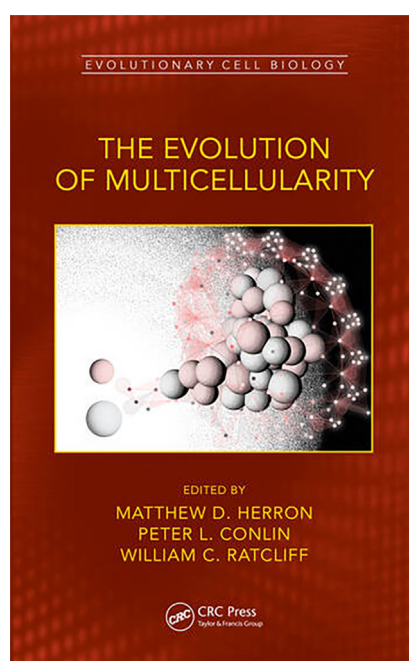


Book Review

Coming together
to understand
multicellularityCarl Simpson ^{1*}

What features do all multicellular organisms share due to the common evolutionary problems and what differences are due to the constraints imposed by their unicellular ancestors? That is no easy task; not least because the answers to those questions span all biological disciplines. The new volume, *The Evolution of Multicellularity* edited by M.D. Herron *et al.*, pulls together current thought on multicellularity from workers across a constellation of fields. This volume does a wonderful job covering the issues: from how to recognize multicellularity (Chapter 2), multilevel selection (Chapter 3), to multicellularity in fungi (Chapter 14), algae, and plants (Chapters 15 and 16).

For me, the theory (Chapters 3, 4, and 12) and history (Chapter 13) are of particular interest. Brunet and King's (Chapter 13) history of hypotheses about the ancestors of animals is a thrilling read. I did not realize that even as recently as Gould's [1] book *Wonderful Life*, animal polyphyly was considered a possibility. This history of putative animal ancestors Brunet and King highlight goes to show just how intertwined the empirical and theory aspects of multicellularity are.

The theory chapters (3, 4, and 12) expand beyond previously published work and put the theoretical challenges organisms face when evolving multicellularity, life cycles, and division of labor in a broader context. One of the challenges faced head on by these chapters is tackling what it means for fitness to pass from the cell level to the organismal level. Lots of theoretical work on multicellularity is burdened by theory developed to solve altruism [2]. In these chapters we see a way past this by focusing on life cycles and division of labor. A surprisingly large variety of possible life cycle types are outlined in Chapter 4 by Staps *et al.*, and yet they show that the conditions in which specific types of life cycles can evolve are bounded. Reading this chapter reminded me of the second to last chapter in Buss [3], where he outlined a space of possible life cycles structured by cellular features (e.g., presence or absence of cell walls). Buss estimated that there are >900 possible life cycles but only 27 realized life cycles. The fact that multicellularity evolved so far in the geological past yet is not recorded in the fossil record, puts the onus on theoreticians to imagine the life cycles and the evolutionary steps needed to evolve multicellularity. As a consequence, the details of how models of multicellularity are constructed matter (Chapters 10–12) as they represent a subset of possible life cycles. Yet, as Buss showed us [3], comparative biology is full of a rich diversity of organisms that span degrees of individuality but all

share a restricted set of life cycles. The work of Van Valen [4] might help to further broaden the theoretical approaches to match the biological variety we know occurs.

It might seem that we are close to understanding the origins of multicellularity, but I doubt it. There remain pieces of the puzzle that are missing from this volume; pieces that largely sit at the intersection of emerging fields and disciplines. For one example, we need a serious consideration of the ecology of early multicellularity. To accomplish this we need a mechanism for how the physics of feeding and motility change with multicellularity and how those changes fit into the biotic and environmental contexts that occurred in the deep geological past when multicellular groups originated.

It is tempting, for example, to use the fact that choanoflagellates and sponges both eat bacteria to equate them ecologically. However, this masks how different they are in terms of how they feed – the physics of their feeding – and how that in turn affects their ecologies. Sponges are able to deplete suspended food from huge volumes of water, allowing for the possibility of competition among suspension feeders [5]. In part, sponges can be such effective filter feeders because their generation times and feeding rates are significantly greater than the generation times of their prey bacteria. How efficiently do choanoflagellates deplete their local volume of bacteria? As the generation times of choanoflagellates and their prey bacteria are both short, depletion of prey is not as clear here as it is in sponges. Koehl points out how the various forms of life stage phenotypes in choanoflagellates aid to locate patches of bacteria, exploit them, and then move on to a new patch [6]. However effectively choanoflagellates prey on bacteria, their ecological interactions are likely to be dominantly predator–prey in nature. For

sponges, in contrast, their ecological interactions are broader, including competition with other filter feeders.

To a large extent, the ecological changes that come with multicellularity are due to the shift in the dominant physics that the organisms experience [6–8]. Even eukaryotic unicellular organisms have low Reynolds numbers, so much of their ecology is constrained by their local environments due to the dominance of viscous forces. In contrast, motile multicellular organisms with larger Reynolds numbers are able to manipulate and control their local environments.

Then there is the geological context in which clonal multicellularity evolved. Metazoans and a set of multicellular red and green algal lineages may have all evolved during an ~100 million year window (around 800–700 million years ago) during the Neoproterozoic Era. At this time, much of the Earth system was in flux – it included 70 million years of the global Snowball

Earth glaciations, massive global erosion, and the rise of atmospheric oxygen [9]. Oxygen was long thought to be the driver of multicellularity, but it likely rose to metabolically useful levels only after the origin of multicellularity [10]. Given the possibility that multicellularity could be adaptive in cold seawater [8] and cold supraglacial habitats [11] during Snowball glaciation, the oxygen stress that occurs at high temperatures [12] post-Snowball during the Ediacaran Period could have acted to suppress diversification until the cooler global temperatures emerged in the Cambrian Period, ultimately causing a long fuse between the origin of multicellularity and the Cambrian explosion.

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