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The Rise of Amphibians: 365 Million Years of Evolution

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the remaining salt marshes are diked, drained, fragmented, isolated, polluted, and invaded; we are still losing the battle for their survival. This book makes a strong case for salt marsh restoration as a means to reverse the destructive legacy of this "unnatural history."

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RECONSTRUCTING THE ROOTS OF THE AMPHIBIAN TREE

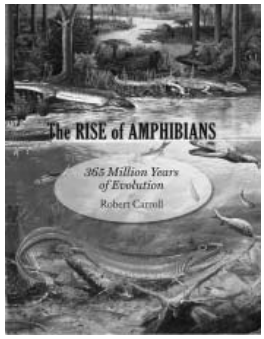
The Rise of Amphibians: 365 Million Years of Evolution. Robert Carroll. Johns Hopkins University Press, 2009. 392 pp., illus. $65.00 (ISBN 9780801891403 cloth).

Amphibian systematics is experiencing an era of change. Integrative taxonomy and increased exploration, especially of tropical regions, have led to an explosion in species numbers, with more than a thousand species discovered and described between 2000 and 2009. Some of these new species were breakthroughs of great biogeographic importance, such as *Karsenia koreana*, the first Asian plethodontid salamander, or *Nasikabatrachus sahyadrensis*, a representative of a morphologically unique family of frogs in India. Furthermore, important advances in our knowledge of the deep phylogeny of extant amphibians have been achieved through the analysis of DNA sequences, and molecular clocks are coming to a consensus in dating the major nodes of the amphibian tree—leading to an improved understanding of how vicariance and dispersal shaped the current distribution of amphibians and created opportunities for their radiations. These major breakthroughs are reflected in new proposals for amphibian classification at the genus and family levels, which, although still partly disputed, reflect evolutionary history better than previous schemes.

These novel developments all concern extant amphibians—a clade named the Lissamphibia that comprises salamanders, frogs, and caecilians. However, back at the roots of amphibian evolution, lissamphibians were just one—eventually very successful—offshoot. A diverse array of early amphibians dominated terrestrial habitats of Earth in the Carboniferous and Permian periods, and paleontologists have in recent years compiled extensive new data on these first vertebrate conquerors of land. *The Rise of Amphibians: 365 Million Years of Evolution*, by Robert Carroll, aims to bridge the gap between paleontological and neontological advances in amphibian research and invites the reader to join a fascinating voyage of discovery into the early origins and more recent evolution of these animals.

The book starts deep—very deep—in the past. The first of 14 chapters reviews the early history of Earth and the origins of life. The second chapter, on the ancestry of vertebrates, exemplifies one major strength of the book: Although Carroll's main expertise and research are on the paleontology of vertebrates, he admirably integrates evidence from other disciplines, as in the case of early metazoan and vertebrate evolution. The result is a detailed overview of the importance of *Hox* gene duplication for vertebrate evolution. Evidence from evolutionary developmental biology is also an excellent complement in following chapters (e.g., in the discussion of the genetic bases of changes in the locomotion system).

The third chapter starts with an overview of the transition of sarcopterygian fishes to the first Devonian amphibians. This is one of the chapters in which the recent advances in knowledge, from both fossils and molecules, are most obvious. It was only a few years ago that we witnessed fierce discussions about whether, among extant taxa, the coelacanth or the lungfishes are the closest relatives of tetrapods, and complained about missing links in the transition from aquatic to terrestrial vertebrates. Carroll's tree summarizes the current consensus. Lungfishes are closer than the extant actinistian coelacanth *Latimeria* to tetrapods as indicated by molecules, but the extinct rhipidistian coelacanths, such as *Eusthenopteron*, are the last



aquatic taxa splitting off the branch that further includes *Pandrichthys* and the spectacular, recently discovered *Tiktaalik*. This is of course the branch that led to the first creatures that can be considered amphibians—the probably largely aquatic *Acanthostega* and the more terrestrial *Ichthyostega*. Missing links? Yes, they exist: Fossils are scant that would link the first Devonian amphibians with the diverse faunas recovered from the upper Carboniferous, and the Paleozoic radiations with lissamphibians. But it is exciting to realize that the transition from water to land, from "fishes" to amphibians, is now well documented by many no-longer-missing links.

