



Zootaxa 3829 (1): 001–081
www.mapress.com/zootaxa/

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Monograph

ISSN 1175-5326 (print edition)

ZOOTAXA

ISSN 1175-5334 (online edition)

<http://dx.doi.org/10.11646/zootaxa.3829.1.1>

<http://zoobank.org/urn:lsid:zoobank.org/pub:75210CDC-AC6A-4624-A6F1-1BC969BC7CAA>

ZOOTAXA

3829

Systematics of the blindsnakes (Serpentes: Scolecophidia: Typhlopoidea) based on molecular and morphological evidence

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Magnolia Press
Auckland, New Zealand

Accepted by P. Passos: 23 May 2014; published: 8 Jul. 2014

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(*Zootaxa* 3829)

81 pp.; 30 cm.

8 Jul. 2014

ISBN 978-1-77557-437-8 (paperback)

ISBN 978-1-77557-438-5 (Online edition)

FIRST PUBLISHED IN 2014 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

<http://www.mapress.com/zootaxa/>

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ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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Abstract

The blindsnake superfamily Typhlopoidea (Gerrhopilidae, Typhlopidae, and Xenotyphlopidae) is a diverse, widespread part of the global snake fauna. A recent systematic revision based on molecular phylogenetic analyses and some morphological evidence presented a preliminary solution to the non-monophyly of many previously recognized genera, but additional clarification is needed regarding the recognition of some species and genera. We rectify these problems here with a new molecular phylogenetic analysis including 95 of the 275 currently recognized, extant typhlopoids, incorporating both nuclear and mitochondrial loci. We supplement this with data on the external, visceral, and hemipenial morphology of nearly all species to generate a revised classification for Typhlopoidea. Based on morphological data, we re-assign *Cathetorhinus* from Typhlopidae to Gerrhopilidae. Xenotyphlopidae maintains its current contents (*Xenotyphlops*). In Typhlopidae, one monotypic genus is synonymized with its larger sister-group as it cannot be unambiguously diagnosed morphologically (*Sundatyphlops* with *Anilios*), and two genera are synonymized with *Typhlops* (*Antillotyphlops* and *Cubatotyphlops*), as they are not reciprocally monophyletic. The genus *Asiatyphlops* is renamed *Argyrophis*, the senior synonym for the group. We erect one new genus (*Lemuriatyphlops*) for a phylogenetically distinct species-group in Asiatyphlopinae. Fourteen of eighteen recognized typhlopoid genera are maintained in four subfamilies: Afrotyphlopinae (*Afrotyphlops*, *Grypotyphlops* [re-assigned from Asiatyphlopinae], *Letheobia*, and *Rhinotyphlops*), Asiatyphlopinae (*Acu-*

totyphlops, *Anilius*, *Cyclotyphlops*, *Indotyphlops*, *Malayotyphlops*, *Ramphotyphlops*, and *Xerotyphlops*), Madatyphlopinae (*Madatyphlops*), and Typhlopinae (*Amerotyphlops* and *Typhlops*), some with altered contents. Diagnoses based on morphology are provided for all 19 typhlopoid genera, accounting for all 275 species. This taxonomy provides a robust platform for future revisions and description of new species.

Key words: Serpentes, Scolecophidia, Typhlopoidea, Typhlopidae, *Typhlops*, blind snakes

Introduction

With the recent separation of the genera *Gerrhopilus* and *Xenotyphlops* into the families Gerrhopilidae and Xenotyphlopidae (Vidal *et al.* 2010), the superfamily Typhlopoidea now contains three families: Gerrhopilidae, Typhlopidae, and Xenotyphlopidae (Table 1). Gerrhopilidae inhabits south and southeast Asia and the East Indies, and Xenotyphlopidae occurs only in northeastern Madagascar. In contrast, Typhlopidae is globally distributed, containing at least 257 species (see McDiarmid *et al.* 1999 and Wallach *et al.* 2014 for species accounts and synonymies), and represents a clade with significantly elevated rates of net diversification in snakes (Pyron & Burbrink 2012). Major radiations occur in the New World tropics, Africa, Madagascar, South Asia, Southeast Asia, and Australia (Vitt & Caldwell 2009). New species are commonly reported from all of these areas (Wallach 1993a; Wynn & Leviton 1993; Khan 1999; Wallach 1999; 2001; Franzen & Wallach 2002; Broadley & Wallach 2007; Thomas & Hedges 2007; Wynn *et al.* 2012; Marin *et al.* 2013; Pyron *et al.* 2013a, etc.).

The true diversity of the group is likely much higher, as evidenced by a recent molecular study of Australian *Ramphotyphlops*, which showed that the actual number of species is 200–340% greater than currently recognized (Marin *et al.* 2013). Discovery and description of new species is limited in some ways by their fossorial nature (making them difficult to encounter), and relatively conserved morphology (making them difficult to diagnose and delimit). As a result, there has been little in-depth phylogenetic analysis or systematic investigation of the group, usually restricted primarily to single geographic areas and relatively few characters (McDowell 1974; Roux-Estève 1974; Rabosky *et al.* 2004; Broadley & Wallach 2009).

Throughout most of their recent history (e.g., Boulenger 1893; Werner 1921; Hahn 1980), all blindsnakes were included in the genus *Typhlops*. In the mid-20th century, solid coiled hemipenes and paired retrocloacal sacs were discovered in the Australasian radiation (Robb 1960, 1967), leading these species to be separated into *Ramphotyphlops* (Robb, 1967). The name *Typhlina* (Wagler, 1830) was also applied to this group (McDowell 1974), but was found to be in the synonymy of both *Ramphotyphlops* and *Leptotyphlops*, and was thus later suppressed (Opinion 1207) by the International Commission on Zoological Nomenclature on appeal (ICZN 1982). Until very recently (Broadley & Wallach 2009; Hedges *et al.* 2014), most species were placed in *Typhlops* and *Ramphotyphlops* (McDiarmid *et al.* 1999).

Other genera were erected or resurrected and species moved between them on the basis of morphological characters, but rarely, if ever, from phylogenetic analysis of either morphological or molecular data (see in den Bosch & Ineich 1994; Wallach 1995, 1998a; Broadley & Wallach 2007, 2009). These include the African radiation (*Letheobia*, *Rhinotyphlops*, *Afrotyphlops*, and *Megatyphlops*), and two morphologically divergent groups from Oceania (*Acutyphlops* and *Cyclotyphlops*). The genus *Cathetorhinus* was resurrected for the morphologically divergent *Typhlops melanocephalus* (Wallach & Pauwels 2008), which was previously considered *incertae sedis* (McDiarmid *et al.* 1999). The genus *Grypotyphlops* was resurrected for *Rh. acutus*, the only Indian member of a group otherwise found solely in Africa (Wallach 2003).

Multiple species groups were identified within these larger genera (particularly *Typhlops*), based on shared morphological features such as the number of lateral and transverse scale rows, supralabial imbrication patterns, hemipenial morphology, and lung architecture (Wallach 1993b, 1998a, b). The differences between these groups suggested that current taxonomic arrangements did not describe monophyletic genera. This suspicion was confirmed by recent molecular phylogenetic analyses, which revealed that numerous taxonomic problems existed within Typhlopidae, and that previous nomenclature did not reflect monophyletic groups revealed in the available phylogenies (Vidal *et al.* 2010; Pyron *et al.* 2013b).

The morphological distinction between *Ramphotyphlops* and *Typhlops* was not corroborated by molecular evidence, and species from these and other genera interdigitated with each other in molecular phylogenies (Vidal *et*

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