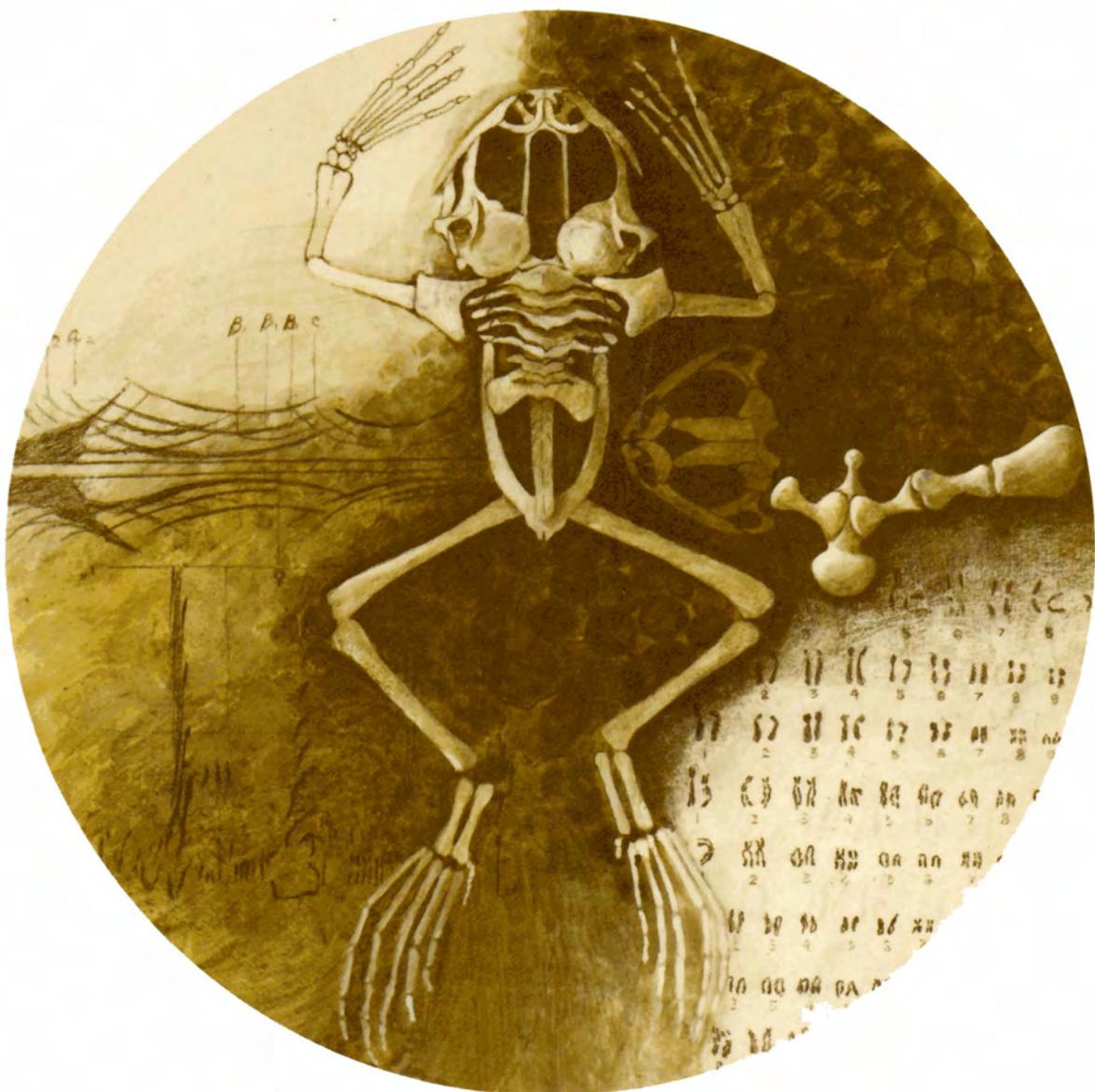
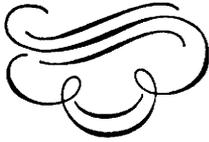

EVOLUTIONARY BIOLOGY OF THE ANURANS

Contemporary Research on Major Problems

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*University of Missouri Press
Columbia, 1973*

PREFACE



Because amphibians exhibit certain general characteristics, particularly a biphasic life cycle, external fertilization, and a unique occupancy of the transitional aquatic-terrestrial environment, they have proven to be excellent organisms for the study of many basic biological phenomena. During the forty-one years since the publication of G. K. Noble's classic reference, *The Biology of the Amphibia* (1931), there has been an almost exponential increase of information about these vertebrates. Of amphibians, the frogs and toads are an incomparably successful and dynamic group. The nearly 2,000 known species display a remarkable range of adaptations that has enabled them to occupy an array of diverse habitats in most areas of the earth. Studies of anurans in both the field and the laboratory have been a source of much of our current knowledge of embryology, physiology, genetics, ecology, population dynamics, systematics, evolution, and biogeography.

