Physical Aspects of Evolutionary Transitions to Multicellularity

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A fundamental issue in evolutionary biology is the emergence of multicellular organisms from unicellular individuals. The accompanying differentiation from motile *totipotent* unicellular organisms to multicellular organisms having cells specialized into reproductive (germ) and vegetative (soma) functions, such as motility, implies both costs and benefits, the analysis of which involves the physics of buoyancy, diffusion, and mixing.

In this talk, I discuss recent results from an investigation of the uni- to multicellular transition in a model lineage: the volvocine green algae. These range from *Chlamydomonas*, a unicellular, biflagellated, photosynthetic green alga less than 10 microns in size to *Volvox*, a colonial organism that can reach 1 mm across, composed of thousands of somatic cells (structurally like *Chlamydomonas*) on the surface of a sphere which contains a small number of germ cells. An important issue is thus the relationship between metabolic requirements and environmental metabolite exchange with increasing size.

For organisms whose body plan is a spherical shell, the current of needed nutrients grows quadratically with radius, whereas the rate at which diffusion alone exchanges molecules grows linearly, leading to a bottleneck radius beyond which the diffusive current cannot meet metabolic demands. How has nature dealt with this conundrum? Organized beating by the somatic cells' flagella clearly allows these organisms to swim, but could the resultant fluid flow play a role in the metabolic activity? In other words: Is there a link between *motility*, *mixing*, and *multicellularity*? I describe two approaches to this problem.

First are experiments that quantify the role of advective dynamics in enhancing productivity in germ-soma differentiated colonies. We found [1] that that *deflagellated* colonies lose productivity relative to normal colonies, but forced advection returns productivity to normal. Imaging of fluid motion around colonies reveals flows with very large characteristic velocities U extending to length scales comparable to the colony radius R. For a typical metabolite diffusion constant D,the associated Peclet number $Pe = 2UR/D \gg 1$; advection dominates diffusion, with striking augmentation at the cell division stage. Second, we have found [2] that the flagella-driven advection generates a boundary layer of concentration of a diffusing solute, and that concentration gradient produces an exchange rate which is quadratic in the radius, as required, thus circumventing the bottleneck and facilitating evolutionary transitions to multicellularity and germ-soma differentiation in the volvocine green algae.

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[1] C.A. Solari, S. Ganguly, J.O. Kessler, R.E. Michod, and R.E. Goldstein, *Proc. Natl. Acad. Sci. (USA)* **103**, 1353 (2006).

[2] M.B. Short, C.A. Solari, S. Ganguly, T.R. Powers, J.O. Kessler, R.E. Michod, and R.E. Goldstein, *Proc. Natl. Acad. Sci. (USA)* **103**, 8315 (2006).