Texto sobre algas Volvocales (extraido de Gilbert, Development Biology, 3rd ed.

In *Volvox*, almost all the cells are somatic, and very few of the cells are able to produce new individuals. In some species of *Volvox*, reproductive cells, as in *Pleodorina*, are derived from cells that originally look and function like somatic cells before they enlarge and divide to form new progeny. However, in other members of the genus, such as *V. carteri*, there is a complete division of labor: the reproductive cells that will create the next generation are set aside during the division of the original cell that is forming a new individual. The reproductive cells never develop functional flagella and never contribute to motility or other somatic functions of the individual; they are entirely specialized for reproduction.

Thus, although the simpler volvocaceans may be thought of as colonial organisms (because each cell is capable of independent existence and of perpetuating the species), in *V. carteri* we have a truly multicellular organism with two distinct and interdependent cell types (somatic and reproductive), both of which are required for perpetuation of the species (Figure 2.11F). Although not all animals set aside the reproductive cells from the somatic cells (and plants hardly ever do), this separation of germ cells from somatic cells early in development is characteristic of many animal phyla and will be discussed in more detail in Chapter 19.

WEBSITE 2.4 ***Volvox* cell differentiation.** The pathways leading to germ cells or somatic cells are controlled by genes that cause cells to follow one or the other fate. Mutations can prevent the formation of one of these lineages.

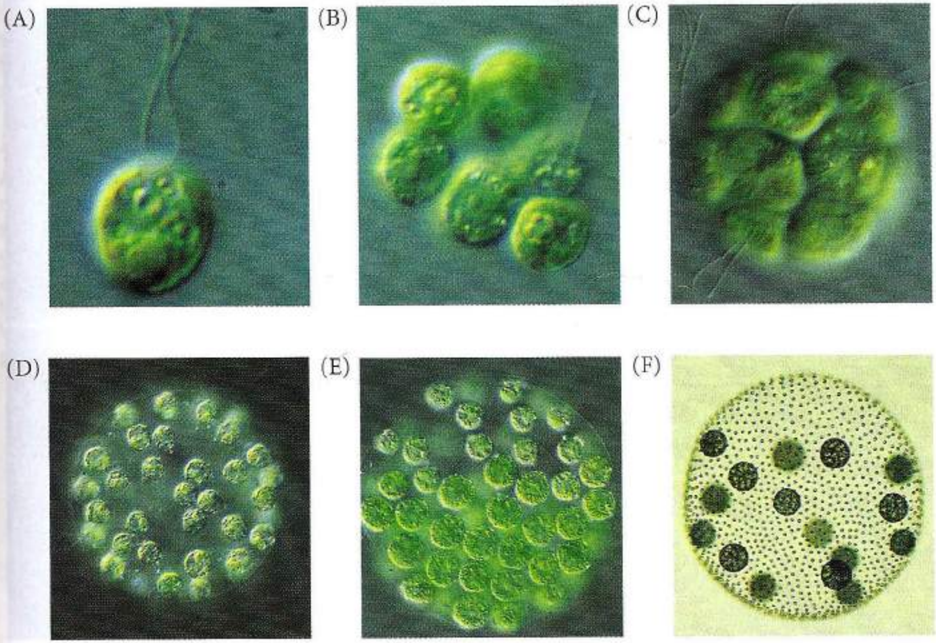


Figure 2.11
Representatives of the order Volvocales. All but *Chlamydomonas* are members of the family Volvocaceae. (A) The unicellular protist *Chlamydomonas reinhardtii*. (B) *Gonium pectorale*, with 8 *Chlamydomonas*-like cells in a convex disc. (C) *Pandorina morum*. (D) *Eudorina elegans*. (E) *Pleodorina californica*. Here, all 64 cells are originally similar, but the posterior ones dedifferentiate and redifferentiate as asexual reproductive cells called gonidia, while the anterior cells remain small and biflagellate, like *Chlamydomonas*. (F) *Volvox carteri*. Here, cells destined to become gonidia are set aside early in development and never have somatic characteristics. The smaller somatic cells resemble *Chlamydomonas*. Complexity increases from the single-celled *Chlamydomonas* to the multicellular *Volvox*. (Photographs courtesy of D. Kirk.)

