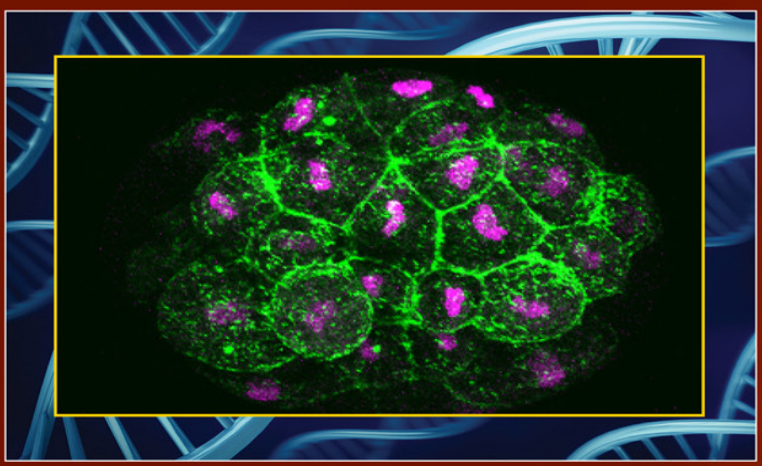
EVOLUTIONARY CELL BIOLOGY

ORIGIN AND EVOLUTION OF METAZOAN CELL TYPES



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Origin and Evolution of Metazoan Cell Types

Evolutionary Cell Biology

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Series Preface

In recent decades, evolutionary principles have been integrated into biological disciplines such as developmental biology, ecology and genetics. As a result, major new fields emerged, chief among which are Evolutionary Developmental Biology (or Evo-Devo) and Ecological Developmental Biology (or Eco-Devo). Inspired by the integration of knowledge of change over single life spans (ontogenetic history) and change over evolutionary time (phylogenetic history), evo-devo produced a unification of developmental and evolutionary biology that generated unanticipated synergies: Molecular biologists employ computational and conceptual tools generated by developmental biologists and by systematists, while evolutionary biologists use detailed analysis of molecules in their studies. These integrations have shifted paradigms and enabled us to answer questions once thought intractable.

Major highlights in the development of modern Evo-Devo are a comparison of the evolutionary behavior of cells, evidenced in Stephen J. Gould's 1979 proposal of changes in the timing of the activity of cells during development—heterochrony—as a major force in evolutionary change, and numerous studies demonstrating how conserved gene families across numerous cell types "explain" development and evolution. Advances in technology and in instrumentation now allow cell biologists to make ever more detailed observations of the structure of cells and the processes by which cells arise, divide, differentiate and die. In recent years, cell biologists have increasingly asked questions whose answers require insights from evolutionary history. As just one example: How many cell types are there and how are they related? Given this conceptual basis, cell biology—a rich field in biology with history going back centuries—is poised to be reintegrated with evolution to provide a means of organizing and explaining diverse empirical observations and testing fundamental hypotheses about the cellular basis of life. Integrating evolutionary and cellular biology has the potential to generate new theories of cellular function and to create a new field, "*Evolutionary Cell Biology*."

Mechanistically, cells provide the link between the genotype and the phenotype, both during development and in evolution. Hence the proposal for a series of books under the general theme of "*Evolutionary Cell Biology: Translating Genotypes into Phenotypes*", to document, demonstrate and establish the central role played by cellular mechanisms in in the evolution of all forms of life.

Brian K. Hall and Sally A. Moody

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Preface

Animals intrigue us with their different lifestyles, the many ways they are adapted to their environments, and the fascinating means by which they survive and reproduce. Animals tend to have complex behavior, and the ways in which this behavior is carried out makes them different from other multicellular branches such as plants and fungi. This volume focuses on the evolution of metazoan cell types that have given rise to this diversity of animal body plans, lifestyles, and complex behaviours.