This volume is the progeny of a symposium presented during the 13th annual meetings of the Society for the Study of Amphibians and Reptiles, held on the Kansas City campus of the University of Missouri from August 27 to August 30, 1970. During the concluding sessions of the 1969 SSAR meetings, the idea for a symposium on anuran biology arose from my discussions with Dr. Kraig Adler (Cornell University) and Dr. William E. Duellman (University of Kansas). We met several times during the following weeks to develop a program with a unifying theme that, we had concluded, could be best embodied in an evolutionary approach. After composing lists of topics and of the outstanding authorities in each subject, we tried to balance the selection of participants between those who have been long established and those who have achieved more recent recognition. The purpose of mixing "old guards" and "young turks" was to increase the opportunity for an incisive, critical evaluation of the evidence.

The response from the invited specialists greatly reinforced our original optimism about the amount of interest the program would receive. They all shared our opinion that such a synthesis was overdue, and each labored for nearly a year, exchanging and revising early drafts in preparation for the meetings. However, because the time limitations imposed by the formal sessions restricted the length of the material, the authors were allowed further opportunity to revise and elaborate upon their manuscripts until press time in 1972. Thus, the papers as published here have a recency and a greater body of evidence than the original presentations. Except for a minor rearrangement in sequence, the organization of this book follows that of the symposium.

The salient problems in anuran evolution and those areas of investigation likely to produce significant resolutions are identified in Blair's introductory paper.

In Part I, Estes and Reig interpret early evolutionary lineages; from their meticulous re-examination of Mesozoic proanuran and anuran fossils, they derive support for the lissamphibian hypothesis of common origin for frogs, salamanders, and caecilians. Variation and trends in the evolution of skeletal morphology are assessed by Trueb. Her evidence suggests a greater adaptive lability in osteological features than has been generally recognized. Lynch reviews the substance of previous anuran classifications and, after presenting extensive and detailed character analyses, proposes an alternative phylogeny to delineate the archaic, transitional, and advanced frog families. The application of modern biochemical techniques to determine genetic relationships is described and evaluated by Guttman.

In Part II, Rabb compares variation and progressive complexities in components of reproductive behavior among anuran taxa, emphasizing the roles of hormonal and neurological mechanisms. Salthe and Duellman find simultaneous relationships in body size, clutch size, ovum size, and mode of reproduction, all of which impose adaptive limitations on the evolution of reproductive strategies. Starrett focuses upon functional anatomy of the branchial chambers, chondrocranium, and musculature to diagnose the significant evolutionary features of larval morphology. Four distinctive developmental patterns provide a framework for her definitions of the anuran suborders. Diverse modes of tadpole social behavior are recognized by Wassersug as responses to environmental variables, which he interprets in terms of adaptive and evolutionary trends.

In Part III, Schiøtz examines the ecological role of mating calls in the context of social interactions and sound environments. He concludes that voices are important determinants of evolutionary processes but of little use in phylogenetics. Straughan's complementary study deals with mating calls as functional units of communications systems that exhibit modular characteristics subject to selective pressures. An operational definition and application of the techniques of ecological genetics is provided by Merrell, and chromosomal mutations are used by Bogart to postulate derivations from ancestral karyotypes. Savage reconstructs the historical origins of modern frog distribution from his analyses of concurrent events in continental drift, paleoecological opportunities, and macroevolution.

Each of the above parts, which represent the program's sessions, is followed by an open discussion in which the contributors and moderator are identified by surname only. Other speakers are identified by their full names and professional affiliations at the point of their initial statements and subsequently by surnames only. The editing of these tape-recorded sessions has been necessarily severe. I have, however, tried to leave intact the informal atmosphere of the discussions, as well as to retain the innuendoes and syntax of the speakers.

During the preparation and presentation of the symposium, several students in the Biology Department at the University of Missouri—Kansas City, particularly Thomas J. Berger, James R. Stewart, Donald D. Smith, Cathy Ewart, Cathy Hunt, and Roger Jensen, offered their generous assistance. I also benefited by the experience of Dr. William W. Milstead, who organized and edited a noteworthy symposium on lizard ecology in 1965. Dr. Harold C. Burdick, Acting Chairman of the Biology Department, provided funds for staff assistance and communication

expenses. Paul Anderson and Linda Folkman of the Division for Continuing Education managed most of the procedural details during the meetings.

