Introduction: the evolution of multicellularity in context

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Abstract

The goal of this book is to provide an overview of the evolution of multicellularity: the types of multicellular groups that exist, their evolutionary relationships, the processes that led to their origins and subsequent evolution, and the conceptual frameworks in which their evolution is understood. In four main sections, the contributors review the philosophical issues and theoretical approaches to understanding the evolution of multicellularity, the evolution of aggregative multicellularity, the evolution of clonal multicellularity, and the evolution of multicellular life cycles and development. While the subject is too broad to cover in a truly comprehensive way, the contributors have done an outstanding job of synthesizing the critical information on their respective topics. We hope that this book will serve as a starting point for readers interested in the evolution of multicellularity, a reference for researchers on the subject, and a jumping-off point to stimulate future research.

"If indeed it is true that all living bodies are productions of nature, we are driven to the belief that she can only have produced them one after another and not all in a moment. Now if she shaped them one after another, there are grounds for thinking that she began exclusively with the simplest, and only produced at the very end the most complex organisations both of the animal and vegetable kingdoms." (Lamarck, 1809, p. 129)

1.1 Introduction

Barbara Kingsolver called it "audacious" to send a piece of writing out into a world that "already contains *Middlemarch*." (Kingsolver, 2001) To ask readers to spend time on your creation, when they could instead choose from a raft of powerful, wise, profound novels that already exist, it had, she concluded, "better be important." In the context of this collection, our *Middlemarch* is the outstanding work that has already been done on the evolution of multicellularity. Excellent books by David Kirk (1998), John Tyler Bonner (2000), and Richard Kessin (2001), as well as collections edited by David Whitworth and colleagues (2008), by Iñaki Ruiz-Trillo and Aurora Nedelcu (2015), and by Karl Niklas and Stuart Newman (2016), have been dedicated to the topic, not to mention thousands of scholarly papers.

Our audacity comes from the conviction that an open niche still exists, a sort of book on multicellularity that hasn't previously been written. Our goal has been to organize a set of chapters that would collectively serve as an in-depth review of the subfield of evolutionary biology that deals with the origins of multicellularity. We intend the book to serve as a jumping-off point, stimulating further research by summarizing the topics that students and researchers of the evolution of multicellularity should be familiar with.

We hope that it will provide a sufficient overview so that a reader unfamiliar with the relevant literature (a beginning graduate student, for example) will come away with an understanding of the major issues. What types of multicellular organisms exist? What are their evolutionary relationships? What processes led to their origins and subsequent evolution? In what conceptual frameworks can their evolution be understood? Crucially, what questions remain to be answered (see Chapter 18 for a detailed discussion)? In addition to providing an overview for newcomers to the field, we hope the book will serve as a reference for more established researchers.

1.2 Background

The idea that multicellular animals and plants evolved from single-celled organisms has been around as long as there has been a coherent theory of evolution. Jean-Baptiste Lamarck, for example, believed that (mostly) unicellular 'infusoria' were constantly arising through spontaneous generation and evolving into more complex forms due to the motion of fluids within their bodies (Lamarck, 1809, Lamarck, 1815) (more details on Lamarck's views can be found in Chapter 13). Although Charles Darwin considered Lamarck's ideas about spontaneous generation "superfluous (and groundless)" (Darwin, 1887, p. 210), he agreed that animals and plants likely descend from "some one primordial form" (Darwin, 1859, p. 425).

In the post-Darwin world, descent of multicellular organisms from unicellular ancestors has by and large been taken as a given. Furthermore, plants and animals have long been considered to have independently evolved multicellularity. Ernst Haeckel, for example, proposed that animals descended from protozoa and plants from protophyta (Haeckel, 1894) (more details on Haeckel's views can be found in Chapter 13). Henry Cadwalader Chapman thought it "probable that Monera in past time divided into animal and vegetal Monera," which gave rise to the animals and plants (including red, green, and brown algae), respectively (Chapman, 1873, p. 83). August Weismann agreed that animals and plants descended from distinct unicellular ancestors (Weismann, 1889).

As the big picture of phylogenetic relationships among kingdoms and phyla began to emerge, it became clear that two origins of multicellularity would not suffice. For example, the fundamental distinction between cells with and without nuclei, recognized by Haeckel (1869) and formalized in the taxonomy of Copeland (1938), necessitates an independent origin in the filamentous cyanobacteria. This did not, however, resolve the extreme heterogeneity of Copeland's Kingdom Protoctista ("Nucleate organisms not of the characters of plants (including green algae) and animals" (Copeland et al., 1956, p. 4)). The recognition of fundamental differences among the phyla within the kingdom, including for example red algae, brown algae, and ciliates, further implied that the multicellular members of each of these groups represents at least one additional independent origin of multicellularity.

Further advances in phylogenetic systematics have shown that even within some of these taxa, multicellularity has evolved more than once. This is almost certainly the case in the green algae (Chapter 9), the fungi (Chapter 14), and the Amoebozoa (Chapter 5), for example. In 2007, Grosberg and Strathmann estimated "at least 25" independent origins of multicellularity (Grosberg and Strathmann, 2007, p. 622), but this is very likely a serious underestimate. Recent phylogenetic reconstructions based on whole transcriptome data suggest that there may have been this many independent origins of multicellularity in the green algal lineage alone (One Thousand Plant Transcriptomes Initiative, 2019). Furthermore, we should not forget that essentially all estimates of the number of origins are based exclusively on extant taxa; there is no telling how many species may have evolved multicellularity and subsequently gone extinct without leaving much of a fossil record.

