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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

of *Leptotyphlops* are currently recognized. In the New World these include the *albifrons*, *bilineatus*, *dulcis*, *septemstriatus*, and *tesselatus* groups (Orejas-Miranda 1967; Peters 1970; Thomas 1965; Thomas *et al.* 1985). In the Old World, these include the *bicolor*, *longicaudus*, *nigricans*, *parkeri*, *reticulatus*, *rostratus*, and *scutifrons* groups (Broadley 1999; Broadley & Broadley 1999; Broadley & Wallach 1997a; Broadley & Wallach 2007; Hahn 1978; Wallach 1996; Wallach 2003; Wallach & Hahn 1997). Primary characters used to distinguish these groups were scalation (e.g., number and relative size of supralabials and number of middorsals and subcaudals), and body proportions (e.g., total length, and body and tail shape).

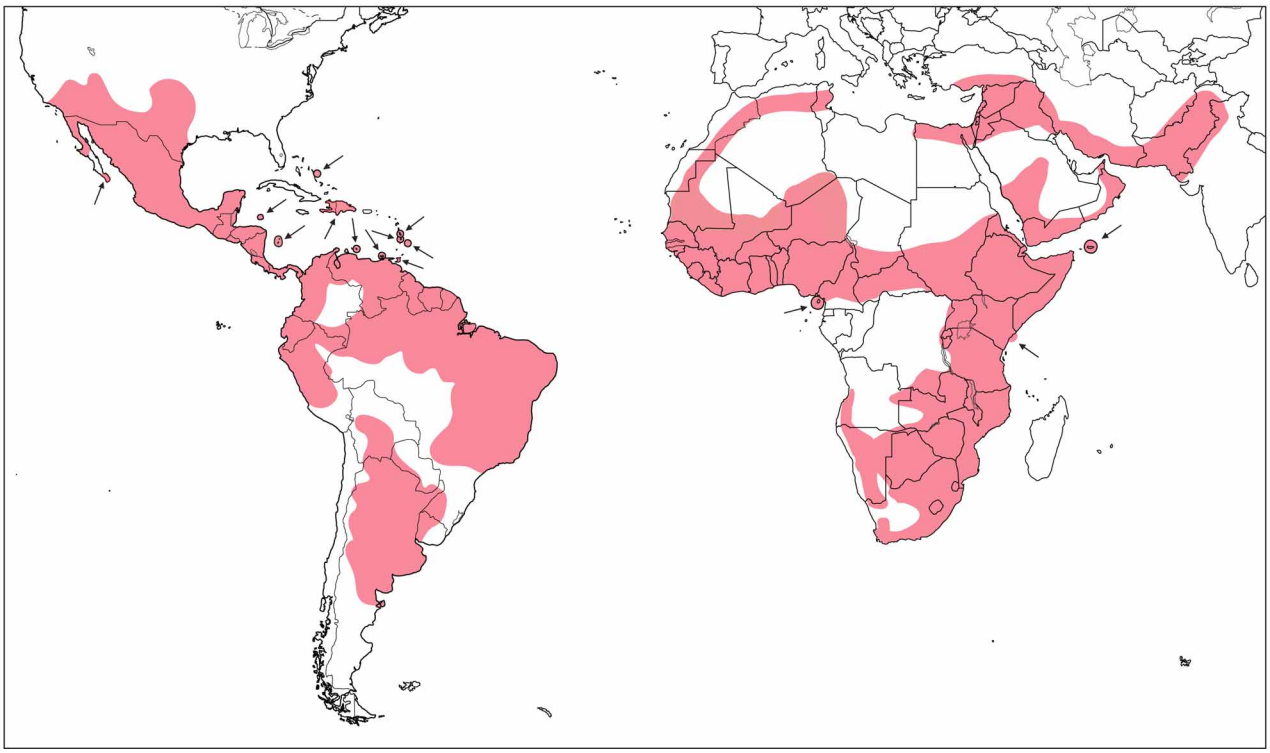


FIGURE 1. Map showing the distribution of the snake Family Leptotyphlopidae.

Remarkably, for a family of terrestrial vertebrates, no phylogenetic analysis—morphological or molecular—has been published on Leptotyphlopidae aside from a sequence analysis of a few closely related species (Hedges 2008). An unpublished PhD dissertation (Wallach 1998) remains the primary phylogenetic and biogeographic work, based on an analysis of morphological data, mostly of measurements of organs and their relative positions in the body cavity. Selected data and conclusions from that study have been noted in several publications (Broadley & Wallach 2007; Wallach 2003; Wallach & Boundy 2005). Wallach's (1998) phylogenetic analysis was presented for species groups rather than individual species. It resulted in a somewhat ladder-like tree of *Rhinoleptus* and species groups of *Leptotyphlops*, with *Rhinoleptus* at the lowest rung (closest relative of all other leptotyphlopids) followed by the *L. parkeri* Group as the next higher branch on the tree. Moving up the tree, several branches led to New World species groups (i.e., paraphyletic with respect to the Old World taxa), and finally the remaining Old World species groups formed a monophyletic group. Within that monophyletic group it was noted (Wallach 1998; Wallach & Boundy 2005) that "… the *L. reticulatus* group is most basal, followed by the *L. bicolor* species group, which is the sister group to the *L. longicaudus* plus *L. rostratus* groups and the *L. nigricans* plus *L. scutifrons* groups." Substantial (> 95%) bootstrap support for the position of *Rhinoleptus* as closest relative of all other leptotyphlopids existed as well as strong support (91%) for the group uniting all leptotyphlopids except *Rhinoleptus* and *L. parkeri*; other nodes, however, were supported by bootstrap values of only 51–77%. Wallach (1998) concluded from his analysis that the family arose in the Guinea region (West Africa), dispersed into South America, and then reinvaded Africa prior to the separation of the two continents (~105 million years ago, Ma). Alternatively, he suggested that "the primitive African lineages may have become extinct."

Here we present analyses of DNA sequence data bearing on the relationships and biogeography of leptotyphlopid snakes. We sampled *Rhinoleptus* and representatives from four of the five species groups of *Leptotyphlops* in the New World (all except the *tesselatus* group) and five of seven species groups in the Old World (all except the *parkeri* and *reticulatus* groups). Our analyses suggest that the diversification of living lineages began as early as the mid-Cretaceous (~100 Ma) and was influenced by continental breakup, and that a much greater diversity of species exists than is currently recognized.

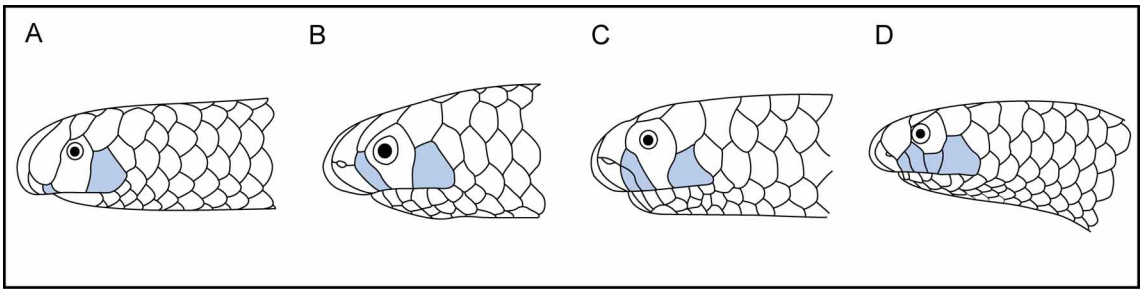


FIGURE 2. Head scalation in leptotyphlopid snakes illustrating variation in the number and size of supralabial scales (blue). (A) Two supralabials, with anterior scale small (*Leptotyphlops kafubi*). (B) Two supralabials, with anterior scale large (*Epictia tenella*). (C) Three supralabials, with anterior scale moderate (*Tricheilostoma koppesi*). (D) Four supralabials, with anterior scale moderate (*Tetracheilostoma bilineatum*).

Materials and methods

Morphology. Variation in widely used morphological characters for the Family Leptotyphlopidae was assembled from the primary literature (mostly species descriptions). Some earlier summaries of these data (Broadley & Broadley 1999; Broadley & Wallach 2007; Wallach 1998) were especially useful. Characters of scalation included midbody (counted around body at half the body length) and midtail scale rows (counted around the tail at half its length), middorsal scale rows (counted from between the rostral scale and terminal spine), subcaudals, supralabials, and the relative height of the anterior supralabial (small if less than one-half of the orbit-lip distance, moderate if 50–90% of orbit-lip distance, and large if reaching lower edge of orbit or above; Fig. 2) (Wallach 1998). Some other characters of scalation (e.g., shape of the cloacal shield) are mentioned where diagnostic for particular clades. Supraocular scales are considered "normal-sized" if they are the same size or larger than the middorsal scales whereas they are "small" if they are smaller than middorsal scales (Orejas-Miranda 1967). Characters of body proportion for each species included (i) maximum total length in mm (the primary length measurement for scolecophidians, as opposed to snout-vent length for other snakes), scored for adults—see Hedges (2008) for discussion of body size variation in leptotyphlopids; (ii) body shape (total length divided by width at midbody); (iii) relative tail length (tail length divided by total length, expressed as a percent); and (iv) tail shape (tail length divided by tail width at midtail). Characters of pattern and coloration included dorsal ground color (usually brown, pale brown, or multicolored (e.g., red, yellow, black, etc.), presence or absence of stripes, and ventral coloration (usually brown, pale brown, or white). In summarizing something as variable as pattern and coloration, it was necessary to overlook some subtle differences and assign species to the nearest character state, and therefore these data should not be interpreted, necessarily, as discrete classes. Also, in nearly all cases information on pattern and coloration was taken from the literature and was not verified by examination of museum specimens, which could lead to imprecision in characterization of some aspects of coloration. For example, one author might consider the absence of pigmentation to be "white" whereas another author might refer to this condition as "pink" because of the pinkish hue of underlying tissues unobscured by pigments. Despite this possibility of confusion, we are convinced that broad aspects of coloration have some taxonomic value and thus we include them in the accounts below. Histograms were constructed for several characters that appeared to be of diagnostic value, using species ranges as the primary data.