Sidelights & Speculations

Sex and Individuality in Volvox

Simple as it is, *Volvox* shares many features that characterize the life cycles and developmental histories of much more complex organisms, including ourselves. As already mentioned, *Volvox* is among the simplest organisms to exhibit a division of labor between two completely different cell types. As a consequence, it is among the simplest organisms to include death as a regular, genetically regulated part of its life history.

Death and Differentiation

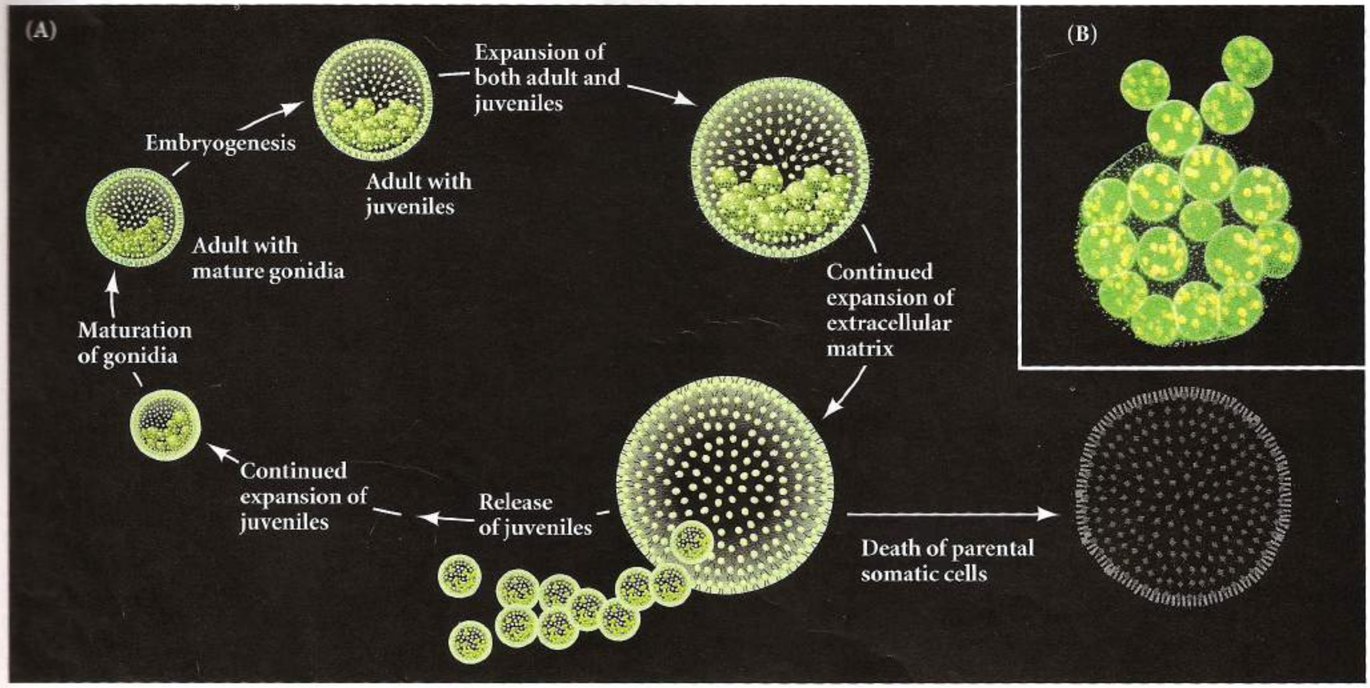
Unicellular organisms that reproduce by simple cell division, such as amoebae, are potentially immortal. The amoeba you see today under the microscope has no dead ancestors. When an amoeba divides, neither of the two resulting cells can be considered either ancestor or offspring; they are siblings. Death comes to an amoeba only if it is eaten or meets with a fatal accident, and when it does, the dead cell leaves no offspring.

