From one cell to many: How did multicellularity evolve?

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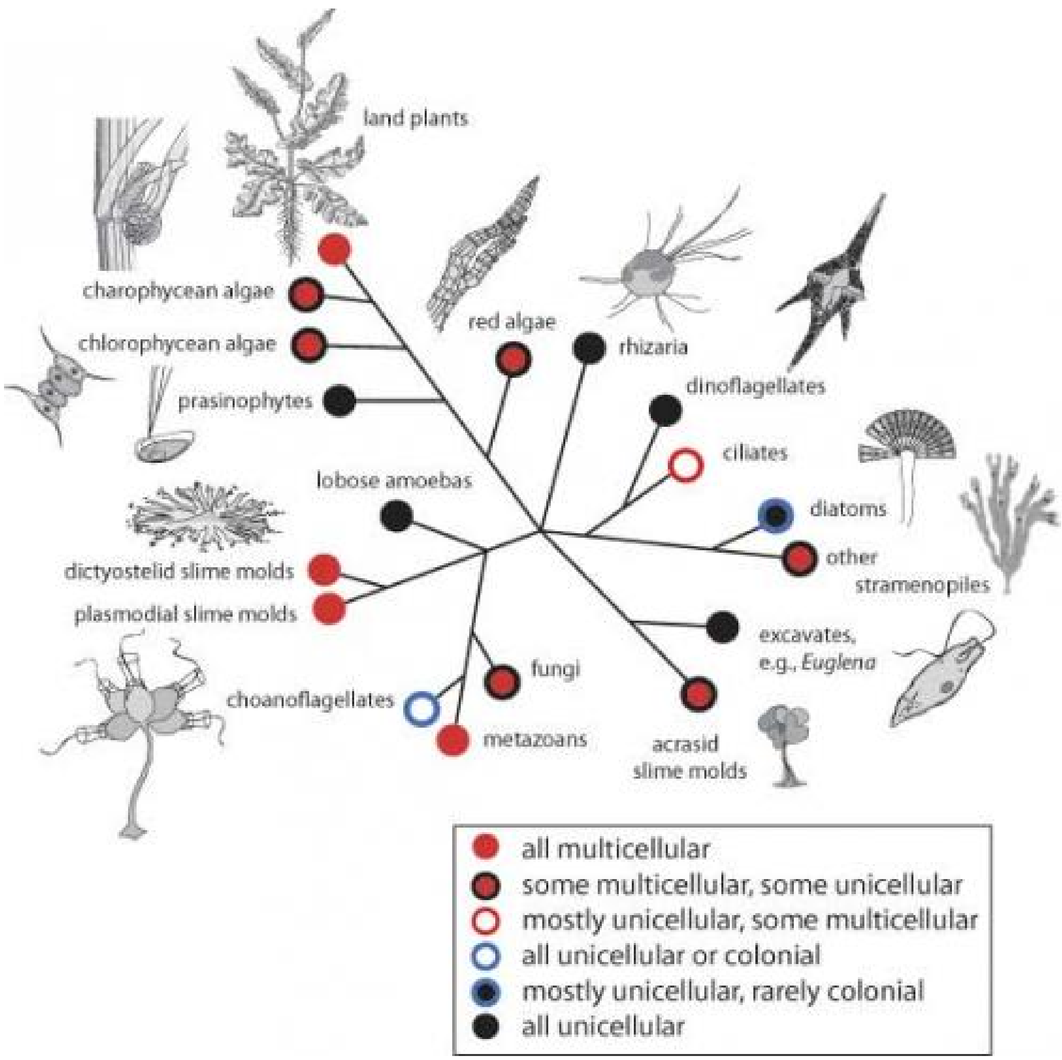

Representative diverse origins of multicellularity are shown on a highly redacted and unrooted phylogenetic diagram of the major eukaryotic clades (modified from a variety of sources). Although some lineages or clades are entirely unicellular or multicellular (e.g., lobose amoeba and the land plants, respectively), most contain a mixture of body plans such as the unicellular and colonial body plans (e.g., choanoflagellates) or a mixture of the unicellular, colonial, and multicellular body plans (e.g., ciliates and stramenopiles). In general, early-divergent persistent (EDP) lineages are dominated by unicellular species (e.g., prasinophytes in the chlorobiontic clade), whereas later-divergent lineages contain a mixture of body plans (e.g., chlorophycean and charophycean algae). Species-rich, late-divergent persistent (LDP) lineages tend to be exclusively multicellular (e.g., the land plants and metazoans). Credit: Karl Niklas.

