



## Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata)

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## Abstract

The family Leptotyphlopidae (116 species) includes the smallest and thinnest species of snakes, often called threadsnakes (or wormsnakes). They are burrowing, have small eyes, and they feed on several life history stages of social insects. Leptotyphlopids have a West Gondwanan distribution, occurring primarily in Africa and the Neotropics (South America, Middle America, and the West Indies). The family is one of the most poorly known of all terrestrial vertebrates from the standpoint of systematics and ecology. No published phylogenetic studies of higher-level relationships exist, either from morphological or molecular data. Here we present DNA sequence analyses of 91 individuals representing 34 recognized species of leptotyphlopids, from nine mitochondrial and nuclear genes. The results show divergences among living lineages as early as the mid-Cretaceous, 92 (113–75) million years ago (Ma) and evidence that the breakup of West Gondwana into South America and Africa, and the separation of West Africa from South and East Africa by high sea levels in the Cretaceous, influenced the biogeographic history of the family through isolation. A Late Cretaceous (78 Ma; 98–63 Ma) transatlantic dispersal from West Africa to South America may explain the origin of the monophyletic New World radiation. Mid-Cenozoic divergences among Middle and North American species indicate that leptotyphlopids dispersed to those regions from South America, by rafting over water, prior to the emergence of the Isthmus of Panama. A revised classification recognizes two subfamilies, Epictinae subfam. nov. (New World and Africa) and Leptotyphlopinae (Africa, Arabia, and Southwest Asia). Within the Epictinae we recognize two tribes (Epictini trib. nov. and Rhinoleptini trib. nov.), three subtribes (Epictina subtrib. nov., Tetracheilostomina subtrib. nov., and Renina subtrib. nov.), and eight genera (*Epictia*, *Guinea* gen. nov., *Mitophis* gen. nov., *Rena*, *Rhinoleptus*, *Siagonodon*, *Tetracheilostoma*, and *Tricheilostoma*). Three tribes are recognized within the Leptotyphlopinae (Epacrophini trib. nov., Myriopholini trib. nov., and Leptotyphlopini trib. nov.) and four genera (*Epacrophis* gen. nov., *Myriopholis* gen. nov., *Leptotyphlops*, and *Namibiana* gen. nov.). The significant non-monophyly of some species and the estimated long period of time (tens of millions of years) separating populations of currently recognized species indicate that an unusually large number of species exist that are unrecognized. This combined with small distributions and high levels of deforestation in these areas argue for increased awareness of leptotyphlopids and other burrowing reptiles in conservation planning.

**Key words:** Africa, burrowing, Cretaceous, dispersal, Middle America, South America, transatlantic, vicariance, West Indies

## Introduction

Leptotyphlopids (116 species) include the thinnest and smallest species of snakes, all of which are burrowers. They are known as threadsnakes or wormsnakes, with the former noted as being more appropriate due to their often extreme thinness (Branch 1998; 2005). Together with two other families of burrowing and worm-like snakes with small eyes—Typhlopidae and Anomalepididae—they comprise the Scolecophidia, the closest relative of all other snakes (Alethinophidia).

Leptotyphlopids are distributed almost exclusively in Africa and the Neotropics (Middle and South America and the West Indies), with a few species occurring in southern North America, Arabia, and southwest Asia (Fig. 1). They occupy a wide variety of habitats and elevations, occurring in deserts (e.g. Branch 1998; Broadley & Wallach 2007), forests (e.g. Broadley & Wallach 1999a), wetlands, savannas (Broadley & Broadley 1999; Broadley & Wallach 2007), and transformed habitats (Thomas *et al.* 1985), from below sea level to 3250 meters (Thomas *et al.* 1985; Zug 1977). They feed frequently (Cundall & Greene 2000; Greene 1997), primarily on small, social insects, and particularly their eggs and larvae (Webb *et al.* 2000). Some leptotyphlopids occur on islands that were never connected to mainland areas (see below), indicating that they must have arrived by rafting over ocean waters. Nonetheless, the overall distribution of the family is, in biogeographic terms, West Gondwanan, raising the possibility that the separation of South America and Africa in the mid-Cretaceous (~105 million years ago, Ma) may have influenced the evolutionary history of the group through vicariance.

Nearly all systematic work on the family Leptotyphlopidae has been the description of new species. All species have been placed in the Genus *Leptotyphlops*, except a single species from West Africa with a horn-like rostral scale that is placed in the Genus *Rhinoleptus* (Orejas-Miranda *et al.* 1970). Twelve species groups