Cells are the units of life, and with the evolution of multicellularity, cells were able to undergo a tremendous diversification and functional specialization. These novel cellular features are made possible by the evolution of distinct cell types that are highly specialized, for example, for protection from the environment, uptake of nutrients, transport, sensing and transmitting information, and reproduction, and by their interactions. Expansion into ecological niches, competition, and predation among early animals provided the framework for continuous evolutionary change, transforming simple epithelia into transport tubes, and specialization of cells as blood for transporting nutrients and gases, sequestering the germ lineage in cells and organs, and distinguishing cells for paracrine, endocrine, and neuronal signalling.

It has been argued (Valentine et al., 1994) that the number of cell types is an effective measure of organismal complexity with vertebrates having more types and more complexity than invertebrates and non-bilaterians. Such hierarchical views of complexity have dominated the evo-devo discussion on the evolution of metazoan cell types and body plans (Scholtz, 2004; Dunn et al., 2015). And while there is good evidence from a broad range of studies that cell types are conserved within some lineages (Erkenbrack and Thompson, 2019), it turns out that it is difficult to detect homologies between cell types across longer evolutionary distances (Sebé-Pedrós et al., 2018a; Sebé-Pedrós et al., 2018b). Convergence, not very long ago considered unlikely, is now widely accepted to have happened at all biological levels (cells, tissues, body plans).

Cellular evolution shares parallels across the different multicellular groups (plants, fungi, animals), for example, mechanisms of adhesion in epithelia of slime molds (*Dictyostelium*) and placozoans (Dickinson et al., 2012; Weis et al., 2013; Smith and Reese, 2016). Although in many cases multiple origins are inferred for cell types with the same function, it seems likely that some already specialized cell types in the earliest metazoans do share a common ancestry (are homologous). Discriminating between homology and homoplasy of cell types has always been problematic due to the lack of a resolved phylogeny of organisms, but new tools have been developed in recent years that go beyond ultrastructural comparisons and cellular physiology.

While ultrastructural similarity and cellular function were previously used to determine cell types (Valentine et al., 1994), recent effort has been in sequencing, and most recently in single cell RNAseq methods. Although these data bring a new perspective to the definition of a cell type, they also add some blur to the picture and do not in fact increase our understanding of the basic categories used. Surprisingly,

estimates of the minimum number of cell types in different organisms (not including neuronal subtypes) in the human body has not changed from Valentine's (1994) estimates even with scRNAseq techniques (Trapnell, 2015; Cao et al., 2017). Instead, with the introduction of sequencing approaches to investigations of cell complements of organisms, new definitions, such as cell states and sub-cell-types have had to be introduced to provide a better semantic framework that describes the biological observations. This has led to the co-existence of different perspectives what a cell type actually is (e.g., Mak, 2017).

Comparative developmental data using cell lineage tracers, gene expression, single cell genomics/transcriptomics, and gene knockout approaches can provide support for shared gene networks that designate specific cell types as similar to each other. A less studied data set includes physiological function determined by complement of ion channels, receptors, paracrine molecules, and even cell behavior. These tools however, are also influencing the picture of what we understand and identify as a cell type and could provide a level of novel definition.

What is special about the evolution of cell types as a unit is that each cell in the body carries the genomic information that contains all modules used by other cell types. Since this information is also inherited by the next generation via the germ line, we can expect the independent and recurrent emergence of similar cell types in many lineages. To discriminate between homology and convergence on the level of cell types will be one of the greatest challenges in the future, because of the easiness of the horizontal transfer of cellular submodules by activation of cis-regulatory elements. This is similar to what is observed in the vast exchange of genetic material between species in prokaryotes which still poses the major problem in resolving prokaryote phylogeny, the aptly named "ring of life" (Rivera and Lake, 2004).

