Blindsnake evolutionary tree reveals long history on Gondwana

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Blindsnake evolutionary tree reveals long history on Gondwana

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Worm-like snakes (scolecophidians) are small, burrowing species with reduced vision. Although largely neglected in vertebrate research, knowledge of their biogeographical history is crucial for evaluating hypotheses of snake origins. We constructed a molecular dataset for scolecophidians with detailed sampling within the largest family, Typhlopidae (blindsnakes). Our results demonstrate that scolecophidians have had a long Gondwanan history, and that their initial diversification followed a vicariant event: the separation of East and West Gondwana approximately 150 Ma. We find that the earliest blindsnake lineages, representing two new families described here, were distributed on the palaeolandmass of India+Madagascar named here as Indigascar. Their later evolution out of Indigascar involved vicariance and several oceanic dispersal events, including a westward transatlantic one, unexpected for burrowing animals. The exceptional diversification of scolecophidians in the Cenozoic was probably linked to a parallel radiation of prey (ants and termites) as well as increased isolation of populations facilitated by their fossorial habits.

Keywords: biogeography; squamates; snakes; dispersal; vicariance

1. INTRODUCTION

Of the two major divisions of snakes, scolecophidians are the most poorly known in terms of species diversity, phylogeny, biogeography and ecology (Greene 1997). They feed on small social insects (ants, termites and their larvae), and do so on a frequent basis (Cundall & Greene 2000). They include the smallest snakes and rarely exceed 30 cm in length (Hedges 2008). Most species have greatly reduced eyes and head scolation, a pinkish or brownish, tubular-shaped body with smooth scales, and are frequently mistaken for earthworms by non-scientists. Scolecophidians are distributed on all continents except Antarctica, but most species inhabit the southern continents and tropical islands (Uetz et al. 2010).

Scolecophidians include approximately 400 species divided into three families: Anomalepididae (anomalepids, approx. 17 species), Leptotyphlopidae (threadsnakes, approx. 120 species) and Typhlopidae (blindsnakes, approx. 260 species) (Adalsteinsson 2009; Uetz et al. 2010). All three occur in the New World tropics, with the anomalepids restricted to that region. Threadsnakes also occur in Africa, Arabia and southwest Asia, whereas blindsnakes are even more broadly distributed, occurring in Africa, Madagascar, southeastern Europe, southern Asia and Australia (Adalsteinsson et al. 2009).

Remarkably, for a lineage of terrestrial vertebrates, only two higher level scolecophidan phylogenies are available. The first one is an unpublished PhD dissertation based on an analysis of mostly internal anatomy (Wallach 1998). The second is a recent molecular study of threadsnakes using sequences of nine mitochondrial and nuclear genes (Adalsteinsson et al. 2009).

Snakes in general and scolecophidians in particular have a Gondwanan origin (Vidal et al. 2009). Threadsnakes originated on West Gondwana (Africa and South America), as did anomalalepids (Adalsteinsson et al. 2009). The wide distribution of blindsnakes on Gondwana, and their fossorial (burrowing) habits, suggests that continental drift influenced the early evolutionary history of this family as well. However, they lack a significant fossil record and therefore details are unclear. Did oceanic dispersals also occur? If so, which continents were occupied by blindsnakes ancestrally and which ones were colonized later by dispersal? These are questions that we address here with a new molecular dataset.

2. MATERIAL AND METHODS

We constructed a molecular dataset for 96 scolecophidian species from the three recognized families, with detailed sampling of the largest family, Typhlopidae. The dataset comprised of five nuclear protein-coding genes (recombination-activating gene 1: RAG1, amelogenin: AMEL, brain-derived neurotrophic factor: BDNF, neurotrophin 3: NT3 and bone morphogenetic protein 2: BMP2) for 101 taxa (85% of the sequences were newly determined, i.e. 402 sequences that have been deposited in GenBank under accession numbers GU902304–GU902705). Phylogenies were built using probabilistic approaches (maximum-likelihood (ML) and Bayesian inferences) and dating analyses were performed according to the Bayesian relaxed molecular clock approach (figure 1; electronic supplementary material).

3. RESULTS AND DISCUSSION

The resulting ML and Bayesian phylogenetic trees show remarkable consistency. Among Scolecophidia, five main clades diverged in the Jurassic and Cretaceous, between 159 (154–167) and 97 (112–81) Myr ago: these are (i) anomalalepids; (ii) threadsnakes; (iii) Typhlops hedraeus (Philippines) and Typhlops mirus...
Figure 1. (Caption opposite.)
The earliest divergence in the typhlopoid tree (figure 1). The palaeolandmass of Indigascar, it can be inferred that oceanic dispersal should not be dismissed as a possible biogeographical mechanism for these snakes also makes them more prone to isolation. Transatlantic journeys during the Cenozoic would require and most likely travelling along with their invertebrate prey. Our molecular timing results support the conclusion that oceanic dispersal should not be dismissed as a possible biogeographical mechanism for organisms that otherwise appear to be poorly adapted to the prevailing westward water currents (Vidal et al. 2008; Adalsteinsson et al. 2009). Transatlantic journeys during the Cenozoic would have taken at most six months (Houle 1999), not an insurmountable task for vertebrates with a low food requirement and most likely travelling along with their invertebrate prey. Our molecular timing results support the conclusion that oceanic dispersal should not be dismissed as a possible biogeographical mechanism for organisms that otherwise appear to be poorly adapted for an overseas journey (Vidal et al. 2008). Thus, blindsnakes—and scolecodophiids in general—have had a long evolutionary history that has been influenced by both continental drift and ancient ocean currents.

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