Dean Edwin J. Westermann and Associate Dean Henry A. Mitchell of the UMKC College of Arts and Sciences supported the project by subsidizing the travel expenses for the foreign participants, arranging for the availability of facilities, and making possible my reduced teaching commitment during some of the months required for editing. Provost Wesley J. Dale also arranged some financial support for travel of foreign participants.

I have been aided greatly in the editorial work by two persons who deserve special recognition: Kay Earnshaw, who did the difficult transcription of discussion sessions and typed the many manuscript drafts that were necessary, and Thomas J. Berger, who has been of continued assistance in overseeing many editorial details.

To all of these, and others not individually mentioned, I wish to express my sincere gratitude. At a time when scientific specialists must search through an extensive body of literature in order to maintain professional competence and biologists with more general interests encounter equal difficulty in finding other than vintage references, I hope this volume will accomplish the intended objectives of providing a contemporary review, re-examination, and synthesis of those fields that significantly relate to anuran evolution.

J.L.V.

University of Missouri—Kansas City
August, 1972



Participants in the Symposium on Evolutionary Biology of the Anurans. *Seated, left to right:* Arne Schiøtz (Danmarks Akvarium, Charlottenlund, Denmark), Sheldon I. Guttman (Miami University, Ohio), Priscilla H. Starrett (University of Southern California), W. Frank Blair (University of Texas—Austin), Linda Trueb (University of Kansas), Stanley N. Salthe (Brooklyn College of the City University of New York), James P. Bogart (Louisiana Tech University). *Standing, left to right:* Jay M. Savage (University of Southern California), John D. Lynch (University of Nebraska), George B. Rabb (Chicago Zoological Society), Ian R. Straughan (James Cook University of North Queensland, Australia), Dean E. Metter (University of Missouri—Columbia), Richard Estes (Boston University), Robert F. Inger (Field Museum of Natural History), Richard J. Wassersug (University of California—Berkeley), David J. Merrell (University of Minnesota), William E. Duellman (University of Kansas), Osvaldo A. Reig (Universidad Austral de Chile, Valdivia, Chile). *Not shown:* Joseph A. Tihen (University of Notre Dame).

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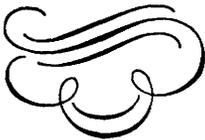
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EVOLUTIONARY BIOLOGY OF THE ANURANS

INTRODUCTION

MAJOR PROBLEMS IN ANURAN EVOLUTION

W. Frank Blair



INTRODUCTION

I am taking two approaches in this introductory statement. One is addressed to the accuracy of our present knowledge of the evolutionary history and degree of diversification (speciation) of the anurans. This approach, of course, raises the question of the accuracy of present schemes that represent presumed phyletic relationships of the anurans at all levels up to the highest taxa. The second approach is addressed to the use of anurans as materials by which we can elucidate evolutionary mechanisms and principles. The two approaches are not mutually exclusive and can be discussed as parallel, rather than isolated, entities.

With respect to evolutionary history, we are concerned with such questions as the following: What has been the area of origin of major evolutionary breakthroughs leading to the establishment of new phyletic lines—to new higher taxa in our schemes of classification? What has been the history of expansion of these lines into other areas? What has been the time scale within which these events have occurred? There are obviously related questions. What has been the ancestral group? How much has our understanding of phylogenetic relations been clouded by convergent evolution? How much by differential rates of evolution within various subgroups? How much by differential rates of change in different biological systems?

With respect to evolutionary mechanisms, we can also ask of our anuran material a number of significant questions: What is the real meaning of ecological diversity? Why are some genera monotypic and seemingly have been monotypic or nearly so throughout their histories, while others split into many species? Why is there greater diversity in the tropics than in extratropical regions? Why does diversity of taxa decrease and numbers of individuals increase as one ascends a tropical mountain range? How are major specializations initiated and perfected? What are the mechanisms of speciation? Why do evolutionary strategies differ so much between taxa, such as *Rana* and *Bufo*? Are these differences due to different ecological roles of the two genera, or do they relate back to basic differences in their genetic constitutions? Some of these questions have moderately satisfactory answers; some have no answers at all.

In raising these questions and in suggesting possible approaches that might provide answers, I am going to stress the multidisciplinary approach, particularly