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Biol. Lett. 2010 **6**, 558-561 first published online 31 March 2010
doi: 10.1098/rsbl.2010.0220

Supplementary data

"Data Supplement"

<http://rsbl.royalsocietypublishing.org/content/suppl/2010/03/25/rsbl.2010.0220.DC1.html>

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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).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.0220> or via <http://rsbl.royalsocietypublishing.org>.

Received 3 March 2010
Accepted 8 March 2010

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 scalation, 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 (anomalepidids, approx. 17 species), Leptotyphlopidae (threadsnakes, approx. 120 species) and Typhlopidae (blindsnakes, approx. 260 species) (Adalsteinsson *et al.* 2009; Uetz *et al.* 2010). All three occur in the New World tropics, with the anomalepidids 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 scolecophidian 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 anomalepidids (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) anomalepidids; (ii) threadsnakes; (iii) *Typhlops hedraeus* (Philippines) and *Typhlops mirus*

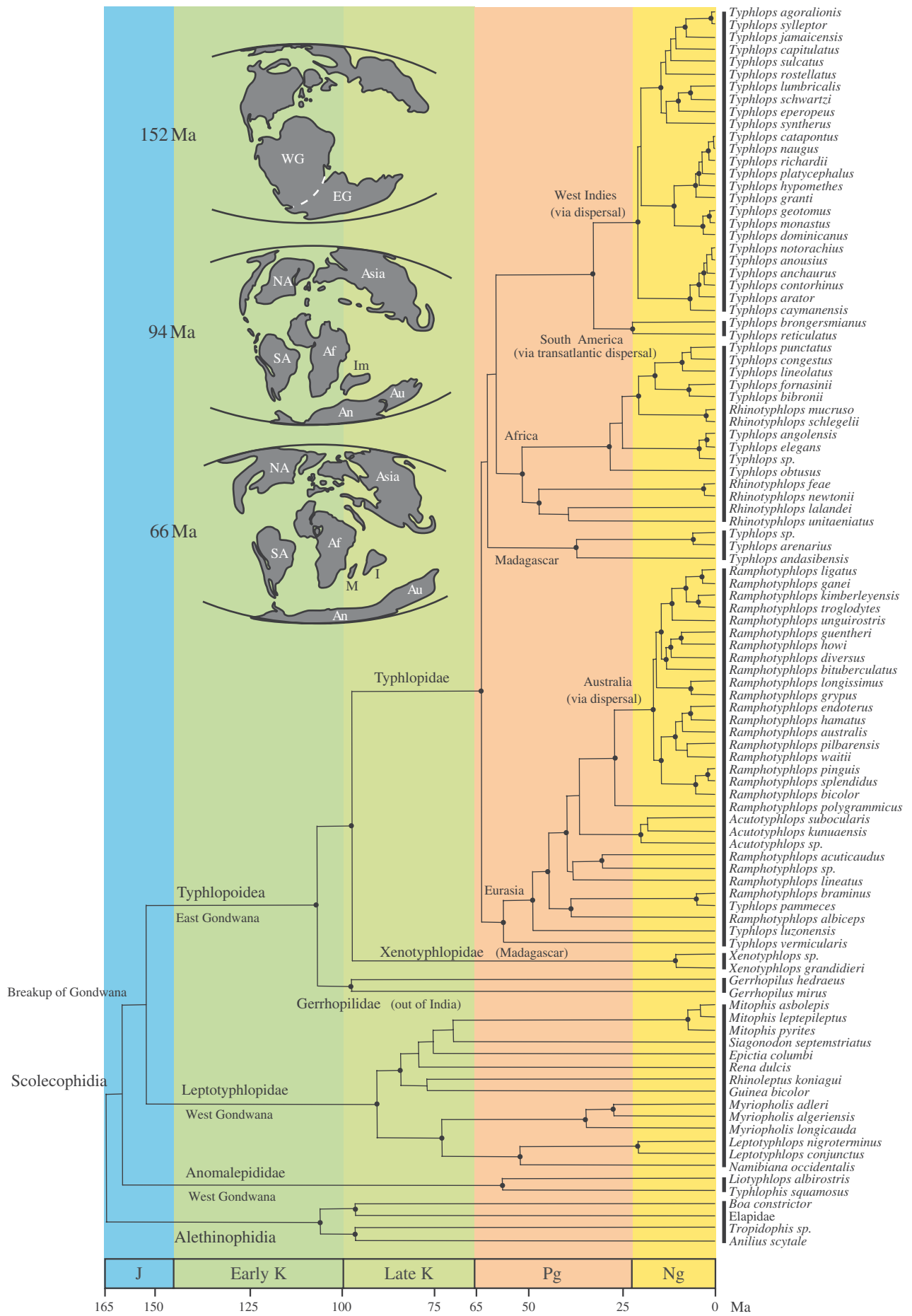


Figure 1. (Caption opposite.)

Figure 1. (*Opposite.*) A timetree of scolecophidians based on the analysis of DNA sequences from five nuclear protein-coding genes. Inferred biogeographical events are indicated at nodes on the timetree (clades also defined by vertical bars next to taxon names). Nodes with black circles are supported by posterior probability > 95% and ML bootstrap probability > 70%. Inset in the upper left shows positions of the continents at three periods in the Earth's history, after Scotese (2009): Late Jurassic (152 Ma), mid-Cretaceous (95 Ma) and Mesozoic–Cenozoic boundary (66 Ma). Labels on landmasses are: Af (Africa), An (Antarctica), Au (Australia), EG (East Gondwana), I (India), M (Madagascar), Im (Indigascar), NA (North America), SA (South America) and WG (West Gondwana). Labels on the time scale are K (Cretaceous), J (Jurassic), Ng (Neogene) and Pg (Palaeogene).

