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Review of Teiid Morphology with a Revised Taxonomy and Phylogeny of the Teiidae (Lepidosauria: Squamata)

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Abstract

Despite advances within particular groups, systematics of the Teiidae has long been unsatisfactory, because few morphological characters have been described for this family. Consequently, most species have been assigned to the large, polyphyletic, and poorly defined genera *Ameiva* and *Cnemidophorus*. We describe 137 morphological characters and score them for most species of Neotropical Teiidae. Important, but previously undescribed, character suites include pupil shape; the frontal ridge; longitudinal division of the interparietal; the rostral groove; patterns of supraciliary fusion; the preauricular skin fold; the "toothy" first supralabial; modified apical granules; the pectoral sulcus; expansion of scales at the heel; tibiotarsal shields; scales between the digital lamellae along the postaxial edges of the toes; scale surface microstructure of macrohoneycomb, macroridges, or lamellae; distribution patterns and morphology of lenticular scale organs; types of epidermal generation glands; and several hemipenial structures. We propose a new taxonomy of the Teiidae based on recovered evolutionary history and numerous morphological characters surveyed in this study. We recognize three subfamilies: Callopistinae **new subfamily**, Teiinae Estes *et al.*, and Tupinambinae Estes *et al.* To resolve polyphyly of *Ameiva* and *Cnemidophorus*, we erect four new genera for various groups of Neotropical Teiidae: *Ameivula* **new genus,** *Aurivela* **new genus,** *Contomastix* **new genus,** and *Medopheos* **new genus.** We resurrect *Holcosus* Cope from the synonymy of *Ameiva* and *Salvator* Duméril and Bibron from the synonymy of *Tupinambis*. On the basis of shared derived characters, we propose new species groups of our redefined *Ameiva* and *Cnemidophorus*. We incorporate our new characters into a key to the genera and species groups of Teiidae. A phylogenetic hypothesis of Teiidae based on morphological characters differs substantially from hypotheses based on mitochondrial DNA. The phylogeny based on morphology is consistent with well-established biogeographic patterns of Neotropical vertebrates and explains extreme morphological divergence in such genera as *Kentropyx* and *Aurivela*.

Key words: *Ameivula* new genus, *Aurivela* new genus, Callopistinae new subfamily, *Contomastix* new genus, generation glands, *Holcosus, Medopheos* new genus, scale surface morphology, *Salvator*

Introduction

Prior to Boulenger's systematic rearrangement of lizards, the various teiid genera were scattered among several families. In his key to genera, Boulenger (1885b) divided the teiids up into four groups; his Group I was defined by nasals not separated medially by a frontonasal, limbs well developed, and body moderate to large. The group included the various genera of "macroteiids," a term perhaps first used by Ruibal (1952). The remaining groups included various genera of microteiids and are currently assigned to the Gymnophthalmidae. Later, the macroteiids were placed in a separate subfamily containing two clades formally recognized as the tribes Teiini and Tupinambini by Presch (1970, 1974a). Little doubt remains that the Teiidae and Gymnophthalmidae are monophyletic groups (Castoe *et al.* 2004; Pellegrino *et al.* 2001), and Presch's clades are generally regarded as subfamilies (Estes *et al.* 1988). Recognition of these subfamilies has received mostly unambiguous support from separate analyses of chromosomal (Gorman 1970), hemipenial (Böhme 1988), osteological (Presch 1974a), integumental (Vanzolini & Valencia 1965), myological (Rieppel 1980, but see Abdala & Moro 2000), neurological (Northcutt 1978), and mitochondrial DNA (Giugliano *et al.* 2007) character sets. A third subfamily Chamopsiinae accommodates extinct genera from North America and may be the sister group of the extant subfamilies (Denton & O'Neill 1995; but see note added to proof of Sullivan & Estes 1997). The Teiidae is almost certainly the sister group of the Gymnophthalmidae, and teiids likely arose in the middle Cretaceous from a common ancestor shared with the extinct Polyglyphanodontidae (Conrad 2008; this group has been considered an additional subfamily of the Teiidae by some authors, e.g., Estes 1983a; Gao & Norell 2000).

The genus-level taxonomy of the Teiidae has long been unsatisfactory. This problem is particularly acute within the speciose radiation of cnemidophorines in which most tropical species are assigned to the large polyphyletic genera *Ameiva* and *Cnemidophorus*. Polyphyly urgently requires resolution, because teiids are often the most conspicuous elements of many New World herpetofaunas and have been the subject of numerous detailed ecological studies. As researchers make ecological comparisons among teiid species, draw inferences about their biogeography, propose conservation strategies, and conduct other studies of their comparative biology, polyphyly of genera such as *Ameiva*, *Cnemidophorus*, and *Tupinambis* will likely produce what Bortolus (2008) called "error cascades," where seemingly trivial taxonomic problems become magnified in the development of scientific knowledge. However, the problem is not just one of polyphyly. Some genera have never been adequately diagnosed, whereas others are defined by apparent symplesiomorphies. These problems contribute to misidentification in the field and incorrect or uncertain assignment of newly discovered species.