Preface

Multicellularity has evolved independently in ten different major clades and over 25 times in individual lineages within these clades, each of which had a unicellular ancestral condition. Its evolution involved the appearance of physiological mechanisms resulting in cell-to-cell adhesion and sustained intercellular communication among adjoining cells. A comparative approach among extant lineages shows that these two requirements have been achieved in different ways among different plant, animal, and fungal groups; for example, cell-to-cell adhesion and communication in metazoans typically involves membrane-bound glycoproteins and cell-cell junctions whereas land plant cell adhesion and communication results from a pectinaceous middle lamella and plasmodesmata. Critical questions in this context are these: What are the genomic and developmental commonalities among multicellular lineages that permit cell-to-cell adhesion and communication, and what are the unique features of the lineages? What are the selective advantages and disadvantages of these defining features of multicellular organisms? What physical consequences follow from the multicellular state of life, and can these provide insight into the origins of morphological novelties?

In addition, the evolutionary transition from the unicellular to the multicellular condition represents a major change in the definition of individuality since a new kind of organism emerges from the interactions and cooperation among subunits (cells). Until recently, discussions about this transition have been characterized by two divergent schools of thought, one focusing on the so-called "unicellular bottleneck" between alternating generations, and another focusing on "soma–germ" specialization. More recently, the focus has become more synthetic by considering the unicellular bottleneck in terms of an "alignment-of-fitness" phase (wherein genetic similarity among cells prevents internal conflict) and soma–germ specialization in terms of an "export of fitness" (wherein cellular components become interdependent and collaborate in reproductive effort). This perspective raises a number of important questions. For example, does the unicellular bottleneck in the life cycles of multicellular organisms ensure an alignment of fitness? Does multicellular "individuality" evolve as the result of a gain in fitness achieved by cellular specialization?

Finally, recent knowledge of the physical underpinnings of morphogenesis and pattern formation in multicellular organisms raises questions that go beyond the adaptationist framework of traditional evolutionary theory. In particular, to what extent are morphological motifs inevitable physical outcomes of a new scale of cellular life that afford opportunities to explore and create entirely novel niches? What is the implication of such morphological inevitabilities (which may be brought about by nonlinear processes) for phyletic gradualism? Is the evolution of multicellularity typically a "left wall"—that is, is it a generally irreversible event in the history of many, if not the majority of lineages, and if so, why?

In view of the importance of understanding the origins and consequences of the evolution of multicellularity, a group of scholars active in these areas gathered at the Konrad Lorenz Institute, Klosterneuburg, Austria, September 25–28, 2014, to share their views and to explore new avenues of research. The results of these discussions, which continue to the present, along with contributions from several key investigators in this field not present at the workshop, are contained in the 14 chapters of this book. These chapters, which collectively cover a broad spectrum of organisms, perspectives, and approaches, are organized into five sections focusing on selected topics that present particular challenges.

Part I provides insights from the fossil record regarding the paleoecological circumstances in which animal multicellularity evolved and a consideration of the ancient physiological, biochemical, and developmental predispositions for the evolution of multicellularity in general. The first chapter explores the phyletic distribution of the different methods heterotrophs use to acquire food and reviews the sequence of their appearance in the fossil record (Knoll and Lahr). One conclusion emerging from this analysis is that different methods of nutrient acquisition may have driven the evolution of simple and complex multicellularity in some lineages. Next, certain molecular aspects of cell type specification and elaboration are explicated (Niklas and Dunker). It is hypothesized that the functional repertoire of eukaryotic proteomes has been evolutionarily expanded (without increasing the size of genomes) by the evolutionary innovation of proteins containing intrinsically disordered domains, as exemplified by the ubiquitous and metabolically versatile pan-kingdom calmodulin and calmodulin-like proteins.

Part II focuses on plants, here broadly defined to include all photosynthetic eukaryotes, encompassing the algae as well as the land plants. One chapter presents new insights into how the distinction between somatic and germ cell lines may have evolved in the green alga, *Volvox*, by the co-optation of an ancient (premulticellularity) stress-induced transcriptional repressor (König and Nedelcu). A second contribution discusses how the mechanical and chemical coupling of cells and combinations of "dynamical patterning modules" (defined as associations of gene products with the physical forces and effects they mobilize) may lead to the formation of recurrent patterns in plants and aggregates of unicellular entities (Arias, Azpeitia, Benítez, Escalante, Hernández-Hernández, and Mora van Cauwelaert). The final chapter in this section presents a multifaceted view of how the evolution of multicellular plants under constraints of nutrient gathering and escape from predation led to developmental mechanisms that are modular, distributed, self-organizing, integrative, and highly adaptive, without centralized control (Leyser).