(Sri Lanka); (iv) the Malagasy genus *Xenotyphlops*; and (v) all the remaining blindsnakes (Eurasia, Australasia, Africa, Madagascar, South America, West Indies). The deep splits between the three main blindsnake clades ((iii)–(v) above) are strongly supported (bootstrap probability values, 91–100%; posterior probability values, 100%) and are older than divergences among all other families of living snakes (Vidal *et al.* 2009). For this reason, we erect the two newly discovered clades ((iii)–(iv) above) to familial rank and redefine the Superfamily Typhlopoidea to include only the three blindsnake families.

Gerrhopilidae Vidal, Wynn, Donnellan and Hedges, new family, with the genus *Gerrhopilus* Fitzinger, 1843 as type genus. Included genus: *Gerrhopilus*. *Gerrhopilus* comprises the former *Typhlops ater* species group (McDowell 1974), diagnosable by the presence of gland-like structures 'peppered' over the scales of the head (minimally the rostral and nasals, but often other scales on the head and chin). A divided preocular and/or ocular is common and all species have overlap of the preocular (or subpreocular when present) by the second supralabial (except *G. tindalli*). Included species are: *G. andamanensis*, *G. ater*, *G. beddomii*, *G. bisubocularis*, *G. ceylonicus*, *G. depressiceps*, *G. floweri*, *G. fredparkeri*, *G. hades*, *G. hedraeus*, *G. inornatus*, *G. mirus*, *G. mcdowelli*, *G. oligolepis* and *G. tindalli*.

Xenotyphlopidae Vidal, Vences, Branch and Hedges, new family, with the genus *Xenotyphlops* Wallach and Ineich, 1996 as type genus. Included genus: *Xenotyphlops*. *Xenotyphlops* is distinguishable externally by its greatly enlarged and nearly circular rostral shield that is nearly vertical in the lateral aspect and a single enlarged anal shield. Internally *Xenotyphlops* is unique among blindsnakes in lacking a tracheal lung and possessing an unexpanded tracheal membrane, type G tracheal foramina and a long heart–liver gap (Wallach *et al.* 2007). Included species are *X. grandidieri* and *X. mocquardi*.

