

# Distributions, Relationships, and Zoogeography of Lowland Frogs The *Leptodactylus* Complex in South America, with Special Reference to Amazonia

W. Ronald Heyer  
and Linda R. Maxson

**ABSTRACT** An analysis of the distributions and evolutionary relationships of lowland frogs of the species-rich *Leptodactylus* complex is presented. Composite species distributions are derived and carefully examined for general patterns. Centers of species diversity are defined and compared with the present distribution of morphoclimatic domains. The high species diversity observed in the *Leptodactylus* complex is attributed to the occurrence of two major ecological groupings of frogs and three distinct adaptive patterns of these frogs.

Our joint work has been supported by the Director's Office, National Museum of Natural History, Smithsonian Institution, and the Smithsonian Research Awards program.

Raymond F. Laurent and Roy W. McDiarmid provided muscle samples from Argentina and Peru, respectively.

Roy W. McDiarmid, Alan H. Savitzky, and P. E. Vanzolini have read over the manuscript and offered constructive comments.

WHR's work on systematics of the *Leptodactylus* complex has been supported by the Smithsonian Institution Research Foundation, the Smithsonian Research Award Program, and the Smithsonian Amazon Ecosystem Research program.

WHR expresses special thanks to P. E. Vanzolini for a personal introduction to the Amazon.

LMR's work on biochemical systematics of leptodactylid frogs has been generously supported by the Department of Genetics and Development, University of Illinois, Urbana.

We thank these institutions and individuals for their support.

Evolutionary relationships among representative *Leptodactylus* species based on comparative studies of albumin sequence differentiation are also described. This work reveals that speciation events are Tertiary, not Pleistocene events, and that there exists some intraspecific variation that appears to extend back into the Pliocene.

The refuge theory accounts for very few distributional events and no speciation events in the *Leptodactylus* complex.

The *Leptodactylus* complex of frogs has been the subject of extensive systematic analyses by the senior author for the past twelve years. More recently we have initiated biochemical analyses of these same species in hopes of providing new insights into the relationships among this interesting but enigmatic assemblage of frogs. This symposium has provided us the impetus to synthesize our current understanding of the distributions and evolutionary relationships of the members of the *Leptodactylus* complex. Because much systematic and biochemical work is still going on, what we present here must be construed as a progress report. However, we believe that at this time we are able to make some basic statements concerning the distribution, evolutionary relationships, and zoogeography of the group.

The focus of this symposium is the testing of what has come to be called the refuge theory (Simpson & Haffer 1978), based on studies of avifaunas primarily in