Death becomes an essential part of life, however, for any multicellular organism that establishes a division of labor between somatic (body) cells and germ (reproductive) cells. Consider the life history of *Volvox carteri* when it is reproducing asexually (Figure 2.12). Each asexual adult is a spheroid containing some 2000 small, biflagellated somatic cells along its periphery and about 16 large, asexual reproductive cells, called **gonidia**, toward one end of the interior. When mature, each gonidium divides rapidly 11 or 12 times. Certain of these divisions are asymmetrical and produce the 16 large cells that will become a new set of gonidia in the next generation. At the end of cleavage, all the cells that will be present in an adult have been produced from the gonidium. But the resulting embryo is "inside out": it is now a hollow sphere with its gonidia on the outside and the flagella of its somatic cells pointing toward the interior. This predicament is corrected by a process called **inversion**, in which the embryo turns itself right side out by a set of cell movements that resemble the gastrulation movements of animal embryos (Figure 2.13A–H). Clusters of bottle-shaped cells open a hole at one end of the embryo by producing tension on the interconnected cell sheet (Figure 2.13I). The embryo everts through this hole and then closes it up. About a day after this is done, the juvenile *Volvox* are enzymatically released from the parent and swim away.

What happens to the somatic cells of the "parent" *Volvox* now that its young have "left home"? Having produced offspring and being incapable of further reproduction, these somatic cells die. Actually, these cells commit suicide, synthesizing a set of proteins that cause the death and dissolution of the cells that make them (Pommerville and Kochert 1982). Moreover, in death, the cells release for the use of others, including their own offspring, all the nutrients that they had stored during life. "Thus emerges," notes David Kirk, "one of the great themes of life on planet Earth: 'Some die that others may live.'"

In *V. carteri*, a specific gene, *somatic regulator A*, or *regA*, plays a central role in regulating cell death (Kirk 1988, 2001a). This gene is expressed only in somatic cells,

Figure 2.12
Asexual reproduction in *V. carteri*. (A) When reproductive cells (gonidia) are mature, they enter a cleavage-like stage of embryonic development to produce juveniles within the adult. Through a series of cell movements resembling gastrulation, the embryonic *Volvox* invert and are eventually released from the parent. The somatic cells of the parent, lacking the gonidia, undergo senescence and undergo programmed cell death, while the juvenile *Volvox* mature. The entire asexual cycle takes 2 days. (B) Micrograph showing young adult spheres of *Volvox carteri* being released from parent to become free-swimming individuals. (A after Kirk 1988; B from Kirk 2001b.)



