Nutrient Uptake Constraints, Multicellularity, and Increased Complexity in Volocales. C. A. Solari, Biología Comparada de Protistas, IBBEA, CONICET-UBA, Buenos Aires, 1428, Argentina. Email: casolari@bg.fcen.uba.ar.

On Earth and maybe on other planets, life originated and evolved in a world of low Reynolds number, *Re* = $RV\rho_w / \eta$ <1 [1], where *R* can be a microorganism's radius, *V* its swimming or flow speed around it, η water viscosity, and ρ_w water density. In this "creeping flow" or "Stokes" regime, motion is dominated by friction, flows are linear and time reversible, and transport is dominated by diffusion. The transport of dissolved nutrient molecules into the organism is proportional to the molecular concentration gradient. The magnitude of this gradient depends on the remote concentration of the molecules and on the rate at which those molecules are absorbed. This is the basic conventional wisdom regarding the dynamics of microorganisms.

Selective pressures, such as predation, pushed microorganisms to increase in size [2]. Yet, general constraints set an upper limit to cell size, such as the decrease in the surface to volume ratio. Given these constraints, certain organisms increased in size by increasing cell number, generating multicellular organisms.

However, increased size entails novel costs. Nutrient consumption increases proportionally with size, creating an increased boundary layer of nutrient depletion. This transport limitation can be circumvented by passive solutions, such as the formation of elongated cells, or by active solutions in which collective flagellar beating move liquid medium past the cellular cluster. The flows associated with swimming can greatly increase transport rates by advection and mixing of molecules.

The relative importance of these processes can be evaluated by a ratio of time constants for diffusion ($t_{diff} = L^2/D$) and advection ($t_{adv} = L/V$) called Peclet number ($Pe = LV/D$), where *V* is again a fluid or swimming speed, *L* a characteristic dimension such as the organism's radius, and *D* the diffusion coefficient of a molecule such as O_2. If *Pe*<1, diffusion is faster than the transport of molecules by advection via the flowing medium, whereas if *Pe*>1, advection is important.

The volvocine green algae are an ideal model system for studying the unicellular-multicellular transition since they comprise an assemblage of lineages featuring varying degrees of complexity in terms of colony size, colony structure, and cell specialization [3-5] (Fig. 1A-E). These motile freshwater bi-flagellated organisms range from unicellular species such as *Chlamydomonas* (A), to 4-64 celled colonies with no cellular differentiation, e.g., *Gonium* (B), *Eudorina* (C) to multicellular ~10^3-10^4 celled individuals with complete germ-soma separation, e.g., *Volvox* (E).

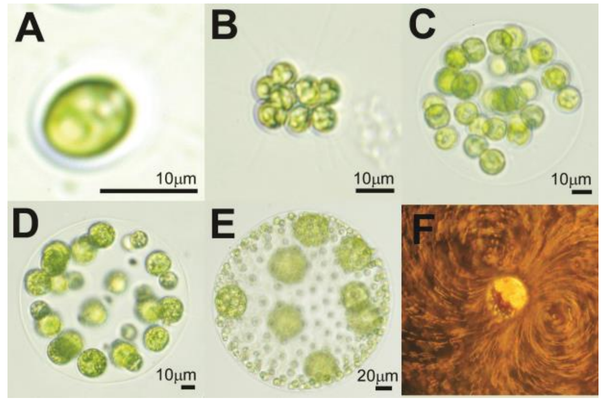

Fig. 1. Volvocales arranged according to organism size. *Chlamydomonas reinhardtii* (A), *Gonium pectorale* (B), *Eudorina elegans* (C), *Pleodorina californica* (D), *Volvox carteri* (E), and time-exposure of *V. carteri* self-generated flows (F).

For organisms whose body plan is a spherical shell, such as the Volvocales, 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 where the diffusive current cannot meet metabolic demands [6]. But, the evolution of cell differentiation allowed the viability of large Volvocales. The flagellar beating of the surface somatic cells enhances nutrient uptake by mixing the boundary layer of the diffusing solute, producing an exchange rate that is quadratic in the radius, thus circumventing the bottleneck (Fig. 1F). The collective flagellar beating increases the speed (*V*) and distances (*L*) of the flows, so *Pe* >> 1 for large multicellular colonies. For example, *Pe*<1 for *Chlamydomonas* (A), but in large *Volvox* spheroids (E-F), *Pe*>>1 [7].

In short, advection is not important for a unicell or a small colonial organism, but is important for a large multicellular species. If life evolves and there is a selective pressure to increase in size, multicellularity and increased complexity (i.e., germ-soma separation) might be a solution to counteract the increasing costs of reproducing a larger organism [8].

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