Distribution maps. Distributions of taxa were constructed from records in the primary literature. These were supplemented by unpublished museum records (Herpnet 2009). A map of the family (Fig. 1) was constructed from a synthesis of all available records.

Sequence data collection. Specimens and localities sampled are listed in Appendix 1. DNA extraction for all tissue samples was carried out using the DNeasy Tissue Kit from Qiagen. Primer sets used in amplification and sequencing are listed in Appendix 2. Both complementary strands were sequenced using an ABI 3100 or 3730 Nucleic Acid Analyzer at Pennsylvania State University. All chromatograms were fully inspected, and all sequences were compared against their reverse complement to detect any call errors. Embedded primer sequences were deleted from all sequence fragments before assembly or alignment. Sequenced fragments and their complements were combined in MEGA 4.0 (Tamura 2007), and have been deposited in GenBank under accession numbers GQ468987–GQ469284 (Appendix 1). Alignments for the cytochrome b, tRNA-valine, amelogenin, BDNF, C-mos, NT3, and RAG1 were performed using ClustalW (Thompson *et al.* 1994), with default parameters, in MEGA 4.0 (Tamura 2007).

Ribosomal RNA genes 12S and 16S were aligned according to secondary structure using an alignment of squamate sequences from the European ribosomal RNA database (Wuyts & Van de Peer 2004) in Muscle (Edgar 2004); alignments are available from the corresponding author. To eliminate hypervariable loop regions, the program GBlocks (Castresana 2000) was used on 12S and 16S alignments with default parameters under the least stringent settings: (1) allow smaller final blocks, (2) allow positions with gaps within the final blocks, and (3) allow less strict flanking positions. Approximately 80% of sequence data was retained using these settings. Two data sets were used in subsequent analyses and tree-building. The first was a concatenation of mitochondrial gene alignments: 12S (870 sites), tRNAval (72 sites), 16S (1,212 sites), and cytochrome b (810 sites) for all 91 individuals (total of 2,971 sites), referred to as the "four-gene" data set. The second was a concatenation of mitochondrial gene alignments: 12S (892 sites), tRNAval (68 sites), 16S (1,219 sites), cytochrome b (809 sites) and nuclear gene alignments: amelogenin (323 sites), BDNF (670 sites), C-mos (566 sites), NT3 (495 sites), and RAG1 (513 sites) for 24 taxa representing species groups (total of 5,563 sites), referred to as the "nine-gene" data set.

Phylogenetic analysis. Maximum Likelihood (ML) and Bayesian methods were used to construct phylogenies, and the following taxa were used as outgroups: *Ramphotyphlops braminus* (Typhlopidae; a scolecophidian), *Boa constrictor* (Boidae), *Python regius* (Pythonidae), and either Naja or Dendroaspis (Elapidae), depending on the gene. ML and Bayesian analyses were conducted using RAxML-VI-HPC v2 (Stamatakis 2006) and MrBayes 3.1 (Ronquist & Huelsenbeck 2003), respectively. Analyses of both data sets treated 12S, tRNAval, and 16S as one gene. Because of the different models of sequence change expected for RNA genes versus protein-coding genes, some partitioning of the data was necessary in the analyses. Protein-coding data sets are often partitioned by either gene (e.g., Heinicke *et al.* 2007) or codon position (e.g., Hedges *et al.* 2009). Here, we performed analyses using both types of partitions to compare results. Initially, the nine-gene data set was partitioned by gene: 12S-tRNAval-16S; cytochrome b; amelogenin; BDNF; C-mos; NT3; RAG1. The four-gene data set also was partitioned by gene: 12S-tRNAval-16S; cytochrome b. For alternative analyses, the nine-gene data set was partitioned by codon position (of protein-coding genes): 12S-tRNAval-16S; codon positions 1, 2, 3 of cytochrome b; and codon positions 1, 2, 3 of nuclear genes and the four-gene data set was partitioned similarly: 12S-tRNAval-16S; and by codon positions 1, 2, 3 of cytochrome b. ML trees were built from 100 alternative runs under the GTR + model. Nodal support for final trees was obtained using non-parametric bootstrapping (BP) with 1000 replicates. Bayesian analyses for both data sets were performed using the same partitions, with four Markov chains started at random trees that were run for one million generations each, and sampled every 100 generations (burnin = 2500). Nodal support for Bayesian trees was quantified with posterior probabilities (PP). Convergence was assessed by monitoring the standard deviation of split frequencies (<0.01 in all cases). Appropriate models of sequence evolution, as selected by ModelTest using the AIC criterion (Posada & Crandall 1998), were used for each gene partition.

Divergence time estimation. MultiDivTime T3 (Thorne & Kishino 2002; Yang & Yoder 2003) was used for Bayesian timing analyses. Each gene in both data sets was analyzed in PAML 3.14 (Yang 1997) to

determine model parameters, and in estbranches (Thorne *et al.* 1998) to estimate branch lengths. Both programs were run with default parameters, using the topology from the ML trees. Saturation may be problematic for timing analyses when fast-evolving genes are used (Halanych & Robinson 1999). Mitochondrial and nuclear genes were tested for saturation by plotting the ratio of transitions/transversions against the corresponding pairwise differences. The plot for cytochrome b indicated that this gene had become saturated, a problem that is especially a concern for time estimation which relies on accurate, quantitative estimates of sequence change and proportionality among branch lengths. Therefore, cytochrome b was excluded from final divergence time estimates on both data sets (its inclusion or not in phylogenetic analyses did not have a significant effect on topology). Two leptotyphlopid fossils known from the Pleistocene-Holocene boundary (van Devender & Mead 1978; van Devender & Worthington 1977) were too recent to provide useful calibrations. A lizard outgroup, *Heloderma suspectum*, was used to root the tree and permit the use of Cretaceous fossil calibrations within snakes.

The oldest caenophidians are from the Cenomanian (100–94 Ma) (Rage & Werner 1999) and therefore the divergence of Elapidae (Caenophidia) and Boidae ("Henophidia") was set at a minimum of 94 Ma. Some objection has been raised to the identity of the fossils and their use in calibrating dating analyses (Head *et al.* 2005; Sanders & Lee 2008) and so we also ran separate analyses with that calibration removed. In the absence of other available fossil calibrations we instead calibrated a different node in the tree, the leptotyphlopid/typhlopid divergence, using Vidal *et al.*'s (2009) time estimate (158 Ma) which was obtained by excluding the 94 Ma calibration. We also used the extremes of the 95% credibility interval (163 and 137 Ma) as calibrations for that node in separate analyses.

All other calibrations were maximums corresponding to geologic dates when West Indian islands became habitable (rose above sea-level). In both data sets, the nodes uniting *Leptotyphlops pyrites* and *L. leptepileptus* (both restricted to the Hispaniolan South Island) were constrained at a maximum of 10 Ma for the Hispaniolan south island (Huebeck & Mann 1985), where both species occur. In the four-gene data set, the node joining the two groups of populations of *L. breuili* was constrained to a maximum of 3 Ma, when St. Lucia emerged above sea-level (Maury *et al.* 1990). Also in the four-gene data set, the node uniting all taxa in the *L. bilineatus* Group (those occurring in the Greater and Lesser Antilles) was constrained at a maximum of 37.2 Ma for the West Indies (Iturralde-Vinent & MacPhee 1999). Analyses were run with the ingroup root (rttm) priors set at the highest, 159.9 Ma (Vidal *et al.* 2009), and lowest, 102.3 Ma (Sanders & Lee 2008) mean estimates for the alethinophidian-scolecophidian divergence, among published estimates. Values for rttmsd, rtrate, rtratesd, brown mean and brownmeansd were set according to the rttm used, following software recommendations. Both data sets had the Markov chain sampled 10,000 times, with 100 cycles between samples, and the first sample was taken after 10,000 cycles.

Results

Phylogenetic relationships. There were 1,915 variable sites in the four-gene data set and 2,767 variable sites in the nine-gene data set; in the latter, the nuclear genes contributed 925 variable sites. Tree topologies from NJ, ML, and Bayesian methods, using different partitions of the same data set, were nearly identical. However, some topological differences were detected between the 4-gene and 9-gene data sets at weakly supported nodes (those < 95% BP) in the 4-gene analysis (Fig. 3); in general, those nodes were better supported in the 9-gene data set. Trees shown here (Figs. 3–4) are the results of analyses that were partitioned by gene. A deep divergence in both trees was seen between a mostly New World clade and an Old World clade, which are both well supported. Notably, *Rhinoleptus koniagui* and *Leptotyphlops bicolor*, two species found in West Africa, cluster together in the New World clade as the closest relative of all other New World species (Fig. 4; 94% BP; 1.0 PP).