Why do we need to know what the origin of a particular cell type is? The evolution of animal diversity is likely strongly affected by the origin of novel cell and tissue types and their interactions with each other. Understanding the evolution of cell types will shed light on the evolution of novel structures and in turn highlight how animals diversified. Several cell types may also have been lost as animals simplified, and a better grasp of the evolutionary history of cell types and how new cell types evolve will allow a better understanding that can discriminate between convergence and homology.

The target audience for this volume is a diverse group that functions at the graduate level and higher, and which crosses all disciplines—physiology, cell, chemical, and molecular biology—and who will be seeking a new approach to understanding the evolution of animal diversity.

In Chapter 1, we start with a stimulating analysis of "What a cell type is." Here, Alessandro Minelli from the University of Padova, Italy, explores the history, philosophy, and semantics of classification of cells by molecules and morphology. He also considers how cell types change with space and time and concludes that we might need to be content with "some degree of taxonomic pluralism" in our understanding of cell type systematics.

The next two chapters examine the protistan origins of animal cell types. In Chapter 2, Najle and Ruiz-Truillo from the CSIC, University of Barcelona and the University of Pompeu Fabra, Spain, argue that unicellular holozoans have different

cell states which are equal to cell types, only so far, these cell states are not known to exist at the same time in the same organism. In Chapter 3, Gavelis, Gile, and Leander from the University of British Columbia, Canada, highlight some particularly complex differentiated cell types in unicellular eukaryotes that function as sensory structures. They look at statocysts, eye-like structures, and harpoon type nematocyst-like structures in different protist groups and argue that homology plays little role in how these structures came about.

Cell types tend to have different phenotypes, whether morphological, molecular, or physiological. But during animal development, all cell types arise from the fusion of the two gametes, and gametes arise from germ cells. How did the germ cell type arise in metazoan evolution? In Chapter 4, Riesgo and Solana, from the Natural History Museum London and Oxford Brooks University, England, focus on early-branching phyla to look for commonalities of germ cell segregation in animals and argue that molecular mechanisms for regeneration hold a clue to how this cell type may have arisen.

One of the more recognizable cell types in animals is the epithelial cell, since it is what lines all tissues and gives sensory, glandular properties to many organs. Yet epithelia are so diverse across metazoans, and in Chapter 5, we learn from Renard, Le Bivic, and Borchiellini, from the University of Aix Marseille, France, that even agreement on what constitutes an epithelium is disputed.

Chapter 6 addresses another iconic metazoan cell type, the neuron. Here Leys, Mah, and Esposito, from the University of Alberta, Canada, examine what a neuron is and assess the morphological and molecular character of neurons as well as sensory cells in non-bilaterians. The problem of bias in interpreting new scRNAseq data is discussed.

In the last chapter, Chapter 7, Andrikou, Gąsiorowski, and Hejnol from the University of Bergen, Norway, examine the origin of nephridia with a careful review of the morphology and transcriptomic profiles of excretory cells in invertebrates. They argue that homology of organelles and even of some excretory cell types does not imply homology of the organs, and they caution against the use of gene combinations to detect cell types without supporting functional data.

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Sally P. Leys is Professor in the Department of Biological Sciences at the University of Alberta, in Edmonton, Canada. She earned her Ph.D. from the University of Victoria under George Mackie in 1996, for which she received the Canadian Society of Zoologists Cameron Award 1997. She held a Commander C Bellairs Postdoctoral Fellowship from McGill University for postdoctoral research in Barbados (1997) and then won an NSERC PDF which she took to the University Aix Marseille, France (1998) and later to the University of Queensland, Australia (1998-2000). She won an NSERC Women's University Research Award in 2000 and was Assistant Professor (Limited Term) at the University of Victoria, British Columbia. In 2002, she was awarded a Canada Research Chair Tier II at the University of Alberta in "Evolutionary and Developmental Biology." Her research interests broadly concern understanding the origin of multicellularity in metazoans and more specifically the cellular and molecular basis of coordination in non-bilaterian animals, sponges, ctenophores, placozoans, and cnidarians.

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