

Quick guide

Volvox

David L. Kirk

What is Volvox? The name comes from the Latin *volvere*, to roll, and -ox, as in *atrox*, fierce. *Volvox* is a spherical multicellular green alga, which contains many small biflagellate somatic cells and a few large, non-motile reproductive cells called gonidia, and swims with a characteristic rolling motion.

Ever since van Leeuwenhoek first viewed these algal 'fierce rollers' with utter fascination in 1700, one biologist after another has pointed to *Volvox* as a model organism that could be used to support or refute some important biological concept of the day, such as spontaneous generation, preformation, epigenesis, the continuity of the germ plasm, and so on. All attempts to exploit *Volvox* as a laboratory model system failed, however, until the 1960s, when Richard Starr's group finally discovered a medium in which the organism would thrive and reproduce in captivity. Starr then circled the globe, bringing into culture all 18 known (and several previously unknown) *Volvox* species. By 1970, he concluded that a mating pair of isolates of *V. carteri* from Japan had the best combination of properties to serve as a genetic model system. Most studies of *Volvox* reported in the last 30 years have used those strains of *V. carteri* or their descendants, and so this guide will be similarly restricted in scope.

How does Volvox reproduce?

Although *V. carteri* has a sexual cycle that can be induced and exploited for Mendelian analysis, the sexual cycle is not used for reproduction in nature; it is used to produce dormant, diploid zygotes that are able to survive adverse conditions. During all active phases, *Volvox* (like other green algae) is haploid and reproduces asexually.

In *V. carteri*, an asexual cycle begins when each mature

gonidium initiates a rapid series of cleavage divisions, certain of which are visibly asymmetric and produce large gonidial initials and small somatic initials. The fully cleaved embryo contains all of the cells of both types that will be present in an adult, but it is inside out, and to achieve the adult configuration it must turn right-side-out in a gastrulation-like process called inversion. Cleavage and inversion together take about 8 hours, and the complete asexual cycle takes precisely two days when it is synchronized by a suitable light-dark cycle.

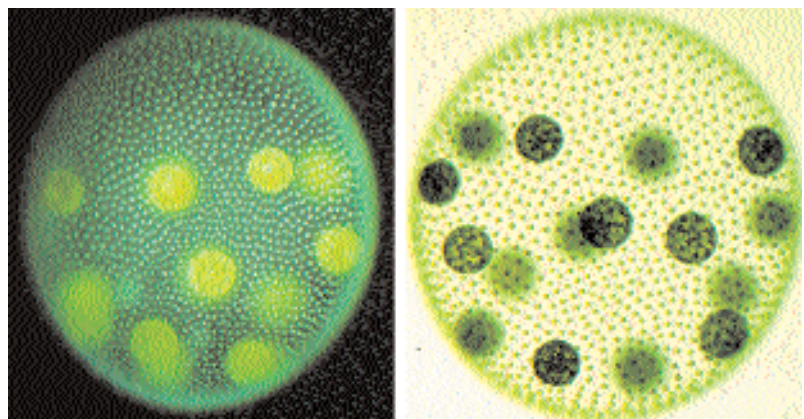
Following inversion, both the adult spheroid and the juvenile spheroids within it increase in size (without further cell division) by depositing large quantities of a glycoprotein-based extracellular matrix. Part way through the expansion phase, the juveniles digest their way out of the parental matrix and become free-swimming. By that time, the somatic cells of the parental spheroids, having fulfilled their function, are already moribund, and will soon be history.

Thus, whereas the gonidia are non-motile and potentially immortal, the somatic cells are specialized for motility, but destined to die when they are only about four days old. This difference raises with particular clarity a central question of developmental biology: how are cells with entirely different phenotypes produced from the descendants of a single cell?

What is the genetic program for germ-soma differentiation in Volvox? In most close relatives of *Volvox*, all cells first execute motility and other vegetative functions, and then they redifferentiate and engage in asexual reproduction. Mutational analysis has defined three types of gene that play the major roles in converting this ancestral program for biphasic development into a germ-soma dichotomy in *V. carteri*: first, the *gls* (gonidialess) genes act during cleavage to permit asymmetric division and formation of large-small sister-cell pairs; then the *regA* (regenerator A) gene acts in the small cells to prevent all aspects of reproductive development, while the *lag* (late gonidia) genes act in the large cells to prevent formation of somatic features such as flagella and eyespots. Genetic and experimental analysis indicates that it is the difference in cell size at the end of cleavage that determines whether *regA* or the *lag* genes will be activated.

Are tools available for molecular analysis of this developmental program?

Although there have never been more than a handful of labs investigating *V. carteri* at any one time, an array of important modern analytical tools have been developed for studying it. These include a transposon-based gene-tagging system, nuclear transformation, inducible-promoter and reporter-gene constructs, GFP-tagging and so on. Such tools have been used to examine in



Darkfield (left) and brightfield (right) micrographs of a young adult spheroid of *Volvox carteri* containing many small somatic cells and a few large, asexual reproductive cells called gonidia.

some detail the functions of the *glsA* gene product, which is required for asymmetric division, and the *regA* gene product, which is required for terminal differentiation of somatic cells. More recently, they have also been used to show that the *invA* gene encodes a novel kinesin that drives inversion.

What can *Volvox* tell us about the evolutionary origins of multicellularity and cellular differentiation? The family Volvocaceae, in which *Volvox* is placed, contains several genera of green flagellates that are intermediate in size and complexity between unicellular *Chlamydomonas* and *Volvox*. Molecular phylogenetic analysis indicates that the family is monophyletic, and shares a common ancestor with *Chlamydomonas* that existed about 50 million years ago. Thus, these algae provide an unrivalled opportunity to analyze a genetic pathway leading from unicellularity to multicellularity with a complete division of labor.

Is there a *Volvox* genome project? Yes. One bacterial artificial chromosome (BAC) library has been produced, a second is in preparation; sequencing of the complete 10^8 base pair *V. carteri* genome is underway.

Where can I find out more?

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Department of Biology, Campus Box 1229, Washington University, St. Louis, Missouri 63130, USA.
E-mail: kirk@biology.wustl.edu

Darwin's dissenter

The Natural History Museum in London is currently celebrating the life of Richard Owen, the naturalist who established the museum and was born 200 years ago last month, but for all his achievements, he was implacably opposed to Darwin's work.

Owen had originally enjoyed a working relationship with the younger Charles Darwin, but as a devout Christian, Owen saw creation as a series of

experiments by a Creator, and he was outraged by Darwin's *On the Origin of Species*.

He is famous for his creation of the word 'dinosaur' and a 25-year campaign to create one of the world's great museums. He secured his reputation as a palaeontologist for his reconstruction of the first archaeopteryx and as an anatomist for the identification of the duck-billed platypus as a mammal.



Museum man: Richard Owen never accepted Darwin's views on evolution but founded one of the world's greatest natural history museums in London. (Picture: Natural History Museum.)