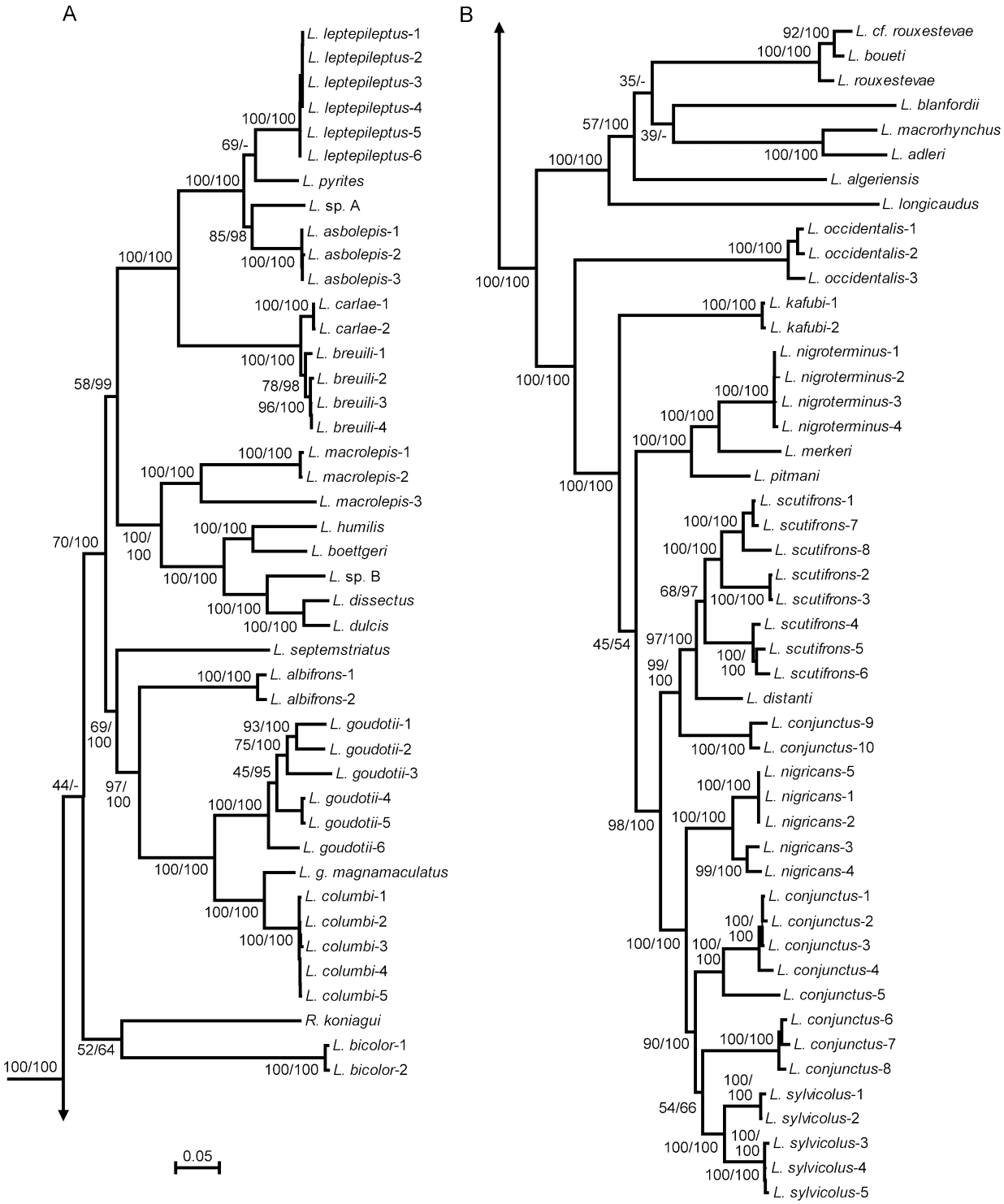


FIGURE 3. A phylogeny of leptotyphlopid snakes based on sequences of four mitochondrial genes (12S rRNA, tRNA-Valine, 16S rRNA, and cytochrome b). Maximum likelihood tree of 91 samples and 2,971 sites. Values are ML bootstrap values followed by Bayesian posterior probabilities. Outgroups are not shown, but included Typhlopidae (*Ramphotyphlops*), Boidae (*Boa*), Pythonidae (*Python*), and Elapidae (*Dendroaspis* and *Naja*). The generic taxonomy in this tree reflects usage prior to this study. See Table 1 and Figure 12 for the new classification proposed here.

Although no identical sequences were found, the four-gene tree (Fig. 3) revealed a pattern whereby sequences of multiple individuals from the same species and population (e.g., within the species *L. asbolepis*, *L. breuili*, *L. columbi*, *L. leptepileptus*, and *L. nigroterminus*) were nearly identical whereas those from different species were considerably more different. However, different populations of the same species

showed variable levels of sequence divergence, with some (e.g., *L. bicolor* and *L. breuili*), showing only small levels and others (e.g., *L. goudotii*, *L. macrolepis*, and *L. scutifrons*) showing larger levels of divergence comparable to that of distinct species.

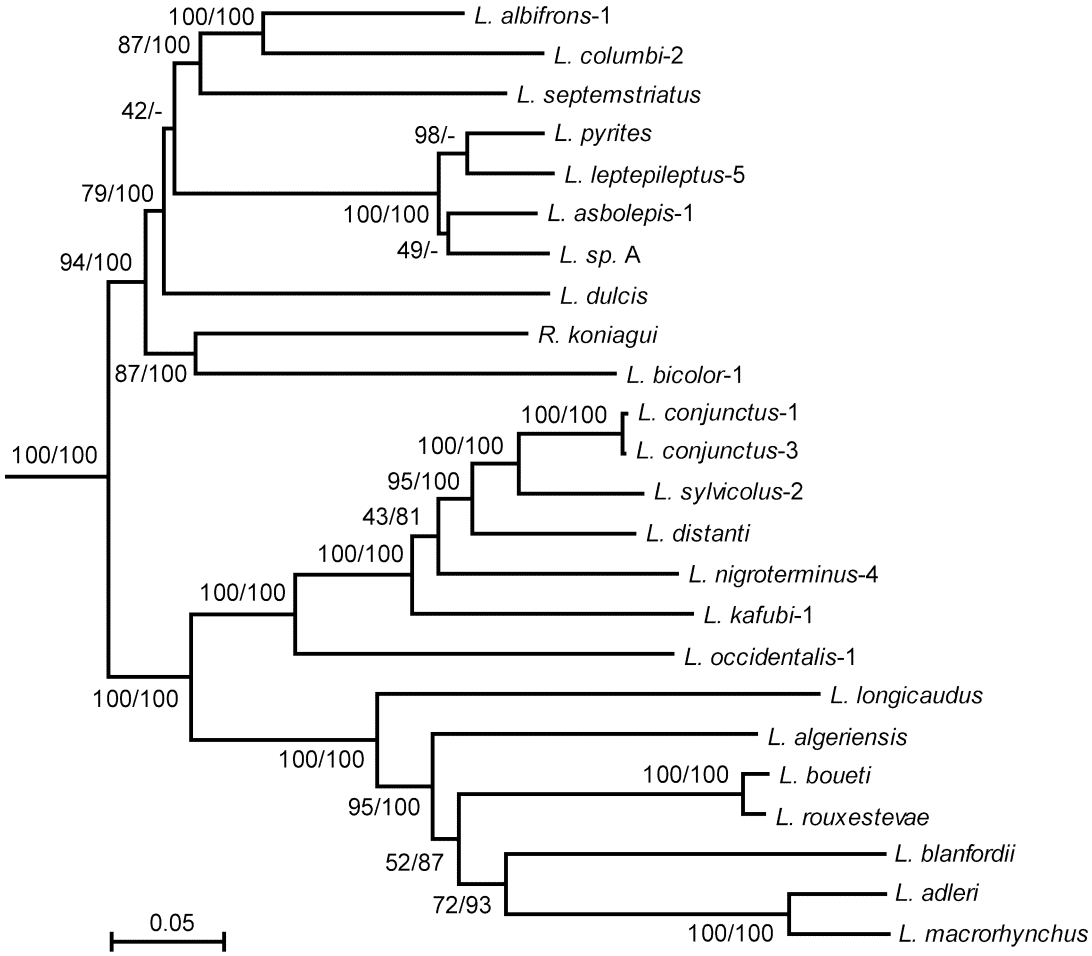


FIGURE 4. A phylogeny of leptotyphlopid snakes based on sequences of nine genes: five nuclear genes nine (amelogenin, BDNF, C-*mos*, NT3, and RAG1) and four mitochondrial and nuclear genes (12S rRNA, tRNA-Valine, 16S rRNA, and cytochrome b). Maximum likelihood tree obtained from the nine-gene data set (24 species; 5,563 sites). Values are ML bootstrap values followed by Bayesian posterior probabilities. Outgroups are not shown, but included Typhlopidae (*Ramphotyphlops*), Boidae (*Boa*), Pythonidae (*Python*), and Elapidae (*Dendroaspis* and *Naja*). The generic taxonomy in this tree reflects usage prior to this study. See Table 1 and Figure 12 for the new classification proposed here.