Chapters 4–6, devoted to the wealth of Carboniferous and Permian amphibians, are the most important; they make up roughly one-third of the book (114 pages). Chapters 7 and 8 look at the escape to and from land; that is, the origins and early evolution of amniotes, and the radiation of largely aquatic stereospondyl amphibians in the Triassic. Being myself mainly interested in recent amphibians, I found these chapters stimulating because of their valuable discussion of the importance of extinction in understanding the biogeography and morphological evolution of amphibians. Today, many basal amphibian lineages are species poor and range restricted, indicating they may be but weak shadows

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of past successful radiations that have since largely disappeared. Carroll's ample discussion reminds us that extinction was even more important in the dawn of amphibian evolution. In a sense, he revives a fascinating and diverse fauna that went almost completely extinct—except for a single lineage that eventually gave rise to the more than 6600 current species in the Lissamphibia.

The recurrent cross-references among the chapters on Paleozoic amphibians highlight a major advantage of this work: Unlike other volumes of its size and breadth, *The Rise of the Amphibians* was written by a single author, giving it a comprehensive and logical structure. The authority of the author and timeliness of the work are beyond question regarding these and earlier chapters on Paleozoic amphibians. However, Carroll's book has some weaknesses when it comes to discussing current phylogenetic knowledge of lissamphibian phylogeny and origins. Not until chapter 9 does he bring up the enigmatic origins of modern amphibians. Chapter 13, "The Success of Modern Amphibians," shows some phylogenetic trees of the Lissamphibia, but all of these date back to 2004. This active field of research, and our understanding of lissamphibian biogeography, has been revolutionized by more recent phylogenetic studies—studies that provided, for example, evidence for phylogenetic links between relict frogs from southern South America (genus *Calyptocephalella*) and the Australian myobatrachid radiation; for relationships between Indian (*Nasikabatrachus*) and Seychellean (Sooglossidae) endemic frogs; for a few amphibian lineages dispersing over the sea to oceanic islands; and for a Tertiary dispersal out of South America of bufonid toads, a group previously considered to be much more ancient. A summary of these findings as reported by San Mauro and colleagues (2005), Frost and colleagues (2006), Roelants and colleagues (2007), and other important contributors would have been welcome. I was disappointed by the absence of an evaluation of the calibration points often used to date molecular trees of amphibians. How reliable are these points, and which ones may have been overlooked that may be more suitable? For amniotes, numerous papers have discussed which calibration points are most suitable and reliable from a purely paleontological point of view; a similar discussion is overdue for amphibians, especially since there is a great need for calibration points from the Tertiary.

The last chapter of *The Rise of Amphibians* is devoted to "The Future of Amphibians," and presents a thorough summary of the current knowledge of amphibian declines, which may represent the forefront of a sixth mass extinction. Despite the alarming signals, this chapter—mainly written by invited author David Green—ends with an optimistic conclusion: Amphibians have proven to be tough survivors of at least three mass extinctions (at the end of the Permian, Triassic, and Cretaceous) and may survive the current crisis of biodiversity as well. It remains to be seen where evolution will drive them. Will some frog lineages overcome the restrictions of their *bauplan* and evolve back into creatures with long vertebrate columns and tails, maybe in subterraneous or aquatic environments where their mainly optical sensory system and saltatory locomotion are disadvantageous? Will there ever be marine amphibians? Will there be neotenic frogs in which the tadpoles become sexually mature, which may then become the ancestors of a radiation with an unprecedented *bauplan* among vertebrates? I would have loved to have read some unbridled speculations about the future of amphibians by one of the major experts of their past. Even without these, however, I enjoyed reading this fascinating book. It will become a landmark and standard reference in early amphibian evolution for years to come.

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INSIDE THE BLUE LINE

The Great Experiment in Conservation: Voices from the Adirondack Park. William F. Porter, Jon D. Erickson, and Ross S. Whaley, eds. Syracuse University Press, 2009. 640 pp., illus. $45.00 (ISBN 9780815632313 cloth).

The Great Experiment in Conservation is a big book about a big subject: a great experiment in conservation that has been running now for over a century inside the "blue line" drawn in 1892, which created the Adirondack Park. Two years later, state-owned lands within the park—most of which had been logged over, acquired for back taxes, and already made a forest preserve to protect timber and water supply—were declared "forever wild" and placed under constitutional protection. The Adirondack Park contains six million acres—it's three times the size of Yellowstone. More than one million acres are motorless wilderness, which amounts to one-quarter of the designated wilderness in the United States east of the Rockies. In 1970, in the face of mounting development pressure, New York State formed the Adirondack Park Agency (APA), giving it broad powers to control private land use within the park and unleashing decades of controversy. These two watershed moments, almost a century apart, have made Adirondack Park one of the great "crucibles of conservation" in American history.

The editors of *The Great Experiment in Conservation: Voices from the Adirondack*

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