Part III is devoted to the Amoebozoa and fungi, and theoretical approaches relevant to these groups. Like the volvocine algae, the cellular slime molds have long provided a robust model system with which to dissect and explore the evolution of multicellularity in large part because of the seminal work of John Tyler Bonner, who has graciously provided a preface to this volume. New insights continue to emerge from their study, such as the extent to which different species, as well as different genotypes of the same species, can cooperate to form fruiting bodies, a phenomenon that calls into question previous conceptualizations of individuality (Nanjundiah). Also called into question is whether multicellularity evolved as an adaptation, an exaptation, or as a nonadaptive happenstance. The available evidence depends on the organisms being examined. Experimental manipulation of yeast under selective regimes rapidly yields "snowflake" aggregates that manifest apoptosis (Conlin and Ratcliff), favoring an adaptationist account (though not necessarily a gradualist one). Whether generalities can be drawn from this remains an open question. Nevertheless, theoretical explorations identify recurrent themes involving a minimal set of generative rules (such as differential adhesion, growth, and cell death) that promote the evolution of multicellularity in simulated systems (Duran-Nebreda, Montañez, Bonforti, and Solé).

Part IV continues with the thematic treatment of multicellularity by focusing on the genomic toolkits of the animals (metazoans) and the mechanisms by which they mediate morphological complexity. For example, are the toolkits required for metazoan multicellularity found in the unicellular ancestors of this vast clade? Although this has been addressed and answered affirmatively, in part, for the choanoflagellates, the closest unicellular relatives, an examination of extant representatives of the more phylogenetically distant Ichthyosporea and Filasterea indicates that this conservation runs even deeper, and that early branching unicellular relatives of the metazoans manifest surprisingly complex genomic repertoires and associated multicellular organizational effects (Ruiz-Trillo). These and other conclusions nevertheless depend on the extent to which phylogenetic relationships are resolved, which lineages are identified as early divergent branches of metazoan evolution and which more closely resemble the colonial ancestors of multicellular animals. Analyses of the characteristics of the choanocytes of marine sponges, for example, and comparisons with choanoflagellates, reveal patterns of gene content and expression that permit a plausible scenario linking the sponges to the ancestral multicellular colonies from which the metazoans evolved (Adamska).

But how do cells achieve the necessary division of labor that permits different functionalities? Mathematical models employing multilevel consistency dynamics shed light on this question. As the number of model cells in an interactive aggregate increases, simulations yield divergent fates among the originally identical systems, a "germ line-soma" separation within the resulting heterogeneous colony from which cells may detach to produce other colonies (Kaneko). Finally, the characteristic animal body plan motifs of tissue multilayering, lumen formation, and tissue elongation are discussed in terms of the ancestry of the genes whose products first mediated these morphogenetic effects in ancient cell clusters. However, such morphologically complex cell aggregates were still not multicellular individuals, and it is proposed that the emergence of an egg stage of development *subsequent* to the origination of the forms was required to produce such entities (Newman).

Part V explores some of the philosophical aspects of what is meant by individuality and how different evolutionary pathways led to the appearance of integrated multicellular phenotypes. The attainment of mutual interdependence between the constitutive and interactive process of a multicellular organism, which thereby achieves an integrated phenotype, is characterized in terms of the "constitutive–interactive closure principle" (Arnellos and Moreno). This chapter also discusses the implications and drawbacks of taking the metazoans as the paradigmatic model system for multicellularity, since fully integrated multicellular organisms appear in other lineages, such as the land plants, although in qualitatively different ways, especially with respect to the relation and interdependence between their constitutive and interactive dimensions. The final chapter identifies a key bifurcation in the broad domain of questions ("problem agenda") concerning the origin of multicellularity (Love). By addressing the phenomenon from the contrasting but interrelated perspectives of evolutionary dynamics (the "when and why" of multicellularity) and developmental biology (the "how" of multicellularity), philosophers of biology, through the activities of reasoning explication and problem clarification, can bring coherence to a scientific effort whose practitioners might otherwise seem at odds with one another.

Collectively, the book's 14 chapters address a broad spectrum of topics, organisms, experimental protocols, and philosophical as well as practical issues.

These chapters show that the evolutionary expansion of preexisting gene families encoding regulatory proteins in combination with novel physical and regulatory interactions resulting from such expansions played critical roles and likely contributed to the evolution of multicellular complexity. Future research is required to identify their targets and to determine their participation in developmental processes. However, as noted by many of the authors, the extent to which the details of transcription factor regulation and gene network architecture carry over from one organism to another is an open question since sequence homologies do not necessarily imply the conservation of function. Likewise, functional homologies are not invariably the result of genomic or developmental homology, as is evident from the broad spectrum of molecules providing cell adhesion, intercellular communication, and so forth.

One of the many interesting questions raised in this volume is whether multicellularity confers any selective advantage. The abundance of extant multicellular organisms gives the impression that it does. However, although it is true that major evolutionary innovations are likely not to be retained within a lineage if they are incompatible with survival and reproduction, it is not always the case that every transition requires a large or even measurable advantage, nor is it the case that phenotypic novelties are invariably adaptive. The retention of multicellularity in some lineages may reflect a random and an adaptively neutral exploration of a body plan morphospace that, once achieved, is, on average, irreversible. These and other speculations will continue to impel researchers to explore the origins and consequences of multicellularity, an effort to which this volume is intended to contribute important information and concepts.