

Preface

Vertebrate origins is a topic that falls into a zoological no-man's land. If it features at all in textbooks of invertebrate zoology, it'll be half a paragraph at the end. In textbooks of vertebrate zoology, it'll be discussed for two or three paragraphs at the beginning. When I was a graduate student in the mid-1980s teaching this subject to undergraduates, I found that the primary literature on the topic was ancient, scattered, obscure, and often contradictory. Students were often told about the ideas of vertebrate origins published by Walter Garstang (1868–1949.) They were never told, however, that his early published ideas are contradicted by his later ones,¹ and that most of what he'd intended to write on the subject never materialized. I resolved that, one day, I'd sort all this out and write the textbook on vertebrate origins I wished I'd had as a teaching aid. The result was *Before the Backbone* (1996). In that book I took a largely historical look at the various ideas proposed to "explain" how vertebrates originated from other animals.

The problem is that vertebrates are so different from other animals that the gap between them has been hard to bridge. Before modern techniques of molecular phylogeny and objective ways of reconstructing evolutionary relationships, the field was clear for any number of imaginative ideas about how vertebrates could have been squeezed out of horseshoe crabs, echinoderms, crustaceans, spiders, scorpions, tunicates, lancelets, mollusks, roundworms, acorn worms, segmented worms, proboscis worms, or even

protozoa.² In *Before the Backbone* I decided to remain above the fray in the hope that readers would be able to make up their own minds.

When *Before the Backbone* appeared, Hox genes, whose organization and function revealed deep connections between the structures of all animals, were relatively newly found. The first genomes were only then being sequenced, and these were of bacteria. Fossils were few. Extant creatures such as acorn worms and tunicates were closed books to geneticists, being very far from the model organisms labs were accustomed to handling.

Twenty years have passed and the face of science is greatly changed. Many organisms relevant to the subject have had their genomes sequenced. Molecular techniques now allow genetic inspection and even manipulation of non-model organisms. Many more fossils have been found and described. Even the shape of animal evolution is conceived differently from the way it was then. The result is that we have a much better idea of how vertebrates fit into the scheme of things, and many interesting ideas have effectively been falsified.

And yet, for all the achievements of the past two decades, the morphological chasm between vertebrates and invertebrates still remains large enough in which to conduct quite a few arguments at once, without much hope of a sure resolution to any of them. The extant relatives of vertebrates were always too few, and the more we learn about them, we find that they have evolved so far along their own courses that they are of questionable help in reconstructing what the latest invertebrate ancestor of vertebrates looked like. The fossils, while more plentiful, offer yet more problems of interpretation. There are, however, clues. They are often fragmentary, possibly misleading and subject to a degree of interpretation—but they are there.

For those who want to delve into the history of the topic, *Before the Backbone* is still in print. The aim of this book, *Across the Bridge*, is to review the state of the field as it is now; to present a synthesis of the more recent literature in a form that will be accessible to students; to see how far we have come in working out how to cross that chasm; and, finally, to venture some ideas of my own. Most of the works cited here have appeared since *Before the Backbone*, and I have generally avoided historical treatments of the subject. This book therefore complements *Before the Backbone* without supplanting it. It is an entirely new work, conceived and constructed from

the ground up. This time, I hope, I'll have succeeded in writing something closer to the book I had intended to write in the mid-1980s.

In *Before the Backbone* I was wary of presenting any kind of novel synthesis, preferring to compare and contrast the ideas of others. I have been less cautious here. In this book I advance some views that will no doubt be controversial. In particular, I suggest that the peculiar Cambrian fossils known as vetulicolians and yunnanozoans, all described since *Before the Backbone* was published, represent successively closer relatives of chordates, the larger group to which vertebrates belong. In doing this, I suggest³ that the segmented trunk region of chordates originated, with vetulicolians, entirely separately from much of the body destined to become the head and viscera, and only later became more integrated with it.

It took me quite a while for me to gather up sufficient confidence to start work on a new book on vertebrate origins. Although various people, notably Christopher J. Lowe, Michael Levine, and Nicholas D. Holland, had been encouraging me from the sidelines, the task seemed too daunting.

What nudged me forward was the opportunity to commission a special supplement of review articles for *Nature* on the origin and early evolution of the vertebrates.⁴ This exercise, and the reviews that resulted, helped me get my thoughts in order. I am grateful to my colleague Ursula Weiss for allowing me to commission the supplement, Melissa Rose for handling the administration, and Jenny Rooke for copyediting.

None of it would have been possible without the willing participation of the authors: Martin D. Brazeau, Marianne E. Bronner, Lionel Christiaen, Nathaniel Clarke, Rui Diogo, Matt Friedman, John Gerhart, Stephen A. Green, Linda Z. Holland, Nicholas D. Holland, Peter W. H. Holland, Philippe Janvier, Robert G. Kelly, Michael Levine, Christopher J. Lowe, Daniel M. Medeiros, Julia L. Molnar, Drew M. Noden, Daniel S. Rokhsar, Marcos Simoes-Costa, Eldad Tzahor, and Janine M. Ziermann—and the guidance of colleagues and anonymous referees.

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As always I owe a debt of gratitude to my family for their support, as well as to the amusement and insight offered by our numerous pets, which together represent all five traditional classes of vertebrate.

Finally, I dedicate this book to the memory of Professor Robert McNeill Alexander, FRS (1934–2016), who died while I was drafting this book. Neill was Professor of Zoology at the University of Leeds when I was an undergraduate there between 1981 and 1984. Then, and since, he was a source of unfailingly wise counsel and friendship. I regard him as having been one of my mentors and keenly feel his loss.