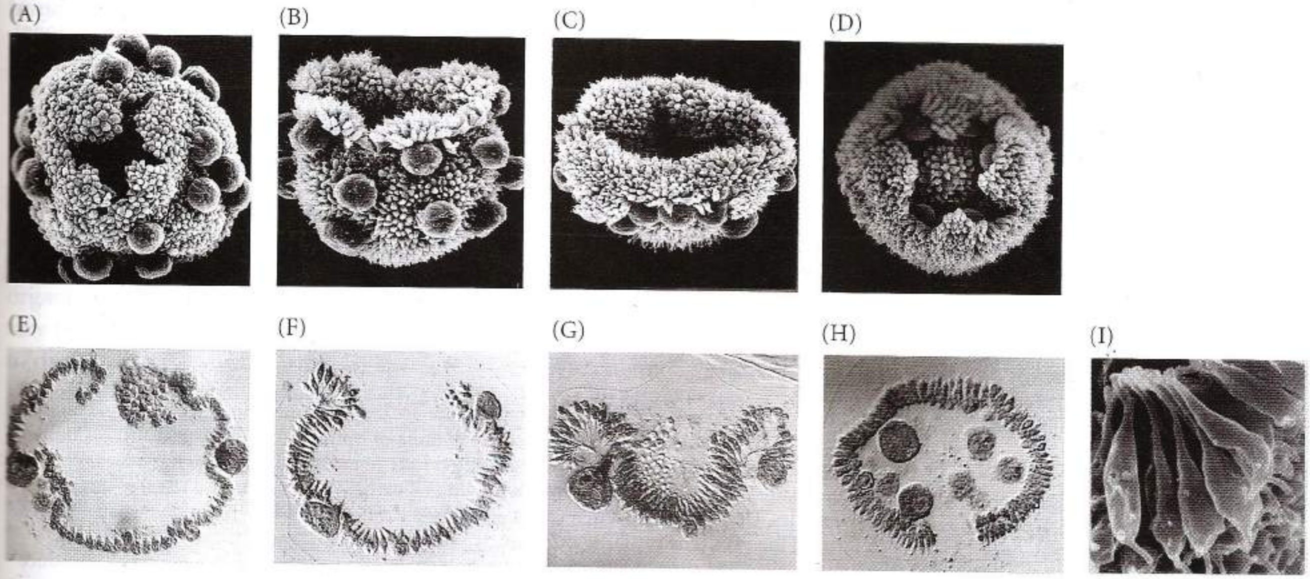


Figure 2.13
Inversion of embryos of *V. carteri*. A–D are scanning electron micrographs of whole embryos. E–H are sagittal sections through the center of the embryo, visualized by differential interference microscopy. Before inversion, the embryo is a hollow sphere of connected cells with the new gonidia on the outside. When the "bottle cells" change their shape, a hole (the phialopore) opens at the apex of the embryo (A, B, E, F). Cells then curl around and rejoin at the bottom (C, D, G, H). The new gonidia are now inside. (I) "Bottle cells" near the opening of the phialopore in a *V. carteri* embryo. These cells remain tightly interconnected through cytoplasmic bridges near their elongated apices, thereby creating the tension that causes the curvature of the interconnected cell sheet. (From Kirk et al. 1982; photographs courtesy of D. Kirk.)

and it prevents their expressing gonidial genes. In laboratory strains possessing regulatory mutations of this gene, somatic cells begin expressing *regA*, abandon their suicidal ways, gain the ability to reproduce asexually, and become potentially immortal (Figure 2.14). The fact that such mutants have never been found in nature indicates that cell death most likely plays an important role in the survival of *V. carteri* under natural conditions.

Enter Sex

Although *V. carteri* reproduces asexually much of the time, in nature it reproduces sexually once each year. When it does, one generation of individuals passes away and a new and genetically different generation is produced. The naturalist Joseph Wood Krutch (1956, pp. 28–29) put it more poetically:

> *The amoeba and the paramecium are potentially immortal. … But for Volvox, death seems to be as inevitable as it is in a mouse or in a man. Volvox must die as Leeuwenhoek saw it die because it had children and is no longer needed. When its time comes it drops quietly to the bottom and joins its ancestors. As Hegner, the Johns Hopkins zoologist, once wrote, 'This is the first advent of inevitable natural death in the animal kingdom and all for the sake of sex.' And he asked: 'Is it worth it?'*

For *Volvox carteri*, it most assuredly is worth it. *V. carteri* lives in shallow temporary ponds that fill with spring rains but dry out in the heat of late summer. Between those times, *V. carteri* swims about, reproducing asexually. These asexual volvoxes will die in minutes once the pond dries up. *V. carteri* is able to survive by turning sexual shortly before the pond disappears, producing dormant zygotes that survive the heat and drought of late summer and the cold of winter. When rain fills the pond in spring, the zygotes break their dormancy and hatch out a new generation of individuals that reproduce asexually until the pond is about to dry up once more.

