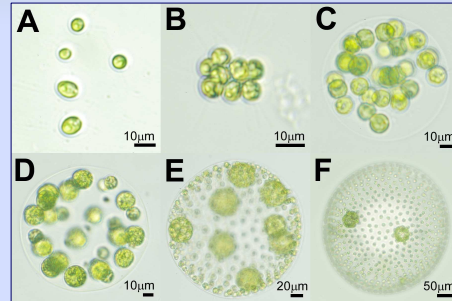


# Artificial Selection for Colony Size in *Pleodorina*

Matthew D. Herron and Richard E. Michod

Department of Ecology and Evolutionary Biology, University of Arizona

**Abstract:** The evolution of mortal somatic cells was a critical step in the evolution of complex body plans and the radiation of multicellular life. The volvocine green algae are a model system for the evolution of differentiation between reproductive and somatic cells. The purpose of this project is to test the hypothesis that the evolution of soma in volvocine algae was driven by trade-offs between motility and fecundity, specifically, by the increasing cost of reproduction in large colonies. The cost of reproduction will be estimated in terms of its effect on motility, an important component of viability. The effect of colony size on this cost will be measured by comparing costs of reproduction across colonies artificially selected for large and small size.



**Figure 1.** Subset of volvocine species: (A) *Chlamydomonas reinhardtii* – one undifferentiated cell, (B) *Gonium pectorale* – a clump of 8 undifferentiated cells, (C) *Eudorina elegans* – a spherical colony of 32 undifferentiated cells, (D) *Pleodorina californica* – a spherical colony of 32 cells of which a few are terminally differentiated, (E) *Volvox carterf* – a spherical colony of up to 4000 terminally differentiated somatic cells and a few specialized reproductive cells, and (F) *Volvox aureus* – a spherical colony of up to 2000 undifferentiated cells and a few specialized reproductive cells. Photos by C. Solari.

## Significance:

Germ-soma (G-S) differentiation is an important threshold on the continuum between groups and individuals<sup>1,2</sup>. By specializing in reproductive and vegetative functions, cells relinquish their individual fitness for that of the group<sup>2</sup>, and the group becomes the unit of selection. Comparisons among volvocine species show that the cost of reproduction increases with colony size<sup>3</sup>, suggesting that G-S differentiation evolved to mitigate such costs. Trends among species, however, may not reflect selective pressures within species, which ultimately drive adaptive evolution. This project will provide a direct test of the hypothesis that G-S differentiation is selected for by an increase in the cost of reproduction as colonies increase in size.

## Overview of project:

### Premises:

- Motility is an important component of viability in volvocine algae.
- Reproduction is costly in terms of motility.
- The cost of reproduction (in terms of motility) increases with increasing colony size across species.

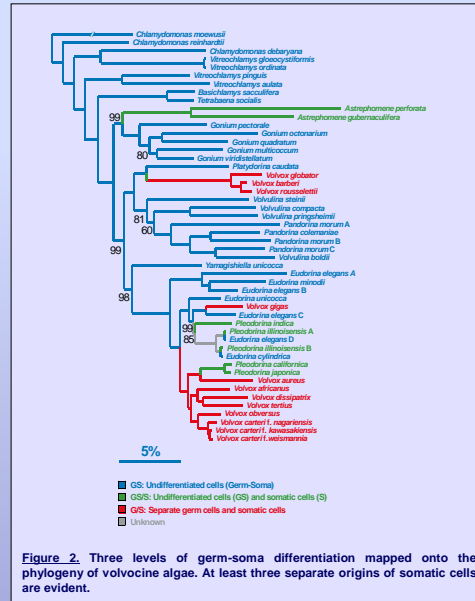
**Hypothesis:** Somatic cells mitigate the cost of reproduction in large volvocine colonies.

### Predictions:

- A measurable genetic trade-off exists between motility and fecundity (the cost of reproduction).
- The cost of reproduction will increase with increasing colony size within a species.
- Colonies will respond to selection on colony size by adjusting their relative investment in somatic cells.

