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An Origin and Evolution of Multicellular Organisms

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Abstract

Multiple eukaryotic lineages that gave rise to plants, fungi, and mammals have evolved multicellularity. Theoretically, this involved cell-to-cell adhesion with an alignment of fitness among cells, cell-to-cell cooperation and specialization with an export of fitness to a multicellular organism, and (3) in some situations, a change from "simple" to "complex" multicellularity. These three stages help to identify a "unicellular) colonial) filamentous (unbranched) branched)) pseudoparenchymatous) parenchymatous" morphological transformation series that is consistent with trends observed within each of the three major plant clades when mapped onto a matrix of morphologies based on developmental and physical rules for plants. Animal and fungal lineages, on the other hand, exhibit a more direct "unicellular) colonial or siphonous) parenchymatous" series. In these circumstances, we talk about the roles that ancestral genomic toolkits and patterning modules played in the cooptation, expansion, and subsequent diversity of multicellularity. We come to the conclusion that different clades and even some closely related lineages differ in the degree to which multicellularity is attained utilizing the same toolkits and modules (and hence the degree to which multicellularity is similar among various animals).

1.1.INTRODUCTION

The birth and spread of eukaryotic multicellular organisms was one of the most amazing developments in evolutionary history (Valentine 1978; Bonner 1998, 2012; Maynard Smith and Szathmáry 1995; Knoll 2011). The fact that this "event" happened independently in various clades may be even more amazing. Depending on how multicellular is defined, estimates of the precise number can differ. Conservative estimates place the evolution of multicellularity—which is best understood as cellular aggregation—at over 25 times (Grosberg and Strathmann 2007). According to more strict definitions that call for ongoing cell-to-cell communication, there have been an estimated ten eukaryotic events, including one each in the Animalia, the Fungi (chytrids, ascomycetes, and basidiomycetes), and the three major plant clades (rhodophytes, stramenopiles, and chlorobionta).

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No matter how many, the many causes of multicellularity and their ensuing effects raise a number of crucial but largely unsolved biological problems. Do multicellular lineages, for instance, share a common series of morphological transformations? What, if any, are the selection pressures that prevent (and promote) multicellularity? Is multicellularity the consequence of chance events that have led to larger animals, or were some lineages' forebears predisposed to produce it? Or, to put it another way, are the morphological themes that appear in multicellular lineages the outcome of adaptive evolution or the unavoidable results of physical laws and processes? Given that all life eventually shared a final common ancestor, are the various origins of multicellularity actually independent?

1.2.EVOLUTIONARY PHASES

Different taxonomic, developmental, morphological, physiological, or genomic frames of reference have led to several definitions of multicellularity. Instead of attempting to define this condition in this article, we will concentrate on two characteristics of multicellular organisms: cell-to-cell adherence, which is a requirement for multicellularity in all clades, and cell-to-cell communication, which is the foundation of multicellular development. Nevertheless, despite these similarities, there are significant differences amongst clades in the cellular and molecular underpinnings of the forms of adhesion and communication. As a result, the middle lamella of the embryophyte cell walls that holds them together has a different chemical makeup from the Type 1 transmembrane cadherin proteins that are important for mammal cell adhesion (Hulpiau and van Roy 2009) or the glycoprotein-based glues generated by many fungi (Epstein and Nicholson 2006). The intercellular connections in the green alga Volvox are also very different from the cell-to-cell communication pathways offered by fungal intercellular septal pores, mammalian gap junctions, and embryophyte plasmodesmata. Cell-to-cell adhesion and intercellular communication can be viewed as "characters" that take on various "character states" depending on a lineage's phyletic history, just like in cladistics.

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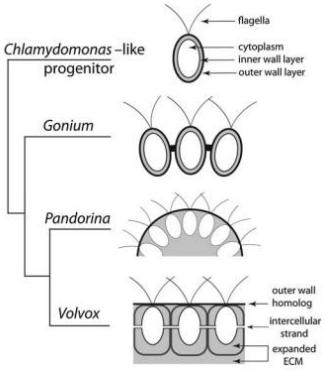

Fig.1. Potential multicellular evolution in volvocine algae (adapted from Kirk 2005). A unicellular Chlamydomonas-like progenitor is altered to form an enlarged extracellular matrix (ECM), in which interconnecting cytoplasmic strands enable multicellularity (e.g., Volvox). In colonial organisms, cells are adhered by the outer cell wall layer (e.g., Gonium).