In the beginning there were single cells. Today, many millions of years later, most plants, animals, fungi, and algae are composed of multiple cells that work collaboratively as a single being. Despite the various ways these organisms achieved multicellularity, their conglomeration of cells operate cooperatively to consume energy, survive, and reproduce. But how did multicellularity evolve? Did it evolve once or multiple times? How did cells make the transition from life as a solo cell to associating and cooperating with other cells such that they work as a single, cohesive unit?

Karl Niklas (Cornell University, Ithaca, NY), a plant evolutionary biologist, is interested in how plants have changed over the past few million years, in particular their size, shape, structure, and reproduction. As the first article in a series of Centennial Review papers celebrating 100 years of the *American Journal of Botany*, Niklas reviews the history of multicellularity and the changes that cells must have had to go through—such as aspects of their shape, function, structure, and development—in order to be able to functionally combine with other cells. He also explores the underlying driving forces and constraints (from natural selection to genetics and physical laws) that influence the evolution of multicellularity.

As a student, Niklas started out being interested in mathematics, but then turned to studying plants because of their "mathematical-like structure." "Multicellularity is a fundamental evolutionary achievement that is capable of mathematical description," comments Niklas, "and one that has occurred multiple times in different plant lineages."

Indeed, no matter how it is defined, scientists agree that multicellularity has occurred multiple times across many clades. Defined in the loosest sense, as an aggregation of cells, multicellularity has evolved in at least 25 lineages. However, even when defined more strictly—requiring that cells be connected, communicate, and cooperate in some fashion or another—it has still notably evolved once in animals, three times in fungi, six times in algae, and multiple times in bacteria.

Multicellularity could have been achieved numerous times based on the premise that selection acts on phenotypes and how well certain combinations of traits work. In other words, even if cells adhere together using different mechanisms, or via different developmental pathways, if the results are cooperative aggregations of cells that function well and thus are able to survive better and, critically, produce more offspring than their unicellular counterparts, then these various evolutionary pathways could all be possible.

"The curtail point," emphasizes Niklas, "is that the evolution of multicellular organisms occurred multiple times and involved different developmental 'motifs,' such as the chemistry of the 'glues' that allow cells to stick together."

Certainly, one of the themes that Niklas drives home in his review is that natural selection acts on functional traits, so multicellularity could have evolved many times via different mechanisms and modes of development, and using different aspects of cellular biology.

However, there are certain sets of requirements that must be met in order for multicellularity to evolve. These include that cells must adhere to, communicate with, and cooperate with each other, and that cells must specialize in their functions (i.e., that not all cells do exactly the same thing, otherwise they would just be a group of cells or a colony). In order to make these things happen, cells must not reject each other. In other words, they must be genetically compatible to some extent—analogous to how our human bodies reject foreign items that are not recognized by our cells. This first step is termed "alignment-of-fitness."

Interestingly, this "alignment-of-fitness" requires a "bottleneck" or unicellular stage when the organism consists of just one cell—a spore, zygote, or uninucleate asexual propagule. This is necessary so that all subsequent cells share similar genetic material.

The "export-of-fitness" stage is the second step necessary to the evolutionary process of multicellularity. This requires that cells work together for a common goal of reproducing more cohesive units, or individuals, like themselves and thereby work in a concerted way toward increasing their fitness. Once this is achieved, a distinct phenotype, or form, of organism exists.

How exactly steps such as cell-to-cell adhesion or communication were achieved in plants, animals, fungi, and algae differs among the major eukaryotic clades, yet an important aspect is that these multicellular organisms all went through a similar series of steps on their way to becoming multicellular, functional organisms.

As Niklas puts it: "This convergent evolution is well summarized by the saying 'There are many roads to Rome, but Rome is not what it used to be'."

In fact, these stages can be mapped on to theoretically possible body plans, illustrating the most plausible series of evolutionary steps—unicellular to colonial to multicellular—that is seen in algae, land plants, and animals. Niklas also posits a plausible alternate evolutionary route, starting with a single cell containing multiple nuclei (e.g., from a siphonous to multicellular form) and finds support for this in the observed forms of some fungi and algae.

"This review of the literature has now brought my attention to 'cooperation'" concludes Niklas, "because multicellularity requires cells to work together. Cheating cells cannot be tolerated over the long run because like a cancer they can gain the upper hand and kill a multicellular organism."

More information: Niklas, Karl J. 2014. The evolutionary-developmental origins of multicellularity. *American Journal of Botany* 101(1):6-25. DOI: 10.3732/ajb.1300314 .
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