The relationships of the species in both analyses (four-gene and nine-gene) corresponded closely to morphological species groups already recognized. For example, all of Greater Antillean and Lesser Antillean species formed a well-supported group, which corresponds to the *bilineatus* Group, defined by the presence of a supralabial scale separating the ocular from the lip (Thomas 1965; Thomas *et al.* 1985). In Africa, species placed in the *longicaudus* Group (Broadley & Broadley 1999; Broadley & Wallach 2007) also formed a well-supported group (Figs. 3–4). However, our inferred relationships of many other African species complexes did not support those proposed by Wallach (1998); *L. nigricans* (*nigricans* Group) appeared nested within an otherwise cohesive *L. scutifrons* Group; the taxa *merkeri* and *pitmani*, both treated as northern races of *L. scutifrons*, exhibit high genetic divergence and did not group with southern African populations assigned to that species (Broadley & Broadley 1999; Broadley & Wallach 2007); *L. kafubi*, previously considered a northern population of *L. nigricans* (Broadley & Watson 1976) was validated as a full species (Broadley & Broadley 1999), but did not associate with *L. nigricans* despite the presence of a discrete prefrontal; and the

taxon *conjunctus*, previously treated as a full species (Broadley & Watson 1976) or as a race of *L. scutifrons* (Broadley & Broadley 1999) was paraphyletic and showed considerable genetic divergence among populations.

Taxonomic implications. The results have implications for the recognition of taxa. Because our analysis included representatives of all but three species groups (of 12), and because the resulting groups, in most cases, can be diagnosed morphologically, we have proposed a new classification for the family (Table 1). It includes two subfamilies, five tribes, three subtribes, and 12 genera. The genera correspond, in most cases, to previously recognized species groups. Seven of those generic names are resurrected whereas five others are newly named. Several of the genera are large and still encompass considerable diversity, both morphological and genetic. Some morphological characters used to define species groups, e.g. the absence of a prefrontal in the *L. scutifrons* complex and its presence in the *L. nigricans* complex (Broadley & Broadley 1999), do not define clades. Our assignment of species for which we do not have molecular data to the revived and newly-described genera is thus provisional. For this reason, and because of the likelihood of many additional species of leptotyphlopids being discovered and described, this classification will almost certainly continue to evolve.

Systematic accounts

Family Leptotyphlopidae Stejneger, 1892

Stenosomata Ritgen, 1828: 255. Type genus: *Stenosoma* Wagler, 1824. [Preoccupied by *Stenosoma* Latreille, 1810: Coleoptera and *Stenosoma* Lamarck, 1817: Mollusca.]
Stenostomi Wiegmann and Ruthe, 1832: 160.
Stenosomina Bonaparte, 1845: 377.
Stenosomatidae Günther, 1885: 85.
Stenostomidae Cope, 1886: 481.
Glauconiidae Boulenger, 1890: 242. Type genus: *Glauconia* Gray, 1845.
Leptotyphlopidae Stejneger, 1892 [dated 1891]: 501.
Type genus. *Leptotyphlops* Fitzinger, 1843:24.

Diagnosis. Small and thin snakes sharing with other members of Scolecophidia cylindrical bodies, ventral scales not enlarged, reduced eyes with a single visual cell type in the retina, and the absence of neural spines. They have solidly constructed skulls with toothless premaxillary, maxillary, and palatine bones sutured to the braincase along with the nasals and prefrontals. They lack a left lung, a tracheal lung, and a left oviduct (Dowling & Duellman 1978; Underwood 1967; Vitt & Caldwell 2009). Except for two species having 16 midbody scale rows and two others having 14 or 16 rows, all of the other members of the family usually have 14 midbody scale rows. The maximum adult size of each species ranges from 104 mm (*Leptotyphlops carlae*) to 460 mm (*Rhinoleptus koniagui*) in total length; see discussion of body size in leptotyphlopid snakes (Hedges 2008).

Content. Two subfamilies, five tribes, three subtribes, 12 genera, and 116 species (Table 1).

Distribution. The family is distributed in the New World and Old World. In the New World it is distributed from North America (California, Utah, and Kansas) south through the Atlantic drainage of Middle and South America (exclusive of the high Andes) to Uruguay and Argentina. It also occurs on San Salvador Island (Bahamas), Hispaniola, the Lesser Antilles, Cozumel Island (Mexico), Islas de Bahia and Swan Islands (Honduras), San Andres and Providencia Islands (Colombia), Bonaire, Margarita Islands, and Trinidad. In the Old World it is distributed throughout Africa (north and south of the Sahara Desert), the Arabian Peninsula, and in southwest Asia (Turkey, Iran, Pakistan, and northwest India); and on islands off the coast of Africa and Arabia (Bazaruto archipelago, Pemba, Manda, Lamu, Bioko, and Socotra) (Fig. 1).

TABLE 1. Classification of snakes of the Family Leptotyphlopidae. The arrangement used in this study is compared with that in previous classifications (e.g., McDiarmid *et al.* 1999; Uetz *et al.* 2009). Abbreviations for geographic regions are: AR (Arabia), CAF (Central Africa), EAF (East Africa), MAM (Middle America), NAM (North America), SAF (South Africa), SAM (South America), SOC (Socotra Island), SWA (Southwest Asia), WAF (West Africa), and WI (West Indies). Species in bold were sampled in the molecular analyses. Undescribed species used in this study are not listed.

This study	Previous classification
SUBFAMILY EPICTINAE	
Tribe Epictini, Subtribe Epictina	
Epictia albifrons (Wagler 1824) SAM	*Leptotyphlops albifrons*
Epictia albipuncta (Jan 1861) SAM	*Leptotyphlops albipunctus*
Epictia alfredschmidti (Lehr, Wallach, Köhler & Aguilar 2002) SAM	*Leptotyphlops alfredschmidti*
Epictia australis (Freiberg & Orejas-Miranda 1968) SAM	*Leptotyphlops australis*
Epictia borapeliotes (Vanzolini 1996) SAM	*Leptotyphlops borapeliotes*
Epictia collaris (Hoogmoed 1977) SAM	*Leptotyphlops collaris*
Epictia columbi (Klauber 1939) WI	*Leptotyphlops columbi*
Epictia diaplocia (Orejas-Miranda 1969) SAM	*Leptotyphlops diaplocius*
Epictia goudotii (Duméril & Bibron 1844) MAM	*Leptotyphlops goudotii*
Epictia magnamaculata (Taylor 1940) MAM	*Leptotyphlops magnamaculatus*
Epictia melanurus (Schmidt & Walker 1943) SAM	*Leptotyphlops melanurus*
Epictia munoai (Orejas-Miranda 1961) SAM	*Leptotyphlops munoai*
Epictia nasalis (Taylor 1940) MAM	*Leptotyphlops nasalis*
Epictia peruviana (Orejas-Miranda 1969) SAM	*Leptotyphlops peruvianus*
Epictia rubrolineata (Werner 1901) SAM	*Leptotyphlops rubrolineatus*
Epictia rufidorsa (Taylor 1940) SAM	*Leptotyphlops rufidorsus*
Epictia signata (Jan 1861) SAM	*Leptotyphlops signatus*
Epictia striatula (Smith & Laufe 1945) SAM	*Leptotyphlops striatula*
Epictia subcrotilla (Klauber 1939) SAM	*Leptotyphlops subcrotillus*
Epictia teaguei (Orejas-Miranda 1964) SAM	*Leptotyphlops teaguei*
Epictia tenella (Klauber 1939) SAM	*Leptotyphlops tenellus*
Epictia tesselata (Tschudi 1845) SAM	*Leptotyphlops tesselatus*
Epictia tricolor (Orejas-Miranda & Zug 1974) SAM	*Leptotyphlops tricolor*
Epictia undecimstriata (Schlegel 1839) SAM	*Leptotyphlops undecimstriatus*
Epictia vellardi (Laurent 1984) SAM	*Leptotyphlops vellardi*
Siagonodon borrichianus (Degerbøl 1923) SAM	*Leptotyphlops borrichianus*
Siagonodon brasiliensis (Laurent 1949) SAM	*Leptotyphlops brasiliensis*
Siagonodon cupinensis (Bailey & Carvalho 1946) SAM	*Leptotyphlops cupinensis*
Siagonodon septemstriatus (Schneider 1801) SAM	*Leptotyphlops septemstriatus*
Tribe Epictini, Subtribe Renina	
Rena affinis (Boulenger 1884) SAM	*Leptotyphlops affinis*
Rena boettgeri (Werner 1899) NAM	*Leptotyphlops humilis*

continued next page.

TABLE 1. (continued)

