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It is time for a new classification of anoles (Squamata: Dactyloidae)

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Abstract

In this essay, we review concepts of taxonomic categories of anoles, reanalyze accumulated characteristics of these lizards, use these analyses to summarize the topology of the phylogenetic tree for anoles, and use consistent major branches of this topology to recommend a classification scheme for this large group of squamates. We then use this new taxonomy to draw inferences about the evolution of habitat use, as well as the geologic ages and geographic distribution of anole lineages. Our taxonomy eliminates problems of paraphyly inherent in previous classifications by elevating eight major lineages to generic status (*Anolis*, *Audantia*, *Chamaelinorops*, *Ctenonotus*, *Dactyloa*, *Deiroptyx*, *Norops*, and *Xiphosurus*), providing diagnoses of those genera, and then doing the same for species groups within each genus. With the exception

of 19 species, the contents of our generic categories are consistent with all recent phylogenetic reconstructions. Thus, the revised taxonomy appears to provide a stable classification for at least 95% of the 387 species currently recognized and included in our treatment of the group. We argue that these lizards originated in South America ~130 ma, where they were large in size and occupied niches focused on the canopy of rainforest trees. The radiation diverged into eight genera 125–65 ma within a volcanic island arc that connected North and South America. This evolutionary diversification generated three genera (*Deiroptyx*, *Dactyloa*, and *Xiphosurus*) that retained an ancestral large size and canopy niche focus and five genera (*Anolis*, *Audantia*, *Chamaelinorops*, *Ctenonotus*, and *Norops*) that became small, with niches focused toward the ground. The complicated divergence and accretion events that generated the current conformation of the Antillean islands, and eventually closed the Panamanian Portal, transported six island genera to their current centers of diversity (*Anolis*, *Audantia*, *Chamaelinorops*, *Ctenonotus*, *Deiroptyx*, and *Xiphosurus*), leaving two genera on the mainland (*Dactyloa* and *Norops*). Our historical reconstruction makes *Norops* a much older radiation than previous reconstructions, allowing basal diversification of this species-rich lineage to occur on mainland terrains that eventually separated from the mainland to become parts of Cuba and Jamaica. This early diversification extended into northern South America, where a basal lineage of *Norops* coevolved with *Dactyloa* prior to the mainland-island separation.

Key words: Reptilia, lizards, systematics, biogeography, ecomorphology, evolution

Introduction

This monograph is about a group of iguanian lizards popularly referred to as anoles and constituting the family Dactyloidae (Townsend *et al*. 2011). For those who regard the family to be monotypic it is often asserted that *Anolis* (*sensu lato*), with nearly 400 valid species, is the largest genus of terrestrial vertebrates (for the sources of the name anole see Appendix I). That the species involved are among the most studied in an array of ecological, behavioral, and physiological contexts is a vital reason for their evolutionary relationships to be critically reevaluated. Systematic progress in this regard has been delayed by an extremely conservative taxonomic approach to recognizing the diversity within the group and its extraordinarily ancient historical roots.

Our primary objective in this paper is to review the classification of the family Dactyloidae and evaluate the evidence for the existing taxonomy. Our second goal is to determine the monophyly of its formal and informal taxa above the species level (i.e., genera and species groups). In order to attain these goals, we perform a phylogenetic analysis based on morphological, molecular, and karyological features to establish relationships among 231 dactyloid species. The principal result of this analysis leads us to propose a new classification consistent with the inferred history and the goal of recognizing major monophyletic lineages. In addition, we use our phylogeny 1) to examine current ideas on ecologic valence for a wide array of dactyloid species and to develop a hypothesis that provides a historical explanation for the evolution of habitat use, and 2) to propose a bold hypothesis of the biogeographic history of the family within the constraints of the phylogeny inferred here, the latest known fossils, and a paleogeographic interpretation of the deep history of the West Indies, North America, Mesoamerica, and South America.

Current Systematic Status

All reviews of the present classification of anoles must begin with an acknowledgement of the monumental work of Richard E. Etheridge (1960). This highly cited—but never published—monograph was the first to comprehensively investigate anole relationships through a comparison of osteological characters polarized via precursors to modern parsimony methods. On the basis of his comparisons, he proposed a hypothesis of relationships and erected a classification scheme for anoles. His conclusions predated modern phylogenetic methods, but were astute in the proposed relationships, many of which were supported by later authors (e.g., Guyer and Savage, 1986, 1992; Poe, 2004), recent molecular studies (e.g., Glor *et al*. 2005; Mahler *et al*. 2010; Nicholson *et al*. 2005), and the present paper. Etheridge (1960) divided the genus *Anolis* into two groups—termed 'alpha and beta sections'—based upon the condition of their caudal vertebrae. The alpha section lacked the anterolaterally-directed transverse processes that are present on the vertebrae of beta section members. He further subdivided each section into groups termed 'series' on the basis of several combinations of osteological characters. Most important among these characters were interclavicle shape, parasternal rib formulae, number of anterior aseptate vertebrae,