

Amphibian Evolution: The Life of Early Land Vertebrates.

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Rainer R. Schoch. 2014, 276 p.
Wiley-Blackwell, UK,
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AMPHIBIAN EVOLUTION: THE LIFE OF EARLY LAND VERTEBRATES. *Rainer R. Schoch.* 2014, 276 p. Wiley-Blackwell, UK, ISBN 978-0-470-67177-1.

This book by R. Schoch addresses the evolutionary history of amphibians, the earliest vertebrates to emerge onto land, with the aim of providing a factual framework to the analysis of a series of significant biological issues, such as morphogenesis, heterochrony, and adaptation, to name a few. It also furnishes a fascinating overview of how the changes in the theoretical basis of biological thinking have impacted the interpretation of raw evidence. Because of the biphasic life of many amphibians, they constitute plausible model-organisms to study the morphological and physiological features involved in the change of habits and habitat.

The book is divided into ten chapters. The Introduction begins with the discussion of the definition of Amphibia, a name that herein is applied to lissamphibians and all the taxa on their stem. The author argues against the past view that salamanders constitute a reasonable model to study the passage from water to land and criticizes the ecological scenarios that putatively forced vertebrates out of the ancestral pond, in view of the most recent studies suggesting the fundamentally aquatic lifestyle of early tetrapods. Some basic topics on the cladistic method to reconstruct the interrelationships of taxa are also briefly described in this chapter. In Chapter 2, the author overviews the history of tetrapods, which spans over 300 million years, including the latest discoveries. He comments on the significance of 12 exaptations in the origin of tetrapods and the appearance of other features that might be interpreted as synapomorphies but, as the fossil record demonstrates, result from convergent evolution. Several significant basal taxa, including *Eusthenopteron*, *Panderichthys*, *Tiktaalik*, *Ventastega*, *Acanthostega*, and *Ichthyostega*, are described. These taxa are mostly from Devonian rocks of scattered high latitude localities of the northern hemisphere and form a crownward series with increasing degree of relatedness to tetrapods. Carboniferous fossils already include representatives of the two diverging lineages of tetrapods that possibly originated the lissamphibian and amniote clades. Stem-group taxa of

the former include dissorophoids; it is within this group that a lifecycle with a brief period of marked morphological change, or metamorphosis, emerges. The climatic and environmental conditions represented in the most important amphibian fossil localities ranging from the Devonian to the Cenozoic, together with their paleogeographic locations, are reviewed exhaustively in Chapter 3. Soft structures, such as cephalic musculature, respiratory organs, and hearing organs, are described and interpreted phylogenetically in Chapter 4. Special attention is paid to the origin of the impedance matching system (middle ear) to maximize sensitivity to airborne sound, owing to the higher impedance of the fluids of the inner ear with respect to that of the air. The evolution of this system is thoroughly described in relation to anatomical changes in the otic region that preceded the acquisition of terrestriality by tetrapods according to available paleontological data. Chapter 5 deals with the evolution of functional systems. Inferences from the use of extant phylogenetic brackets, as in the previous chapter, are complemented by evidence furnished by experimental data and observations in extant exemplars. Accordingly, a scenario of feeding and respiration, tightly coupled in tetrapodomorph fish, is described. Line drawings illustrate the changes of the hyoid arch, which had a pivotal role in the movements of the cheek and operculum involved in the breathing and feeding cycles, during the fish-tetrapod transition. Transformation of the fins into limbs is also analyzed taking into consideration the available picture of the phylogenetic relationships of relevant fossils. Two chapters, 6 and 8, deal with developmental aspects. Not only do these chapters examine the life-cycles of extant lissamphibians but also the rich fossil record of ontogeny for amphibians. Especially interesting is the latter, although, unfortunately, growth series for stem tetrapods are practically unknown. In contrast, hundreds of specimens of a branchiosaurid species that belong to different growth stages have been described; these specimens show subtle morphological

changes throughout ontogeny, with larvae and adults living in the aquatic milieu. In turn, some small dissorophoids underwent more radical changes correlated with a drastic change of habitat. Other examples among temnospondyls and stem-amniotes are reviewed. In addition, the neotenic and metamorphosing developmental trajectories of some Paleozoic amphibians are compared with those of the living groups. The interplay between ontogeny and evolution, how development evolves and what the outcome of this change is and how it affects morphological evolution, are explored. A key concept in this relation is heterochrony, understood as the changes in the rates and timing of developmental processes with respect to the ancestral ontogeny. Changes in the sequences of developmental events document heterochrony. In this regard, comments on developmental sequences of temnospondyls are included in this chapter alongside with the role of heterochrony in the origin of lissamphibians. Also, similar features in the skull ossification sequence of branchiosaurids and that of salamanders, also resembling the sequence in some fishes and amniotes call for a non-adaptive, and broader, explanation. Ecological aspects of the amphibian history are addressed in Chapter 7, whereas ecological aspects of development are explored in Chapter 8. Factors that might affect life-history, with extant and extinct amphibians providing examples of developmental and morphological plasticity, are examined in this chapter as well. Main hypotheses on the origin of the three modern groups are reviewed in Chapter 9, and the last chapter is devoted to macroevolutionary patterns of amphibian evolution and underlying processes.

The treatment of the taxonomy, at odds with the current use of several well known taxon names based on phyloge-

netic definitions, is noteworthy. Many names that designate total groups (*i.e.*, stem plus crown) are applied only to the stem and, thus, to paraphyletic groupings. For example, such is the case of Salientia (which includes Anura as crown clade) and Tetrapodomorpha (which includes Tetrapoda, the last common ancestor of amniotes and lissamphibians and all of its descendants, as crown clade). Because of the possible utility of this book in college, it is a pity that several errors (*e.g.*, the anuran urostyle is a rod composed of fused tail vertebrae (rudimentary caudal vertebral elements plus hypochord); the opercular muscle is attached to the scapula (for suprascapula); outgrowth of the tail (fleshy outgrowth of the cloaca) forms the intromittent organ in *Ascaphus*; metapterygoid (for metapterygial) axis; in anurans and amniotes digits holding the highest number form first (digit 5 may be the last to form)) passed unnoticed through revisions. High quality photographs, some of which lack scales, illustrate different topics. Abundant and updated literature is included at the end of each chapter. In summary, this is a comprehensive work that could be used as a guide to focus on specific aspects of one of the most exciting chapters of vertebrate history.

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