Threadsnakes and typhlopoids are closest relatives and their divergence has been dated back to 154 (163–136) Myr ago (Vidal *et al.* 2009) and 155 (182–129) Myr ago (this study). Because West Gondwana drifted from East Gondwana (Antarctica, Madagascar, India and Australia) 166–116 Myr ago (Ali & Aitchison 2008) and the basal typhlopoid lineages are present on the palaeolandmass of Indigascar, it can be inferred that typhlopoids have an East Gondwanan origin. In turn, this infers that the split between typhlopoids and threadsnakes is the result of a vicariant event: the separation of East and West Gondwana. The subsequent split of Indigascar into India and Madagascar may explain the earliest divergence in the typhlopoid tree (figure 1).

The Typhlopidae includes four major clades: a Eurasian one spawning the Australasian radiation of

species, an African clade, a second Malagasy clade (separate from Xenotyphlopidae) and a South American clade spawning the West Indian radiation. These clades diverged between 63 (78–49) and 59 (74–46) Myr ago, just after the end-Cretaceous extinctions, as was the case with microhylid and ranoid frogs (Van der Meijden *et al.* 2007). This corresponded to a time when sea levels were lower and continental connections were forming (Smith *et al.* 1994; Miller *et al.* 2005), facilitating land or flotsam dispersal among continents and islands. Subsequent diversification of clades during the Cenozoic was parallel to that of primary food sources—ants and termites (Thorne *et al.* 2000; Brady *et al.* 2006). The fossorial habits of these snakes also makes them more prone to isolation. Recent studies have indicated that scolecophidians harbour a large hidden diversity of species (Thomas & Hedges 2007; Adalsteinsson *et al.* 2009).

The large Eurasian/Australasian group must have originated by dispersal northwards from Gondwana—as did afrophidian snakes—either out of Africa through Europe and Asia (Laurasia) or out of India (Gheerbrant & Rage 2006; Ali & Aitchison 2008; Vidal *et al.* 2009). Within this group, the Australian radiation is relatively recent, 28 (19–39) Myr ago, and apparently reached Australia by oceanic (flotsam) dispersal from Southeast Asia or Indonesia. Another insular radiation occurred in the West Indies, originating by dispersal from South America during the mid-Cenozoic, 33 (44–23) Myr ago, as did the vast majority of West Indian terrestrial vertebrates (Hedges 2006). Finally, because all major splits among typhlopids are more recent than 63 (49–78) Myr ago, and because Africa broke from South America 100 Ma, only westward—not eastward—transatlantic dispersal can explain the presence of blindsnakes in South America. Until now, only six or seven transatlantic events were known in terrestrial vertebrates, all following 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 scolecophidians in general—have had a long evolutionary history that has been influenced by both continental drift and ancient ocean currents.

This work was funded by grants from the Service de Systématique moléculaire du Muséum National d'Histoire

- Naturelle to N.V., the NASA Astrobiology Institute and US National Science Foundation to S.B.H., the Australian Department for the Environment, Water, Heritage and the Arts' CERF programme to S.C.D. and by the Consortium National de Recherche en Génomique, Genoscope. We thank E. Rochel for laboratory assistance and those persons and institutions who contributed some of the tissue and DNA samples used in this study, or assisted us in the field: K. Aplin, A. Bauer, C. Austin, L. Chirio, C. Cicero (MVZ), K. Coate, R. Crombie, K. Daoues, D. Dittmann (LSUMZ), P. Doughty, J. Feinstein (AMNH, Ambrose-Monnell), E. Greenbaum, C. Hass, T. Heger, J. Lazell, C. Marty, G. Mayer, R. Murphy (ROM), R. Platenberg, N. Puillandre, S. Richards, C. Ross, S. Thomson, S. Trape, USNM, J. Vindum (CAS), L. Vitt, L. Whitsed and E. Wikramanayake. K. P. Schliep helped with Multidivtime and J. S. Keogh commented on the manuscript.
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