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**New World direct-developing frogs (Anura: Terrarana):  
Molecular phylogeny, classification, biogeography, and conservation**

S. BLAIR HEDGES, WILLIAM E. DUELLMAN, & MATTHEW P. HEINICKE



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## New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation

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## Abstract

New World frogs recently placed in a single, enormous family (Brachycephalidae) have direct development and reproduce on land, often far away from water. DNA sequences from mitochondrial and nuclear genes of 344 species were analyzed to estimate their relationships. The molecular phylogeny in turn was used as the basis for a revised classification of the group. The 882 described species are placed in a new taxon, Terrarana, and allocated to four families, four subfamilies, 24 genera, 11 subgenera, 33 species series, 56 species groups, and 11 species subgroups. Systematic accounts are provided for all taxa above the species level. Two families (Craugastoridae and Strabomantidae), three subfamilies (Holoadeninae, Phyzelaphryninae, and Strabomantinae), six genera (*Bryophryne*, *Diasporus*, *Haddadus*, *Isodactylus*, *Lynchius*, and *Psychrophrynella*), and two subgenera (*Campbellius* and *Schwartzzius*) are proposed and named as new taxa, 13 subspecies are considered to be distinct species, and 613 new combinations are formed. Most of the 100 informal groups (species series, species groups, and species subgroups) are new or newly defined. *Brachycephalus* and *Ischnocnema* are placed in Brachycephalidae, a relatively small clade restricted primarily to southeastern Brazil. Eleutherodactylidae includes two subfamilies, four genera, and five subgenera and is centered in the Caribbean region. Craugastoridae contains two genera and three subgenera and is distributed mainly in Middle America. Strabomantidae is distributed primarily in the Andes of northwestern South America and includes two subfamilies, 16 genera, and three subgenera. Images and distribution maps are presented for taxa above the species level and a complete list of species is provided. Aspects of the evolution, biogeography, and conservation of Terrarana are discussed.

**Key words:** Amphibia, Brachycephalidae, Craugastoridae, DNA sequence, Eleutherodactylidae, evolution, Strabomantidae, systematics, taxonomy

## Introduction

The twenty-first Century has witnessed a renaissance in systematic biology with respect to theory, methodology, and taxonomy, and perhaps most significantly the application of systematics to such diverse fields as ecology, behavior, and conservation, among others. This resurgence has occurred principally with the sequencing of DNA and use of newly developed methods of analysis. Thus, systematists have discovered a new array of tools and characters for the inference of phylogenetic relationships. These innovative approaches are being used from the levels of local phylogeography to ascertaining the relationships among prokaryotes and eukaryotes. The only work that has attempted to determine the phylogenetic relationships among all liv-