Preface

The origin and evolution of chordates is one of the most mysterious and intriguing phenomena in evolutionary developmental biology. Chordates are animals characterized by possession of a notochord, a dorsal neural tube, and pharyngeal gill slits. They consist of three taxa: cephalochordates, urochordates (or tunicates), and vertebrates. Chordates belong to a supraphyletic group of deuterostomes, together with echinoderms and hemichordates, and are thought to have been derived from the common ancestor(s) of deuterostomes. Vertebrates evolved by developing a body plan with the greatest complexity among metazoans.

In 1859, Charles Darwin proposed the concept of organismal evolution. Since then, the origins and evolution of chordates have been studied, discussed, and debated vigorously for more than 150 years. A huge wave of debate followed soon after Darwin's proposal because the question of chordate origins is directly or indirectly related to how vertebrates, including human beings, emerged on the Earth. Many hypotheses were proposed to explain deuterostome evolutionary scenarios and the origins of chordates.

During the 1980s, a new wave of molecular developmental biology revealed that genes encoding transcription factors and signal pathway molecules play pivotal roles in the differentiation of embryonic cells, formation of organs and tissues, and morphogenesis for construction of metazoan body plans. Shortly thereafter, another wave of evolutionary developmental biology (evo-devo) studies revealed that metazoans, from cnidarians to vertebrates, despite their diverse morphologies, utilize a very similar set of transcription factors and signal pathway molecules for body construction; these genes are sometimes collectively called a genetic toolkit.

I have been working on the developmental biology of urochordate (tunicate) ascidians for approximately 40 years. The reason why I selected ascidians as a research target was that I was interested in the mechanisms of the temporal control of development, rather than those of spatial control, on which most researchers in this field have focused. Embryonic development of ascidians is comparatively simple. Ascidians provide an excellent experimental system to study the cellular and molecular mechanisms of temporal control of embryogenesis. After the discovery that embryonic processes are controlled not by a single clock, but by multiple clocks, some associated with zygote cytoplasm and some with embryonic cell nuclei, I became much interested in the

notochord of ascidian larvae. Because the notochord is the most prominent feature of chordates, elucidation of mechanisms involved in notochord formation might advance our understanding of not only ontogenetic mechanisms, but also phylogenetic mechanisms. My laboratory at Kyoto University discovered that *Brachyury*, which encodes a member of the T-box transcription factor family, plays a pivotal role in notochord formation in ascidians and that this gene is also expressed in the archenteron invagination region of nonchordate deuterostome embryos that do not form a notochord.

Understanding of the origins and evolution of chordates advanced relatively little through the late 1980s. However, since the early 1990s, molecular developmental biological techniques allowed these questions to be addressed by evo-devo investigations. Many previous opinions, hypotheses, or theories were reexamined, and/or new hypotheses were proposed for the evolutionary scenarios of deuterostome and chordate origins. One of most discussed hypotheses relates to the inversion of the dorsoventral axis of bilaterians. This theory was rooted in the comparative anatomy of annelids, arthropods, and vertebrates in the early 19th century. It proposes that most of the components for bilaterian body construction had already evolved in their common ancestors and that vertebrates developed by inverting the dorsoventral axis compared with that of annelids. The hypothesis has received great support from molecular developmental biology.

On many occasions after hearing lectures on this story at international meetings and upon reading new manuscripts dealing with this topic, I always thought that even if the dorsoventral axis is inverted, that alone cannot explain the occurrence of the notochord in chordates. Because I had been engaged in evo-devo studies of notochord formation for a decade, I felt that the significance of this structure was being ignored. I conceived this idea in about 2005, and in 2008 I proposed the "aboral-dorsalization hypothesis" of chordate origins, in which I emphasized that the emergence of fish-like larvae having a notochord was a key developmental event to understand chordate origins. Because my explanation of the hypothesis was clumsy and a little bit odd, my hypothesis did not attract much attention of researchers in this field, and in fact it was essentially ignored.

I wished to reconsider this problem more clearly and to better summarize my thinking about this problem. This is the reason why I began preparations for this book. However, the subject of chordate origins and evolution includes dramatic and drastic changes in embryogenesis and adult morphology. The question is so huge that it is far beyond the reach of a single person. I have spent the last 5 months preparing for this endeavor. For the first 3 months, I struggled, mainly because I myself had no clear idea how chordates originated. I cannot support the dorsoventral inversion hypothesis, but then how can one explain mechanisms of chordate origins? I had no clear answer. Several ideas came to mind as images, but most of them had weak points of one sort or another. Therefore, I decided instead to prepare this book in more of an essay style, in which I could express my thoughts more freely, not so constrained by previous hypotheses.

Thereafter, I felt very much liberated from various pressures. Therefore, this book is not always an orthodox biological treatise, replete with cited references on related subjects. Some topics have been intentionally ignored and others have been preferentially and repeatedly cited to explain or promote my ideas about deuterostomes and the origins and evolution of chordates.

At the risk of being repetitious, the question of chordate origins and evolution is so huge and difficult that it may never be fully resolved. There are many potential interpretations of this problem. I anticipate that the subjects discussed in this book will provoke many responses, most negative, and some positive. However, the main reason that I wrote this book was and is to promote further discussion of this subject from various points of view. It is my hope that I will have the opportunity to revise it in the future, including issues and discussions raised by this first version.

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