## Methods:

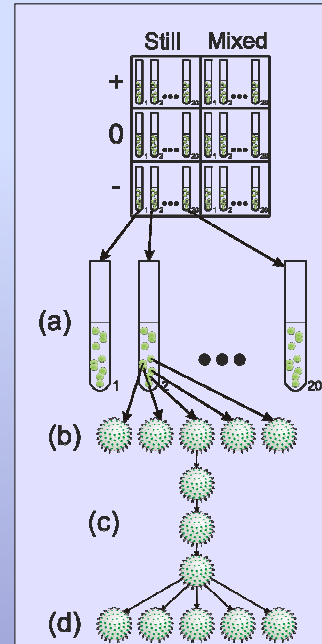
- Found initial populations with sexually produced *Pleodorina starrii* (Figure 1D)
- Artificially select colonies for large and small size (Figure 3)
- Measure cost of reproduction in terms of the effect on motility
- Compare costs of reproduction among colonies of different sizes (Figure 3)
- Compare proportions of somatic cells among treatments
- Induce additional rounds of sexual reproduction if necessary (Figure 4)



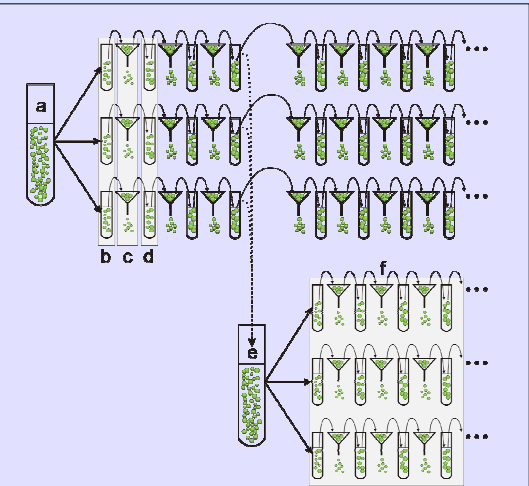
**Figure 2.** Three levels of germ-soma differentiation mapped onto the phylogeny of volvocine algae. At least three separate origins of somatic cells are evident.

## Soma in the volvocine algae:

- At least three separate origins (Figure 2)
- Proportion varies among genera:
  - <15% in *Astrephomene*
  - ~10-50% in *Pleodorina*
  - >99% in *Volvox*
- Only appears in large ( $\geq 32$  cells) colonies
- Proportion generally increases with colony size



**Figure 3.** Experimental design. Each selective treatment ("+" = selection for large size, "-" = unselected control, "-" = selection for small size) will be replicated with twenty populations ("tubes"), a) in still and mixed medium. For statistical analyses, five colonies from each tube will be isolated (b) and propagated for three generations (c) in fresh, still medium to minimize environmental effects. Trait values will be calculated as within-tube means from measurements on five colonies from each tube (d). Differences among colonies within tubes (b, c, d) could include environmental and maternal effects; comparisons of means among tubes (a) are independent comparisons representing genetic differences.



**Figure 4.** Propagation and selection (large size treatment shown). A pool of sexually produced colonies (a) is divided among the initial replicate populations (b). After three generations of asexual propagation, the colonies are filtered (c) and those retained are introduced into fresh medium (d). The process of filtration and asexual propagation is repeated, and the replicate populations are monitored for a leveling-off of the response to selection. If this occurs, subsamples of all replicates within a treatment will be mixed and induced to undergo a second round of sexual reproduction (e). In this case, a second set of replicate populations (f) will be founded from the resulting offspring and maintained in parallel with the original set.

## References:

1. Buss, L. W. 1987. *The Evolution of Individuality*. Princeton University, Princeton, NJ.
2. Michod, R. E. 2006. The group covariance effect and fitness trade-offs during evolutionary transitions in individuality. *PNAS*, 103: 9113-9117.
3. Solari, C. A., J. O. Kessler and R. E. Michod. 2006b. A hydrodynamics approach to the evolution of multicellularity: Flagellar motility and the evolution of germ-soma differentiation in volvocine green algae. *Am. Nat.*, 167: 537-554.

## Acknowledgements:

We thank J. Cushing, G. Davidowitz, R. Ferrière and B. Walsh for helpful advice and C. Solari for providing photographs of volvocine algae.