How do these simple organisms predict the coming of adverse conditions so accurately that they can produce a sexual generation in the nick of time, year after year? The stimulus for switching from the asexual to the sexual mode of reproduction in *V.*

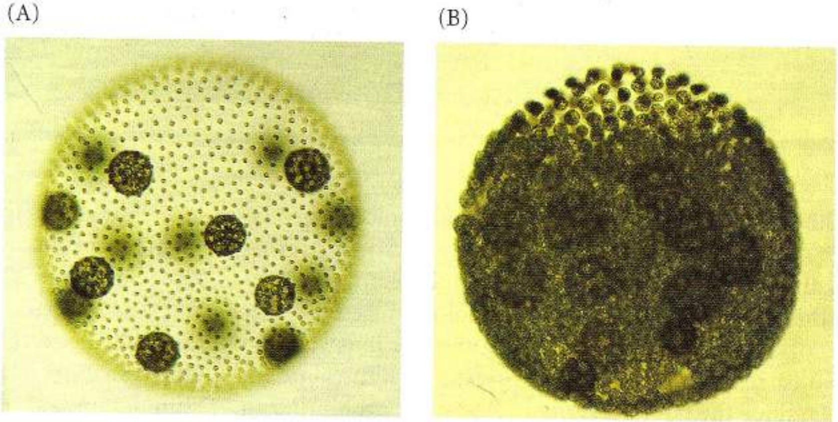
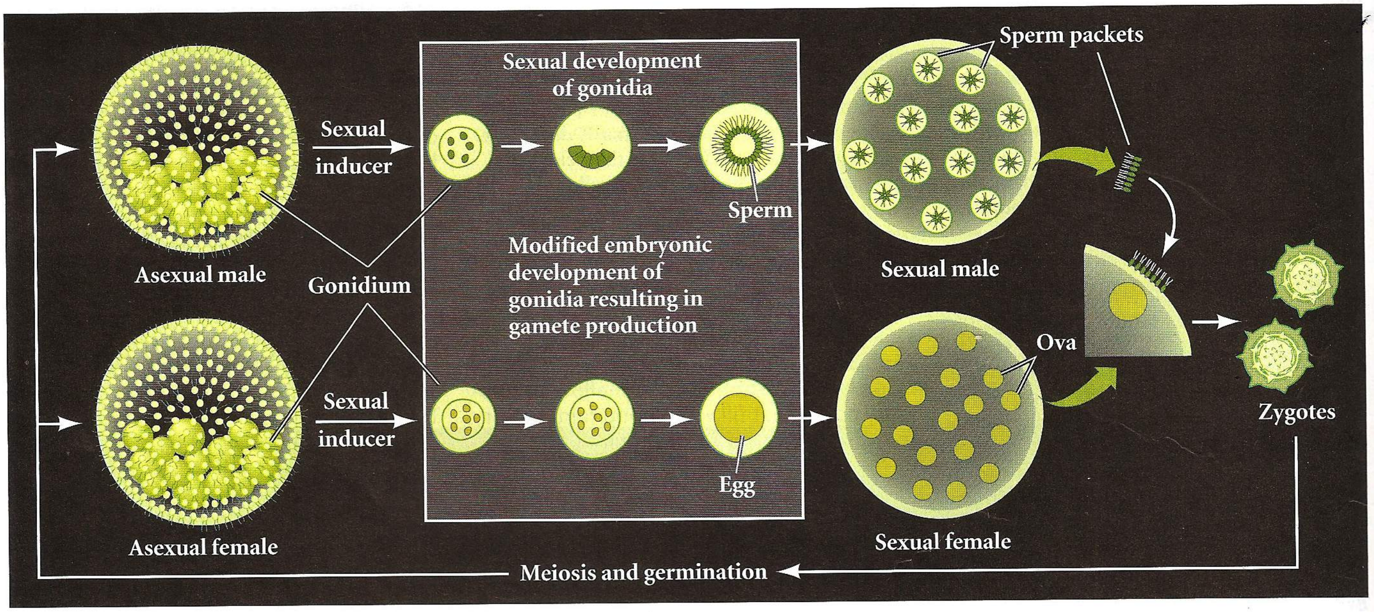


