosphatase activity. In any event, it seems reasonable to suppose that the lysosomal components of the cisternae could account, at least partially, for the rapid degradation and loss of sloughed cisternae.

Fragmentation of mature cisternae is not limited to secretory cells, for some discarded cisternae are always visible in cortical cells and other nonsecretory cells of the maize root tip (see, for example, Fig. 3). Discarded cisternae can also be found in other plant and animal cells. This phenomenon is not restricted to maize root tip cells. These observations suggest that sloughing of mature dictyosome cisternae is a relatively general phenomenon

and might be one of the mechanisms by which dictyosomes maintain uniform numbers of cisternae.

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