This study	Previous classification
Rena bressoni (Taylor 1939) MAM	*Leptotyphlops bressoni*
Rena dimidiata (Jan 1861) SAM	*Leptotyphlops dimidiatus*
Rena dissecta (Cope 1896) MAM, NAM	*Leptotyphlops dissectus*
Rena dulcis (Baird & Girard 1853) MAM, NAM	*Leptotyphlops dulcis*
Rena humilis (Baird & Girard 1853) MAM, NAM	*Leptotyphlops humilis*
Rena maxima (Loveridge 1932) MAM	*Leptotyphlops maximus*
Rena myopica (Garman 1883) MAM, NAM	*Leptotyphlops myopicus*
Rena nicefori (Dunn 1946) SAM	*Leptotyphlops nicefori*
Rena unguirostris (Boulenger 1902) SAM	*Leptotyphlops unguirostris*
Tricheilostoma anthracinum (Bailey 1946) SAM	*Leptotyphlops anthracinus*
Tricheilostoma brevissimum (Shreve 1964) SAM	*Leptotyphlops brevissimus*
Tricheilostoma dugandi (Dunn 1944) SAM	*Leptotyphlops dugandi*
Tricheilostoma fulginosum (Passos, Caramaschi & Pinto 2006) SAM	*Leptotyphlops fulginosus*
Tricheilostoma guayaquilensis (Orejas-Miranda & Peters 1970) SAM	*Leptotyphlops guayaquilensis*
Tricheilostoma joshuai (Dunn 1944) SAM	*Leptotyphlops joshuai*
Tricheilostoma koppesi (Amaral 1955) SAM	*Leptotyphlops koppesi*
Tricheilostoma macrolepis (Peters 1857) SAM	*Leptotyphlops macrolepis*
Tricheilostoma salgueiroi (Amaral 1955) SAM	*Leptotyphlops salgueiroi*
Tribe Epictini, Subtribe Tetracheilostomina	
Mitophis asbolepis (Thomas, McDiarmid & Thompson 1985) WI	*Leptotyphlops asbolepis*
Mitophis calypso (Thomas, McDiarmid & Thompson 1985) WI	*Leptotyphlops calypso*
Mitophis leptepileptus (Thomas, McDiarmid & Thompson 1985) WI	*Leptotyphlops leptepileptus*
Mitophis pyrites (Thomas 1965) WI	*Leptotyphlops pyrites*
Tetracheilostoma bilineatum (Schlegel 1839) WI	*Leptotyphlops bilineatus*
Tetracheilostoma breuili (Hedges 2008) WI	*Leptotyphlops breuili*
Tetracheilostoma carlae (Hedges 2008) WI	*Leptotyphlops carlae*
Tribe Rhinoleptini	
Guinea bicolor (Jan 1860) WAF	*Leptotyphlops bicolor*
Guinea broadleyi (Wallach & Hahn 1997) WAF	*Leptotyphlops broadleyi*
Guinea greenwelli (Wallach & Boundy 2005) WAF	*Leptotyphlops greenwelli*
Guinea sundewalli (Jan 1861) WAF	*Leptotyphlops sundewalli*
Rhinoleptus koniagui Villiers 1956 WAF	*Rhinoleptus koniagui*
Rhinoleptus parkeri (Broadley 1999) EAF	*Leptotyphlops parkeri*
SUBFAMILY LEPTOTYPHLOPINAE Tribe Epacrophini	
Epacrophis boulengeri (Boettger 1913) EAF	*Leptotyphlops boulengeri*
Epacrophis drewesi (Wallach 1996) EAF	*Leptotyphlops drewesi*
Epacrophis reticulatus (Boulenger 1906) EAF	*Leptotyphlops reticulatus*

continued next page.

TABLE 1. (continued)

This study	Previous classification
Tribe Myriopholini	
Myriopholis adleri (Hahn & Wallach 1998) WAF	*Leptotyphlops adleri*
Myriopholis albiventer (Hallermann & Rödel 1995) WAF	*Leptotyphlops albiventer*
Myriopholis algeriensis (Jacquet 1895) WAF	*Leptotyphlops algeriensis*
Myriopholis blanfordii (Boulenger 1890) AR, SWA	*Leptotyphlops blanfordii*
Myriopholis boueti (Chabanaud 1917) WAF	*Leptotyphlops boueti*
Myriopholis braccianii (Scortecci 1929) EAF	*Leptotyphlops braccianii*
Myriopholis burii (Boulenger 1905) AR	*Leptotyphlops burii*
Myriopholis cairi (Duméril & Bibron 1844) WAF, EAF	*Leptotyphlops cairi*
Myriopholis dissimilis (Bocage 1886) EAF	*Leptotyphlops dissimilis*
Myriopholis erythraeus (Scortecci 1929) EAF	*Leptotyphlops erythraeus*
Myriopholis filiformis (Boulenger 1899) SOC	*Leptotyphlops filiformis*
Myriopholis ionidesi (Broadley & Wallach 2007) EAF	*Leptotyphlops ionidesi*
Myriopholis longicauda (Peters 1854) SAF, EAF	*Leptotyphlops longicaudus*
Myriopholis macrorhyncha (Jan 1860) WAF, EAF, AR, SWA	*Leptotyphlops macrorhynchus*
Myriopholis macrura (Boulenger 1899) SOC	*Leptotyphlops macrurus*
Myriopholis narirostris (Peters 1867) WAF	*Leptotyphlops narirostris*
Myriopholis natatrix (Andersson 1937) WAF	*Leptotyphlops natatrix*
Myriopholis nursii (Anderson 1896) EAF, AR	*Leptotyphlops nursii*
Myriopholis perreti (Roux-estéve 1979) WAF	*Leptotyphlops perreti*
Myriopholis phillipsi (Barbour 1914) AR	*Leptotyphlops phillipsi*
Myriopholis rouxestevae (Trape & Mane 2004) WAF	*Leptotyphlops rouxestevae*
Myriopholis tanae (Broadley & Wallach 2007) EAF	*Leptotyphlops tanae*
Myriopholis wilsoni (Hahn 1978) SOC	*Leptotyphlops wilsoni*
Myriopholis yemenica (Scortecci 1933) AR	*Leptotyphlops yemenicus*
Tribe Leptotyphlopini	
Leptotyphlops aethiopicus Broadley & Wallach 2007 EAF	*Leptotyphlops aethiopicus*
Leptotyphlops conjunctus (Jan 1861) SAF	*Leptotyphlops conjunctus*
Leptotyphlops distanti (Boulenger 1892) SAF	*Leptotyphlops distanti*
Leptotyphlops emini (Boulenger 1890) CAF	*Leptotyphlops emini*
Leptotyphlops howelli Broadley & Wallach 2007 EAF	*Leptotyphlops howelli*
Leptotyphlops incognitus Broadley & Broadley 1999 SAF	*Leptotyphlops incognitus*
Leptotyphlops jacobseni Broadley & Broadley 1999 SAF	*Leptotyphlops jacobseni*
Leptotyphlops kafubi (Boulenger 1919) CAF	*Leptotyphlops kafubi*
Leptotyphlops keniensis Broadley & Wallach 2007 EAF	*Leptotyphlops keniensis*
Leptotyphlops latirostris (Sternfield 1912) EAF	*Leptotyphlops latirostris*
Leptotyphlops macrops Broadley & Wallach 1996 EAF	*Leptotyphlops macrops*
Leptotyphlops mbanjensis Broadley & Wallach 2007 EAF	*Leptotyphlops mbanjensis*

continued next page.

TABLE 1. (continued)

This study	Previous classification
Leptotyphlops merkeri (Werner 1909) EAF	*Leptotyphlops merkeri*
Leptotyphlops monticolus (Chabanaud 1917) CAF	*Leptotyphlops monticolus*
Leptotyphlops nigricans (Schlegel 1839) SAF, EAF	*Leptotyphlops nigricans*
Leptotyphlops nigroterminus Broadley & Wallach 2007 EAF	*Leptotyphlops nigroterminus*
Leptotyphlops pembae Loveridge 1941 EAF	*Leptotyphlops pembae*
Leptotyphlops pitmani Broadley & Wallach 2007 CAF	*Leptotyphlops pitmani*
Leptotyphlops pungwensis Broadley & Wallach 1997 SAF	*Leptotyphlops pungwensis*
Leptotyphlops scutifrons (Peters 1854 SAF), EAF	*Leptotyphlops scutifrons*
Leptotyphlops sylvicolus Broadley & Wallach 1997 SAF	*Leptotyphlops sylvicolus*
Leptotyphlops telloi Broadley & Watson 1976 SAF	*Leptotyphlops telloi*
Namibiana gracilior (Boulenger 1910) SAF	*Leptotyphlops gracilior*
Namibiana labialis (Sternfeld 1908) SAF	*Leptotyphlops labialis*
Namibiana latifrons (Sternfeld 1908) SAF	*Leptotyphlops latifrons*
Namibiana occidentalis (Fitzsimons 1962) SAF	*Leptotyphlops occidentalis*
Namibiana rostrata (Bocage 1886) SAF	*Leptotyphlops rostratus*

Remarks. Hahn (1980) and Wallach (1998) reviewed the systematics of the family and McDiarmid *et al.* (1999) provided synonymies of the family and species. A more recent list of species, including synonymies, is provided by Uetz et al. (2009). Several changes in classification at the species level are discussed below. The two subfamilies recognized here correspond to the two major divisions within the family based on the phylogenetic relationships (Figs. 3–4). The first is a mostly New World group, but includes six species from West Africa, and comprises mostly short-tailed species. The second is an entirely Old World assemblage comprising mostly long-tailed species.

Subfamily Epictinae Hedges, Adalsteinsson, & Branch, New Subfamily

Type genus. *Epictia* Gray, 1845: 139.

Diagnosis. Compared with other subfamilies, members of this subfamily tend to have short, thick tails, and the fewest subcaudal scales: relative tail length is 2.1–11.5% total length versus 4.1–18.9% in the Leptotyphlopinae; tail shape is 1.3–6.1 versus 3.2–11.7; and subcaudals number 8–30 versus 12–58 in the Leptotyphlopinae (Table 2; Fig. 5). All leptotyphlopids with more than two supralabials and more than 14 midbody scale rows are in this subfamily. The support for this group was 44% BP and 0% PP for the four-gene tree (Fig. 3) and 94% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Two tribes, three subtribes, eight genera, and 62 species (Table 1).

Distribution. The subfamily is distributed in the New World and in equatorial Africa. In the New World it ranges from North America (California, Utah, and Kansas) south through Middle and South America (exclusive of the high Andes) to Uruguay and Argentina on the Atlantic side. It also occurs on San Salvador Island (Bahamas), Hispaniola, the Lesser Antilles, Cozumel Island (Mexico), Islas de Bahia and Swan Islands (Honduras), San Andres and Providencia Islands (Colombia), Bonaire, Margarita Islands, and Trinidad. It also occurs in equatorial Africa, from southern Senegal, Guinea, and Bioko Island in the west to Ethiopia in the east.