In the second half of the twentieth century, the evolution of multicellularity began to be seen as one example of a broader category of transitions leading to new, more inclusive biological units. John Tyler Bonner, for example, wrote of "cases where in one jump a new level of complexity is reached" (Bonner, 1974, p. 58), including the origins of life, of eukaryotic cells, of multicellularity, and of social groupings. Leo Buss interpreted the hierarchy of life, from genes to species, as resulting from a series of transitions from less to more inclusive units of selection (Buss, 1987). In their foundational book, John Maynard Smith and Eörs Szathmáry treated the evolution of multicellularity as an example of a "Major Transition in Evolution," events in which new levels of biological organization evolved (Maynard Smith and Szathmary, 1995).

Maynard Smith and Szathmáry's book established the Major Transitions as a subfield of evolutionary biology, which has expanded greatly in the last 25 years. In both biology and the philosophy of biology, the evolution of multicellularity has been viewed through this lens. Subsequent authors have revised the list of transitions and continue to do so (Herron, 2021, and references therein), but every version we are aware of has included the evolution of multicellularity.

1.3 Rationale for the structure of this book

Aside from the introductory and concluding chapters, we have organized the book in four sections. The first, Theory and Philosophy, addresses the ways in which the topic of the evolution of multicellularity has informed and been informed by the philosophy of biology (Chapter 2), the theory of multilevel selection (Chapter 3), and the evolution of life cycles (Chapter 4). The evolution of multicellularity has long played a central role in discussions of the nature of biological individuality, which biological units are the bearers of fitness, predictability *versus* contingency in evolution, how complexity is defined and how it evolves, biological hierarchies, the evolution of cooperation, and the diversity of life cycles, among other topics.

Multicellular life cycles are remarkably diverse. In eukaryotes, though, nearly all involve an alternation of haploid and diploid generations, with fertilization establishing the diploid phase and meiosis restoring the haploid condition. Either phase, or both, may undergo mitosis, and the products of mitosis may form multicellular structures in neither, either, or both phases. In some cases, those multicellular structures result from the products of mitosis failing to separate; in others, free-living unicells aggregate to form a multicellular structure. We call these situations clonal and aggregative multicellularity, respectively, and this is a fundamentally important distinction.

In clonal multicellularity, as the name suggests, all of the cells in the multicellular structure are clones of the progenitor cell (zygote, spore, or other propagule) and related to each other by $r \approx 1$. In aggregative multicellularity, relatedness among the cells in an aggregate can take any value, depending on the spatial structure of the population and the efficacy of kin-recognition during group formation. Social evolution theory predicts that very different outcomes will result from this difference in relatedness, namely that altruistic cooperation will evolve more easily and to higher levels in the clonal case, where relatedness among cells is consistently high. These predictions are consistent with observations of multicellular complexity, which is only known to reach high levels in clonal multicellularity.

Because aggregative and clonal multicellularity have such fundamental differences, we have devoted a section of the book to each (Sections 2 and 3, respectively). Each of these sections begins with an overview of the diversity and phylogeny of independent origins of multicellularity of the appropriate type (Chapters 5 and 9), followed by chapters on group formation (6 and 10), group maintenance (7 and 11), and group transformation (8 and 12). This organization was inspired by Andrew Bourke's book *Principles of Social Evolution*, which proposes the formation, maintenance, and transformation of social groups as a general framework for understanding the Major Transitions (Bourke, 2011). While we don't view social group formation, maintenance, and transformation as necessarily sequential stages of a Major Transition in Evolution – because the challenges of social group maintenance may persist / arise even after group transformation has occurred, for example – we feel that Bourke's stages nicely illustrate the primary barriers to a successful transition in individuality. We hope the parallel structure of Sections 2 and 3 will facilitate comparison of aggregative and clonal multicellular organisms, helping readers to identify both similarities and differences between these two modes of multicellular development.

Section 4 addresses the evolution of multicellularity through the lenses of life cycle evolution and the evolution of multicellular development. Where the previous two sections focus largely on the early steps in the evolution of multicellularity across a broad range of taxa, the chapters in this section are largely focused on subsequent steps in particular taxa: animals (Chapter 13), fungi (Chapter 14), algae (Chapter 15), and plants (Chapter 16), which collectively comprise the so-called complex multicellular taxa, those with more than a handful of cell types and that exhibit intercellular communication, three-dimensional tissue structure, and genetically-regulated tissue differentiation (Knoll, 2011). The final chapter in this section (Chapter 17) considers the case of 'organisms' made up of multiple species, such as lichens and other intimate symbioses.

1.4 Conclusion

Our goal for this book was a single resource that summarizes what we know about the evolution of multicellularity. We aimed high and sent invitations to some of the most influential authors in this field, fully expecting that most would decline. To our delight and amazement, nearly all accepted.

The results have far exceeded our expectations. We feel that the chapters cover their respective topics exceptionally well, combining broad overviews with compelling examples and historical context with recent discoveries. Taken as a whole, we think they will serve the roles we had in mind for the book—primer, reference, and catalyst for further research—admirably.

We live in exciting times for the evolution of multicellularity. New theoretical advances, new model systems coming online, and new capabilities for fast, cheap genome sequencing are combining to produce new discoveries at an unprecedented pace and to provide new perspectives for understanding them. Microbial evolution experiments allow direct observations of transitions to multicellular life and tests of adaptive hypotheses. The expansion of CRISPR/Cas9 genome editing into non-model organisms has immense potential to identify genes and gene functions related to the evolution of multicellularity. A new appreciation for the importance of microbial symbionts expands our perspective, not only on how multicellularity can evolve but on what it means to be a multicellular organism. All of these developments mean that our understanding of the evolution of multicellularity is likely to grow at an accelerating pace, and we are excited to see what lies ahead.

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