Figure 2.14
Mutation of a single gene (*somatic regenerator A*) abolishes programmed cell death in *V. carteri*. (A) A newly hatched *Volvox* carrying this mutation is indistinguishable from the wild-type spheroid. (B) Shortly before the time when the somatic cells of wild-type spheroids begin to die, the somatic cells of this mutant redifferentiate as gonidia (B). Eventually, every cell of the mutant will divide to regenerate a new spheroid that will repeat this potentially immortal developmental cycle. (Photographs courtesy of D. Kirk.)

carteri is known to be a 30-kDa sexual inducer protein. This protein is so powerful that concentrations as low as 6×10^{-17} *M* cause gonidia to undergo a modified pattern of embryonic development that results in the production of eggs or sperm, depending on the genetic sex of the individual (Sumper et al. 1993). The sperm are released and swim to a female, where they fertilize eggs to produce dormant zygotes (Figure 2.15). The sexual inducer protein is able to work at such remarkably low concentrations by causing slight modifications of the extracellular matrix. These modifications appear to signal the transcription of a whole battery of genes that form the gametes (Sumper et al. 1993; Hallmann et al. 2001).

What is the source of this sexual inducer protein? Kirk and Kirk (1986) discovered that the sexual cycle could be initiated by heating dishes of *V. carteri* to temperatures that might be expected in a shallow pond in late summer. When this was done, the somatic cells of the asexual volvoxes produced the sexual inducer protein. Since the amount of sexual inducer protein secreted by one individual is sufficient to initiate sexual development in over 500 million asexual volvoxes, a single inducing volvox can convert an entire pond to sexuality. This discovery explained an observation made over 90 years ago that "in the full blaze of Nebraska sunlight, *Volvox* is able to appear, multiply, and riot in sexual reproduction in pools of rainwater of scarcely a fortnight's duration" (Powers 1908). Thus, in temporary ponds formed by spring rains and dried up by summer's heat, *Volvox* has found a means of survival: it uses that heat to induce the formation of sexual individuals whose mating produces zygotes capable of surviving conditions that kill the adult organism. We see, too, that development is critically linked to the ecosystem in which the organism has adapted to survive.

Figure 2.15
Sexual reproduction in *V. carteri*. Males and females are indistinguishable in their asexual phase. When the sexual inducer protein is present, the gonidia of both mating types undergo a modified embryogenesis that leads to the formation of eggs in the females and sperm in the males. When the gametes are mature, sperm packets (containing 64 or 128 sperm each) are released and swim to the females. Upon reaching a female, the sperm packet breaks up into individual sperm, which can fertilize the eggs. The resulting dormant zygote has tough cell walls that can resist drying, heat, and cold. When spring rains cause the zygote to germinate, it undergoes meiosis to produce haploid males and females that reproduce asexually until heat induces the sexual cycle again.



Although all the volvocaceans, like their unicellular relative *Chlamydomonas*, reproduce predominantly by asexual means, they are also capable of sexual reproduction, which involves the production and fusion of haploid gametes. In many species of *Chlamydomonas*, including the one illustrated in Figure 2.10, sexual reproduction is **isogamous** ("the same gametes"), since the haploid gametes that meet are similar in size, structure, and motility. However, in other species of *Chlamydomonas*—as well as many species of colonial volvocaceans—swimming gametes of very different sizes are produced by the different mating types. This pattern is called **heterogamy** ("different gametes"). But the larger volvocaceans have evolved a specialized form of heterogamy called **oogamy**, which involves the production of large, relatively immotile eggs by one mating type and small, motile sperm by the other (see Sidelights & Speculations). Here we see one type of gamete specialized for the retention of nutritional and developmental resources and the other type of gamete specialized for the transport of nuclei. Thus, the volvocaceans include the simplest organisms that have distinguishable male and female members of the species and that have distinct developmental pathways for the production of eggs or sperm.

In all volvocaceans, the fertilization reaction resembles that of *Chlamydomonas* in that it results in the production of a dormant diploid zygote that is capable of surviving harsh environmental conditions. When conditions allow the zygote