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NOTES

ON SQUARE HOLES IN PENNATE DIATOMS

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Square holes observed in the walls of the pennate diatoms may be due to cubic crystals inside the silicalemma that interfere with silica deposition, or cause its dissolution shortly after deposition. Their presence is consistent with models of valve morphogenesis by diffusion limited precipitation of amorphous silica without any pre-pattern.

Idei & Kobayasi (1989) have observed square holes in the outer wall of the alveoli of the pennate diatom *Diploneis finnica*, and noted published examples in *Navicula pygmaea* Kütz. The number of holes varied from 0 to 3 per valve. The holes illustrated in their article were all slightly less than 1 μm on a side. They appear to penetrate into the depth of the valve, which is also about 1 μm thick. Idei & Kobayasi (1989) entertained, but rejected, two external causes for square holes: "It seems difficult to consider them as simple breaks or artifacts... Our observations of the living cells found no trace of parasites such as fungi, etc."

We would like to propose a simple internal mechanism, intimately related to valve morphogenesis: square holes are formed by precipitation of a cubic crystal from the mother liquor inside the silicalemma, at the time of precipitation of silica around the crystal. The strongest suggestion of this hypothesis is the observation: "These openings are usually restricted to positions close to the margin of the valve in the median and polar regions" (Idei & Kobayasi 1989). Since precipitation of the valve occurs inside a small volume of fluid (presumably mostly water) within the silicalemma, as precipitation proceeds and solid silica occupies a higher fraction of the volume, the remaining fluid (the mother liquor) will contain son-silica solutes at ever increasing concentrations. In raphid diatoms silica precipitation seems to proceed from the region of the raphe towards the valve margins (Schmid 1979, 1984). Thus we would anticipate that the mother liquor at the growing edge of the precipitated silica would attain the highest concentration of non-silica solutes. In some cases, substances in the mother liquor might themselves precipitate, because they are driven to concentrations past their threshold saturation points (Fig. 1).

The apparently random orientation of the square holes with respect to the costae (Idei & Kobayasi 1989) suggests that crystal nucleation is not orientated with respect to the direction of growth of the costae. If an epitaxial mechanism of costa formation were involved, such as has been postulated by Hecky *et al.* (1973), we might anticipate alignment of crystals with these authors' hypothesized pre-

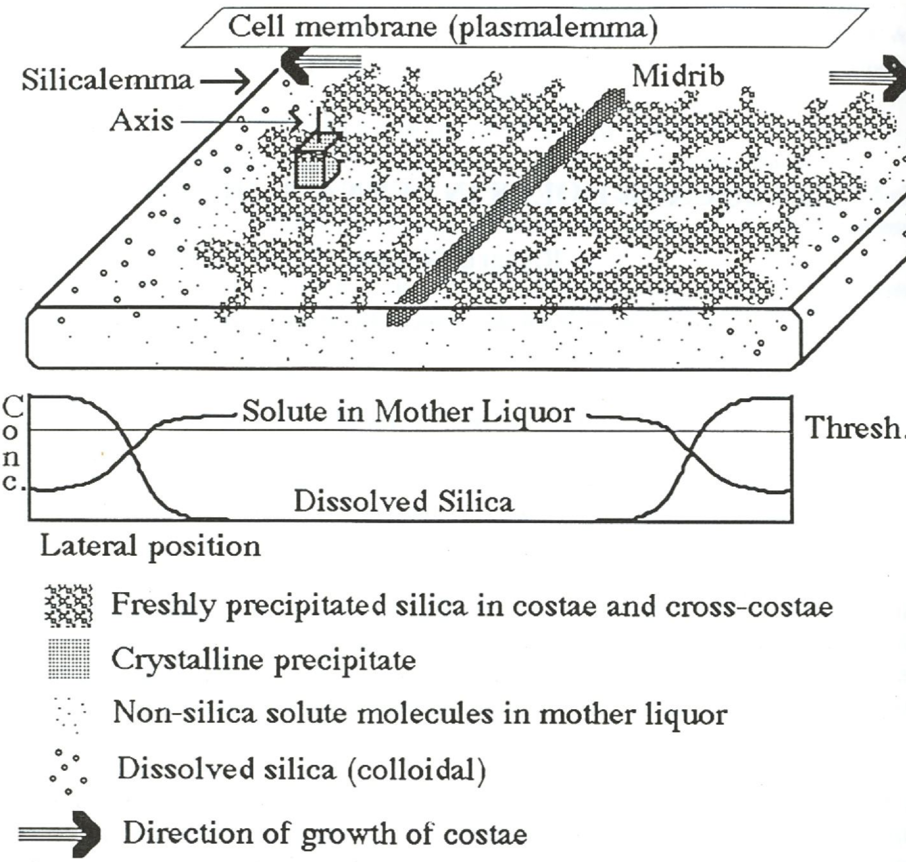

Fig. 1. Schematic diagram of silica precipitation in a pennate diatom. The silica is nucleated at the nascent midrib and grows laterally within the silicalemma in both directions. As it grows, silica is depleted from the aqueous medium within the silicalemma. However, other solutes in the mother liquor increase in concentration (**Conc.**). This increase is greatest at the lateral margins of the silicalemma, where, if the concentration of a non-silica solute passes its threshold (**Thresh.**) for precipitation, a crystal may form. (The crystal may be at any angle around its vertical axis.) The amorphous silica is thus forced to precipitate around the crystal, or redissolve as the crystal grows into it. (Note that the silicalemma lies parallel to and just within the cell membrane.)

pattern mechanism for silica deposition. On the other hand, the presence of randomly orientated cubic crystals inside the silicalemma is consistent with our hypothesis that diatom valve morphogenesis proceeds with no pre-pattern, by undirected diffusion-limited precipitation of amorphous silica (Gordon 1981, Gordon & Aguda 1988). One can imagine that the pattern of silica around the cubic crystals is slightly perturbed by the presence of the crystal, especially near the two holes in fig. 36 of Idei & Kobayasi (1989), where cross-costae are missing. On the other hand, one could equally imagine that growth of a cubic crystal might not finish until after the silica precipitated around it. In this case, the growing crystal might force dissolution of the neighbouring silica, which could leave the valve pattern with a clean hole. The other figures in Idei & Kobayasi (1989) show holes that do not appear to alter the silica pattern. Perhaps both processes occur.

Crystals are the only structures that we can conceive that would form and maintain sharp corners at this size scale, for the time it takes the diatom to construct a valve. Indeed, most of the corners of