BOOK REVIEW

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A review of *tadpoles: the biology of anuran larvae* by Roy W. McDiarmid and Ronald Altig

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Tadpoles: The Biology of Anuran Larvae. McDiarmid, R. W., and R. Altig. 1999. University of Chicago Press, Chicago. xiv + 444 pp. $70. ISBN 0-226-55762-6.

Tadpoles are eating machines. They don't have limbs, so they can't walk (although they do swim). They don't call (although they can hear) and they can't breed. They do have behavior, or at least what ethologists regard as behavior. So what do they do? Basically, they eat, and they do it a lot; approximately half of their biomass is intestine! Indeed, a tadpole's primary ecological *raison d'être* is to get the individual organism that it represents from embryo to (typically) terrestrial adult. In doing so, it tries to take advantage of what frequently are spatially and temporally abundant aquatic food resources. Given the essentially gastronomic theme of this phase of a frog's complex life history, it's only appropriate that a new volume about tadpole biology covers the field from soup to nuts. Amphibian gourmands will not be disappointed with this feast.

The book comprises 12 chapters by 14 authors, plus a glossary, an extensive bibliography (70 pages!), and three indices (author, subject, and taxonomic). Contents are organized topically: an introductory chapter by the editors is followed by one or more treatments of "standard" topics (morphology, neurobiology, physiology, behavior, and ecology), plus two chapters that address the origin, evolution, and maintenance of the anuran larva (and of the complex life history in general) as well as its loss through direct development and related reproductive modes. The final chapter, also by the editors, provides a detailed compendium of tadpole diversity (mostly anatomical, but also ecological) at the levels of families and genera.

Several chapters provide valuable and significant contributions, either by compiling and summarizing existing information from very diverse literature (both classical and recent), or by offering novel syntheses and highlighting important problems deserving of further study. For example, Cannatella (Architecture: Cranial and Axial Musculoskeleton) effectively organizes the often cumbersome and potentially confusing descriptions of musculoskeletal anatomy of tadpoles, which is essential for understanding the physiology and biomechanics of feeding and locomotion, as well as trophic ecology and behavior. Lannoo (Integration: Nervous and Sensory Systems) employs a very effective approach to reviewing tadpole neurobiology by emphasizing how larval features need to be understood in light of the dramatic changes that happen at metamorphosis. These changes, which include the outright loss or significant transformation of many larval-specific traits and *de novo* formation of many adult traits, offer many important lessons that apply equally to several other organ systems. Harris (The Anuran Tadpole: Evolution and Maintenance) takes a primarily population-biological approach to assessing the ecological and genetic context for the origin and retention of the complex life history. Some readers will be disappointed with the limited treatment of phylogenetic, and especially paleontological, evidence that bears on this topic, which is tightly linked to more general questions regarding amphibian origins and relationships. Nevertheless, Harris develops a provocative model for life history evolution, based largely on quantitative genetics, which posits that direct development may represent the ancestral (or primitive) life history for anurans. This hypothesis, which has been offered previously by other authors based on different considerations, is generally regarded as inconsistent with existing paleontological and phylogenetic data. Evidence on either side of the argument, however, is far from unequivocal, and Harris's model is worth evaluating more thoroughly.

Potential readers who might want to pick and choose only a subset of chapters should be forewarned that many of the chapter headings are somewhat misleading, insofar as they don't communicate the topical breadth of the treatment that follows. Thus, Hoff et al. (Behavior: Interactions and Their Consequences) discuss related aspects of physiology, locomotion, neuroanatomy, and ecology. They also include several wonderful natural history accounts and two splendid,

original drawings of tadpole communities ("ecological dioramas") by Kate Spencer, one of which is featured on the front cover of the dust jacket.

I can identify relatively few features of the book that might have been done differently, and in general these define minor quibbles that don't detract significantly from the volume's overall quality and value. Thus, chapters on Behavior and Integration might have followed one another directly instead of being separated by Physiology: Coping with the Environment (Ultsch et al.) and Endotrophic Anurans: Development and Evolution (Thibaudeau and Altig). Similarly, many readers unfamiliar with detailed aspects of amphibian life history evolution may find the latter chapter easier to digest if they first read Ecology: Resource Use, Competition, and Predation (Alford) and The Anuran Tadpole: Evolution and Maintenance, which instead appear near the end of the book. I also was surprised to see so little discussion of the possible—indeed, likely—role of tadpoles in the well-documented decline of many amphibian species worldwide. There already is enough evidence to conclude that larval physiology is a critical link in the chain of causal events leading to the decline of at least some amphibian species. Indeed, some of this evidence is mentioned in passing by both Ultsch et al. and Alford, although nowhere is it dealt with explicitly in this context. The relevance and tragedy of this phenomenon is underscored by the description of the facultative nonfeeding tadpole of *Bufo periglenes*, which is described as representing a critical and possibly unique stage in the evolution of exclusively maternal provisioning of the embryo and larva (i.e., endotrophy; p. 184). This species, the "golden toad" of Costa Rica, has not been seen alive since 1989 and may now be extinct.

I came away from reading this book with two main messages regarding existing knowledge about tadpoles and prospects for future research. The first is a general recognition that current understanding of tadpole biology is based largely on a relatively small number of temperate species, mostly in the genus *Rana* (Ranidae) but also, of course, *Xenopus laevis* (Pipidae). Much of this work is excellent science and extremely valuable. Nevertheless, to the extent that we, as biologists, continue to draw broad conclusions regarding larval amphibian biology from such a biased taxonomic and ecological sampling, we do so at our intellectual peril. Moreover, there is an urgent need for detailed studies of individual species that simultaneously relate important anatomical and physiological features to larval ecology and behavior. Only with such comprehensive studies can we hope to meaningfully address many important questions of adaptation and evolution.

The second message is the tremendous potential for developmental biology to make critical and unique insights into our understanding of tadpole biology. I regard this potential as largely untapped, despite the large amount of information that already has been derived from literally hundreds of studies of early development in the two primary amphibian "model" systems, *X. laevis* and *Ambystoma mexicanum*, and decades of study of the endocrinological basis of metamorphosis in both frogs and salamanders. Much of the potential relevance of development lies beyond what might be viewed as its "traditional" applications in the study of morphology and reproductive biology, and instead to fields such as ecology, behavior, and physiology. Conversely, tadpoles offer excellent (and practical) opportunities for the study of many contemporary and general problems in *evo-devo*, from the origin and evolution of complex features to the developmental basis of homology, from life-history evolution to developmental constraints. The present volume likely will prove to be an indispensable resource in this and related research.