1.3.SIMPLE VERSUS COMPLEX MULTICELLULARITY

A distinction between "simple" and "complex" multicellularity is made by some authors (Butterfield 2000; Schlichting 2003). For example, unbranched filamentous morphologies and organisms with tissue systems, respectively, have internalised some of their cells, while others make contact with their external environment entirely (Knoll 2011).

This distinction is significant for two reasons: (1) it correlates with differences in cell specialisation, energy consumption per gene expressed, and increases in non-protein-coding DNA (Bonner 2004; Lane and Martin 2010; see also Lozada-Chavez et al. 2011); and (2) it aids in determining the likelihood that a multicellular organism can evolve to a unicell state (for example, a complex multicellular to unicell transition is much less likely than a colonial to unicell transition).

Since reaction-diffusion (R-D) morphogenetic systems can develop in response to progressively steep gradients in nutrition availability brought on by growing size or distance, diffusion is in fact a mechanism of communication that can propel cell specialisation. For instance, a one-dimensional R-D system is an Anabena or Nostoc filament. When its concentration exceeds a certain threshold, a diffusible inhibitor produced by heterocysts stops the production of heterocysts (Wilcox et al.

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1973; Risser et al. 2012). The first undifferentiated cell to be triggered in the middle transforms into a heterocyst, releases the inhibitor, and repeats the process when the space between two heterocysts grows (as a result of intervening vegetative cellular divisions). For the formation of stomata and root hairs, analogous R-D systems that operate in two or three dimensions are proposed (Torii 2012). Extant macroscopic algae or the evolution of terrestrial plants can serve as much more intricate examples. As early embryophytes increased in height, passive diffusion eventually became ineffective at supplying aerial tissues with water at rates that were sufficient, necessitating bulk water flow through xylem (Niklas 1997). Similar to the phloem of vascular plants, the inner cortex of the stipes of the big kelp Macrocystis contains specialised "trumpet" cells that transport photosynthates (Bruggeln et al. 1985).

1.4.FUTURE DIRECTIONS

The development of systems capable of establishing and maintaining cellular differentiation both geographically and temporally was necessary for the emergence of multicellular creatures. Each multicellular lineage's unicellular progenitor must therefore have had the ability to express different temporal states of gene expression in response to shifting environmental conditions, and the pre-existing regulatory mechanisms that were responsible for this developmental variability were co-opted to provide the ability to differentiate spatially in the multicellular context.

The mobilization of newly pertinent physical effects and self-organizing dynamics as a result of this new phenotypic context, which was mediated by preexisting attachment and matrix molecules, served as the earliest foundation for spatiotemporal regulation in multicellular organisms (Newman and Bhat 2008, 2009; Hernández-Hernández et al. 2012).

As demonstrated by the basic helix-loop-helix (bHLH) protein family involved in various cellular developmental processes in both plants and animals, the evolutionary expansion of pre-existing gene families encoding regulatory proteins along with novel physical and regulatory interactions resulting from such expansions also played critical roles and may even have driven the evolution of multicellular complexity (e.g., Feller et al. 2011; Pires and Dolan 2012). In fact, bHLH-bHLH interactions as well as synergistic interactions with other regulatory proteins, such MYB, are

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involved in various intracellular processes to build complexes that either activate or repress the expression of groups of target genes (Ramsay and Glover 2005; Feller et al. 2011). These targets must be identified, and their involvement in developmental processes must be determined, through future research. Since sequence homologies do not always indicate the conservation of function, it is important to assess the degree to which the specifics of transcription factor regulation and gene network architecture transfer from one organism to another. Similar to genetic or developmental homologies, functional homologies are not always the outcome, as is shown from the wide range of molecules that support cell adhesion and intercellular communication. Though, we think that future study will demonstrate that three very distinct plant clades, such as unicellular) colonial or siphonous) filamentous (unbranched) branching)) pseudoparenchymatous) parenchymatous, gained multicellularity along a similar morphological transition series.

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