TABLE 2. Morphological variation in the genera of leptotyphlopid snakes, taken from species descriptions (cited in Table 1) and from earlier summaries (e.g., Broadley & Broadley 1999; Broadley & Wallach 2007; Wallach 1998). Abbreviations are: B (brown), BS (body shape = total length/width at midbody), DOR (dorsal coloration), L (large), M (moderate), MBS (midbody scales = rows around middle of body), MDS (middorsal scales from rostral to tail tip), MTS (midtail scales = rows around middle of tail), MU (multi-colored), N (no), PB (pale brown), RTL (relative tail length = tail length/ total length), S (small), SC (subcaudals), SL (supralabials), SL1 (supralabial 1 size), STR (stripes), TOTL (maximum adult total length, mm), TS (tail shape = tail length/ tail width), VEN (ventral coloration), W (white), Y (yes). Character states that are rare or uncommon are denoted by parentheses.

Genus	MBS	MTS	MDS	SC	SL	SL1	TOTL	BS	RTL	TS	DOR	STR	VEN
EPICTINAE													
EPICTINI													
Epictina													
Epictia	14	10 (12)	155–396	10–30	2	L	109–341	28–90	3.3–11.5	2.1–6.1	MU	Y (N)	B
Siagonodon	14	10–14	206–289	8–20	2	S, M, L	202–300	39–130	2.1–6.6	1.3–2.6	MU	Y	W
Renina													
Rena	14	10 (12)	168–312	9–21	2–3	M, L (S)	205–389	26–60	3.1–8.6	1.9–3.8	B	N	W
Tricheilostoma	14	10 (12)	152–253	10–23	3	M	138–400	32–68	3.4–10.7	2–4.4	B	N	B
Tetracheilostomina													
Mitophis	14–16	12	262–414	14–22	3–4	M	143–205	43–94	3.8–5.0	2.3–4.3	B	Y (N)	B
Tetracheilostoma	14–16	10–12	170–192	12–15	4	M	104–113	31–54	5.1–7.0	1.4–2.7	MU	Y	B
RHINOLEPTINI													
Guinea	14	12	173–288	6–16	3 (2)	S (L)	112–188	24–69	2.4–7.0	1.4–4.3	B	N	PB
Rhinoleptus	16	14	302–546	21–28	2–4	S	160–460	67–77	3.7–10	3.5	B	N	B
LEPTOTYPHLOPINAE													
EPACROPHINI													
Epacrophis	14	10	180–248	18–32	2	M	143–201	30–57	7.9–10.9	3.2–5.7	B	N	W
MYRIOPHOLINI													
Myriopholis	14	10–12	165–558	25–58	2	S (M)	103–293	27–138	5.7–18.9	5.0–11.7	PB	N	W
LEPTOTYPHLOPINI													
Leptotyphlops	14	10–12	171–322	18–44	2	S (M)	126–292	36–106	5.1–13.7	3.4–9.2	B	N	B
Namibiana	14	10–12	241–387	12–41	1–2	0–S	192–322	45–142	4.1–10.8	3.8–7.8	B	N	PB

Remarks. The inclusion of six African species (all but one from West Africa) in this otherwise New World group (Table 1; Figs. 3–4) was surprising, and was not found in morphological analyses of visceral and other data (Wallach 1998). Nonetheless, the unusually high scale row count (16) of *Rhinoleptus* has been recorded in two other New World genera in this subfamily, *Mitophis* n. gen and *Tetracheilostoma* (Table 2). Also, the West African members of Epictinae have relatively short and thick tails, low subcaudal counts, and high supralabial counts as in New World Epictinae but in contrast to other Old World leptotyphlopids (Subfamily Leptotyphlopinae).

Tribe Epictini Hedges, Adalsteinsson, & Branch, New Tribe

Type genus. *Epictia* Gray, 1845: 139.

Diagnosis. Members of this tribe have moderate or large anterior supralabial scales, with only two out of 55 species possessing small anterior supralabial scales (*Rena unguirostris* and *Siagonodon cupinensis*). This contrasts with all other leptotyphlopids (except for six African species) which have small anterior supralabial scales (Table 2). Because the West African members of the Epictinae (except *sundewalli*) all have the small anterior supralabial, the moderate and large scale conditions appear to be derived (see biogeography section for discussion on hypothesized evolutionary history). Members of two of the three subtribes in this tribe also have species with striped patterns and multiple colors (including yellow, and in some cases, red) (Fig. 6). In contrast, other leptotyphlopids lack stripes and usually have a brown dorsum. The support for this group was 70% BP and 100% PP for the four-gene tree (Fig. 3) and 79% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Three subtribes, six genera, and 56 species (Table 1).

Distribution. The tribe is distributed in the New World from North America (California, Utah, and Kansas) south through Middle and South America (exclusive of the high Andes) to Uruguay and Argentina on the Atlantic side. It also occurs on San Salvador Island (Bahamas), Cozumel Island (Mexico), Islas de Bahia and Swan Islands (Honduras), San Andres and Providencia Islands (Colombia), Bonaire, Margarita Islands, and Trinidad.

Remarks. This tribe comprises the New World clade of the Subfamily Epictinae.

Subtribe Epictina Hedges, Adalsteinsson, & Branch, New Subtribe

Type genus. *Epictia* Gray, 1845: 139.

Diagnosis. Epictina is distinguished from the subtribe Renina (see below) by having absent or normal-sized supraoculars (small in Renina) and by having a striped pattern and brightly colored dorsum, often with red and yellow (Table 2). Among other leptotyphlopids, only four West Indian species have stripes, and in three of those species the stripes are dull yellow. Epictina is distinguished from the subtribe Tetracheilostomina by having 2 supralabials (3–4 in Tetracheilostomina). The support for this group was 69% BP and 100% PP for the four-gene tree (Fig. 3) and 87% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Two genera and 29 species (Table 1).

Distribution. The subtribe is distributed from southern Mexico (Colima, Veracruz) through the lowlands of Middle America, south to Argentina and Uruguay in South America, but excluding the high Andes. It also occurs on San Salvador Island (Bahamas), Cozumel Island (Mexico), Islas de Bahia and Swan Islands (Honduras), San Andres and Providencia Islands (Colombia), Bonaire, Margarita Islands, and Trinidad.

Remarks. This subtribe comprises the major radiation of leptotyphlopids in South America.

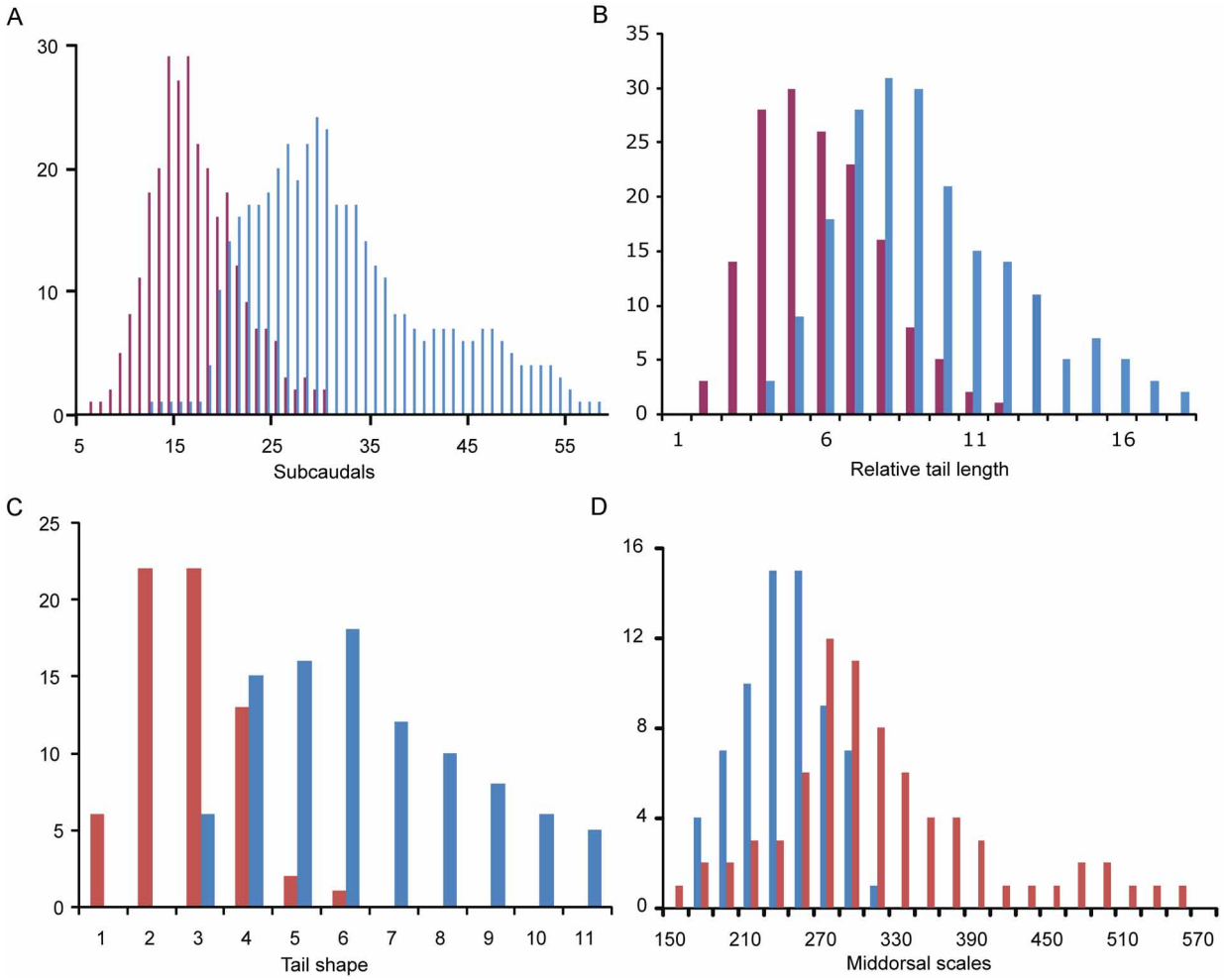


FIGURE 5. Histograms showing differences in scalation and proportions among taxa of leptotyphlopid snakes, assembled from descriptions of species (cited in Table 1) and earlier summaries (e.g., Broadley & Broadley 1999; Broadley & Wallach 2007; Wallach 1998). (A) Subcaudal scales in Epictinae (red, left) and Leptotyphlopinae (blue, right). (B) Relative tail length (tail length/ total length x 100) in Epictinae (red, left) and Leptotyphlopinae (blue, right). (C) Tail shape (tail length/ tail width at midtail) in Epictinae (red, left) and Leptotyphlopinae (blue, right). (D) Middorsal scales in two genera of Leptotyphlopinae: *Leptotyphlops* (blue, left) and *Myriopholis* (red, right). For each panel, frequency is on the Y-axis. In panels B and C, continuous numbers were rounded to integers before binning, and therefore bins are whole numbers as indicated.

Genus *Epictia* Gray, 1845

Stenostoma Wagler, 1824: 68. Type species: *Stenostoma albifrons* Wagler, 1824, by monotypy. [Preoccupied by *Stenostoma* Latreille, 1810: Coleoptera and *Stenostoma* Lamarck, 1817: Mollusca.]
Stenostona Cuvier, 1836: 404. [incorrect subsequent spelling.]
Epictia Gray, 1845: 139. Type species: *Typhlops undecimstriatus* Schlegel, 1839, by subsequent designation by Loveridge, 1957: 246.
Sabrina Girard, 1857: 181. Type species: *Typhlops tesselatum* Tschudi, 1845, by monotypy.
Stenostomophis Rochebrune, 1884: 141. [Replacement name for *Stenostoma* Wagler, 1824.]

Diagnosis. Species of *Epictia* have 14 midbody scale rows, 10 (12 rarely) midtail scale rows, 155–396 middorsal scale rows, 10–30 subcaudals, two supralabials, large anterior supralabials, 109–341 mm maximum adult total length, a body shape of 28–90 (total length/width), relative tail length 3.3–11.5%, a tail shape of 2.1–6.1, striped pattern, multiple dorsal colors common (including reds and yellows), and brown ventral color

(rarely white) (Table 2). Members also have normal-sized supraoculars (supraocular is lacking in *E. nasalis*), and this trait distinguishes *Epictia* from the other genus in the subtribe, *Siagonodon*, which lacks a supraocular. Other traits distinguishing the two genera show overlap, but species of *Epictia* tend to have more midtail scale rows, larger first supralabial (L), and a darker venter (Table 2). The support for this group was 97% BP and 100% PP for the four-gene tree (Fig. 3) and 100% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Twenty-five species (Table 1; Fig. 6).

Distribution. *Epictia* is distributed from southern Mexico (Colima, Veracruz) through the lowlands of Middle America, south to Argentina and Uruguay in South America, but excluding the high Andes. It also occurs on San Salvador Island (Bahamas), Cozumel Island (Mexico), Islas de Bahia and Swan Islands (Honduras), San Andres and Providencia Islands (Colombia), Bonaire, Margarita Islands, and Trinidad (Fig. 8).

Etymology. The generic name is feminine and derived from the Latin *e* (without) and *pictus* (painted), apparently in allusion to absence of colors (only a brown dorsum) in the type species, *Epictia undecimstriata*. This name is ironic because most species in this genus, unknown at that time (Gray 1845), are among the most colorful in the family.

Remarks. Species placed here in *Epictia* include members of both the *albifrons* and *tesselata* groups of "*Leptotyphlops*" (Orejas-Miranda 1967; Peters 1970). The distinction between the two groups has been based on the contact (former *tesselata* Group) or not (former *albifrons* Group) of the first supralabial and the supraocular scale. Given that our molecular phylogenetic analysis did not include any members of the former *tesselata* Group, we were unable to test the validity of these two groups. If the *tesselata* Group is valid, it could take the generic name *Sabrina* Girard. However, considering the great genetic divergence between *E. albifrons* and other members of *Epictia* sampled (Fig. 3), all from the former *albifrons* Group, we are doubtful that additional sampling will support a simple dichotomy of clades corresponding to the two former species groups. Nonetheless, representatives of *Epictia* not sampled here (including all of those in the former *tesselata* Group) all have two supralabials combined with a large anterior supralabial, a condition nearly unique in the family and supporting their placement in this genus. We follow Kretzschmar (2006) in placing "*L.*" *melanotermus* in the synonymy of *Epictia albipunctata*.

Because the sample of *E. goudotii magnamaculata* is closer to *E. columbi* than to other *E. goudotii*, we elevate that subspecies to species status: *Epictia magnamaculata*. The remaining populations of *E. goudotii* sampled are considerably divergent from one another suggesting that multiple species are represented.

Genus *Siagonodon* Peters, 1881

Typhlina Wagler, 1830: 196. Type species: *Acontias lineatus* Reinwardt [*Nomen nudum*] and *Typhlops sentemstriatus* Schneider, 1801, by monotypy; suppressed by ICZN, 1982, Opinion 1207.

Catadon A.-M.-C. Dumeril and Bibron, 1844: 318. Type species: *Anguis septem-striatus* Schneider, 1801, by monotypy. [Preoccupied by *Catadon* Linnaeus, 1761: Cetacea.]

Siagonodon Peters, 1881: 71. Type species: *Anguis septem-striatus* Schneider, 1801, by original description.

Diagnosis. Species of *Siagonodon* have 14 midbody scale rows, 10–14 midtail scale rows, 206–289 middorsal scale rows, 8–20 subcaudals, two supralabials, small or moderate or large anterior supralabials, 202–300 mm maximum adult total length, a body shape of 39–130 (total length/width), a relative tail length of 2.1–6.6%, a tail shape of 1.3–2.6, striped pattern, multiple dorsal colors, and white venter (Table 2). They also lack a supraocular scale. The absence of a supraocular scale distinguishes this genus from the other genus in the subtribe, *Epictia* (except *E. nasalis*). Other traits distinguishing the two genera show overlap, but species of *Siagonodon* tend to have fewer midtail scale rows and a white venter (Table 2). Only one species of this genus was sequenced.

FIGURE 6. Representatives of the snake Family Leptotyphlopidae from the New World. (A) *Epictia albifrons* (Brazil, Tocantins, Parque Estadual de Cantão); photograph by Laurie J. Vitt. (B) *Epictia alfredschmidti* (Peru: Ancash; Malvas); photograph by E. Lehr. (C) *Epictia* cf. *diaplocia* (Brazil: Amazonas; Reserva Adolfo Ducke, 30 km N Manaus); photograph by Laurie J. Vitt. (D) *Siagonodon brasiliensis* (Brazil: Tocantins; Lalapão); photograph by Laurie J. Vitt. (E) *Siagonodon septemstriatus* (Brazil: Roraima; Fazenda Nova Esperança); photograph by Laurie J. Vitt. (F) *Epictia columbi* (Bahamas: San Salvador); photograph by S. Blair Hedges.

Content. Four species (Table 1; Fig. 6).

Distribution. *Siagonodon* is distributed east of the Andes in South America, from southeastern Venezuela, Guyana, and French Guiana in the north to Argentina (Fig. 8).

Etymology. The generic name is masculine and derived from the Greek nouns *siagon* (jaw) and *odon* (tooth), probably in allusion to the presence of teeth only on the lower jaw.

Remarks. Species placed here in *Siagonodon* include members of the *septemstriatus* Group (Orejas-Miranda 1967; Peters 1970). Only one representative (*S. septemstriatus*) was included, and it clustered with a monophyletic *Epictia*, as expected based on character data. However, future molecular studies with additional species are needed to further test the allocation of species to these two genera.

Subtribe Renina Hedges, Adalsteinsson, & Branch, New Subtribe

Type genus. *Rena* Baird and Girard, 1853: 142. Type species: *Rena humilus* Baird and Girard, 1853, by subsequent designation by Stejneger, 1892 [dated 1891]: 501.

Diagnosis. Renina is distinguished from Epictina by having small supraoculars (versus absent or normal-sized in Epictina), lacking a striped pattern, and having a uniform brown (usually dark brown) dorsum, sometimes purplish but not with reds or yellows (Table 1). Renina is distinguished from Tetracheilostomina by having 2–3 (*Rena*) or 3 (*Tricheilostoma*) supralabials versus usually 4 in Tetracheilostomina (one species has 3–4 supralabials). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3); only one species was included in the nine-gene tree (Fig. 4).

Content. Two genera and 20 species (Table 1).

Distribution. Renina is distributed in the New World from North America (California, Utah, and Kansas) south through Middle and South America (exclusive of the high Andes) to Uruguay and Argentina on the Atlantic side.

Remarks. Renina includes the former *macrolepis* Group (now *Tricheilostoma*) and *dimidiatus* Group (now *Rena*) of "*Leptotyphlops*" (Orejas-Miranda 1967; Peters 1970). These two genera are broadly similar in scalation and coloration, supporting the molecular phylogenetic results.

Genus *Rena* Baird & Girard, 1853

Rena Baird and Girard, 1853: 142. Type species: *Rena humilus* Baird and Girard, 1853, by subsequent designation by Stejneger, 1892 [dated 1891]: 501.

Diagnosis. Species of *Rena* have 14 midbody scale rows, 10 (12 rarely) midtail scale rows, 168–312 middorsal scale rows, 9–21 subcaudals, 2–3 supralabials, moderate or large (rarely small) anterior supralabials, 205–389 mm maximum adult total length, a body shape of 26–60 (total length/width), a relative tail length of 3.1–8.6 %, a tail shape of 1.9–3.8, no striped pattern, brown or purplish brown dorsal color, and white venter (Table 2). They also have a small supraocular scale. They are distinguished from the other genus in this subtribe, *Tricheilostoma*, by having a white (not brown or pale brown) venter, usually two supralabials (three in *R. bressoni*, *R. dissecta*, and *R. myopica*), and in having a higher number (on average) of middorsal scales (Table 2). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3); only one species was included in the nine-gene tree (Fig. 4).

Content. Eleven species (Table 1; Fig. 7).

Distribution. *Rena* is distributed from North America (California, Utah, and Kansas) south through Middle and South America (exclusive of the high Andes) to Uruguay and Argentina on the Atlantic side (Fig. 8).

Etymology. The generic name is feminine and derived from the Latin noun *ren* (kidney), apparently in allusion to the kidney color (reddish brown) of the type species.

Remarks. Species placed here in *Rena* include members of the former *dulcis* Group of "*Leptotyphlops*" (Orejas-Miranda 1967; Peters 1970) but exclude those placed by Orejas-Miranda (1967) in the "*macrolepis* Group." Even earlier, Klauber (1940) referred to this assemblage as the *dulcis-humilus* Group. We recognize the species *Rena boettgeri* (southern Baja California, Mexico), originally described as a full species (Werner

1899) but more recently treated as a subspecies (Smith & Larsen 1974) or placed in the synonymy of *R. humilis* (McDiarmid *et al.* 1999). It has a relatively large sequence divergence (Fig. 3) from a nearby sample of *Rena humilis* (Fig. 3) from northern Baja California, and the two taxa have nearly non-overlapping middorsal scale count differences (Grismer 1999; Hahn 1979). Five representatives of *Rena* (*R. boettgeri, R. dissecta, R. dulcis, R. humilis,* and *Rena* sp. B) were included in the molecular phylogenetic analyses, and they formed a strongly supported group, deeply divergent from *T. macrolepis*. Because of this, and the concordance in scalation and coloration distinguishing these two groups of species, we recognize the former "*macrolepis* Group" as the Genus *Tricheilostoma* (see below). However, the original character used to define the group, the relationship between the posterior border of the rostral and the eye level (Orejas-Miranda 1967), is not useful in diagnosing the two genera. Most members (seven of 11) of *Rena* occur in Middle and North America, together with several species in the genus *Epictia* (subtribe Epictina). We concur with the taxonomic arrangement for *R. dulcis* and relatives proposed by Dixon and Vaughn (2003). The species *R. nicefori* was not included in the size range for total length because the adult status of the single specimen (90 mm) is unknown (Hedges 2008).

Rena is distributed in three isolated areas (Fig. 8): North and Middle America (*Rena boettgeri, R. bressoni, R. dissecta, R. dulcis, R. humilis, R. maxima,* and *R. myopica*), northern South America (*Rena affinis, R. dimidiata,* and *R. nicefori*), and Argentina (*R. unguirostris*). Species in these three areas are distinct morphologically as well. Compared with the species from northern South America, the North and Middle American species have relatively high middorsal scale counts (199–309 versus 168–215) and short tails (3.1–6.7 versus 5.7–8.6). In both characters, *R. unguirostris* is similar to the North and Middle American species (241–312 and 3.1–5.1, respectively), but it has a small anterior supralabial scale, which is unusual among New World leptotyphlopids. Based on this evidence, the three groups could be recognized as species groups: the *humilis* Group, the *dimidiata* Group, and the *unguirostris* Group. Future molecular sampling will determine whether the *dimidiata* and *unguirostris* groups belong to the Genus *Rena*.

Genus *Tricheilostoma* Jan, 1860

Tricheilostoma Jan in Jan and Sordelli, 1860:7; 1861: 7; 1861: 190. Type species: *Stenosoma macrolepis* Peters, 1857, by subsequent designation by Loveridge, 1957: 246.

Diagnosis. Species of *Tricheilostoma* have 14 midbody scale rows, 10 (12 rarely) midtail scale rows, 152–253 middorsal scale rows, 10–23 subcaudals, three supralabials, moderate anterior supralabials, 138–400 mm maximum adult total length, a body shape of 32–68 (total length/width), a relative tail length of 3.4–10.7 %, a tail shape of 2.0–4.4, no striped pattern, brown dorsal color, and brown venter (Table 2). They also have a small supraocular scale. They are distinguished from the other genus in this subtribe, *Rena*, by having a brown or pale brown (not white) venter, three supralabials (but also in *Rena bressoni*, *R. dissecta*, and *R. myopica*), and in having a lower number (on average) of middorsal scales (Table 2). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3); no sequences were included in the nine-gene tree (Fig. 4).

Content. Nine species (Table 1; Fig. 7).

Distribution. *Tricheilostoma* is distributed from lower Central America (Panama) south through South America (exclusive of the high Andes) to southeastern Brazil (Fig. 8).

Etymology. The generic name is neuter in gender and derived from the Greek adjective *tri* (three) and Greek nouns *cheilos* (lip) and *stoma* (mouth), in allusion to the presence of three supralabial scales.

Remarks. See comments above, in previous account, regarding the distinction of *Rena* and *Tricheilostoma*. We included three individuals of *T. macrolepis* in the molecular analyses; two from a locality in northern Brazil and a third from Guyana. The deep divergence between sequences from the two sample localities (Fig. 3) indicates that they represent two species. It has already been suggested that this wide-ranging "species" comprises multiple species (Orejas-Miranda 1967).

FIGURE 7. Representatives of the snake Family Leptotyphlopidae from the New World (continued).

(A) *Rena dulcis* (United States: Oklahoma; Beckham County, Packsaddle Wildlife Management Area); photograph by Buddy Brown. (B) *Tricheilostoma koppesi* (Brazil: Tocantins: Parqu Estadual de Cantão); photograph by Laurie J. Vitt. (C) *Tricheilostoma macrolepis* (Brazil: Pará: 101 km S Santarém); photograph by Laurie J. Vitt. (D) *Mitophis asbolepis* (Dominican Republic: Barahona; 0.3 km S, 13.5 km E Canoa); photograph by S. Blair Hedges; (E) *Mitophis leptepileptus* (Haiti: l'Ouest; Soliette); photograph by S. Blair Hedges. (F) *Tetracheilostoma breuili* (Saint Lucia: Maria Major Island); photograph by S. Blair Hedges.

Subtribe Tetracheilostomina Hedges, Adalsteinsson, & Branch, New Subtribe

Type genus. *Tetracheilostoma* Jan, 1861: 191.

Diagnosis. Tetracheilostomina is distinguished from the other two subtribes of Epictini by usually having four supralabials (two in Epictina and 2–3 in Renina) (Table 2). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3); only one of the two genera was included in the nine-gene tree (Fig. 4).

Content. Two genera and seven species (Table 1; Fig. 7).

Distribution. Tetracheilostomina is distributed in the West Indies: on the island of Hispaniola in the Greater Antilles, and on Martinique, Saint Lucia, and Barbados in the Lesser Antilles.

Remarks. Tetracheilostomina includes species in the former "*bilineatus* Group" of "*Leptotyphlops*" (Hedges 2008; Thomas 1965; Thomas *et al.* 1985). The high number (four) of supralabials is rare among leptotyphlopids, otherwise occurring only in *Rhinoleptus*. As a unifying character for this West Indian radiation it is further supported by the molecular phylogeny (Fig. 3). However, the included species are considerably divergent in other scale characters, body size, and coloration. The species from Hispaniola have a high number of middorsal scales, are thin, and pale brown or pink in color. In contrast, the Lesser Antillean species have a low number of middorsals, are stout, and dark brown in color with dull yellowish stripes. The molecular phylogeny supports the distinction of these two groups of species and we recognize them here at the generic level.

Genus *Mitophis* Hedges, Adalsteinsson, & Branch, New Genus

Type species. *Leptotyphlops pyrites* Thomas, 1965

Diagnosis. Species of *Mitophis* have 14 (rarely 16) midbody scale rows, 12 midtail scale rows, 262–414 middorsal scale rows, 14–22 subcaudals, four (3–4 in *M. leptepileptus*) supralabials, moderate anterior supralabials, 143–205 mm maximum adult total length, a body shape of 43–94 (total length/width), a relative tail length of 3.8–5.0 %, a tail shape of 2.3–4.3, no striped pattern (except *M. pyrites*), a pale brown or unpigmented dorsum, and a brown or unpigmented venter (Table 2). They are distinguished from the other genus in this subtribe, *Tetracheilostoma*, by having a high number of middorsal scales (262–414 versus 170–192), thinner body (43–94 versus 31–54), and a pale brown or unpigmented dorsum (not dark brown). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3) and 100% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Four species (Table 1; Fig. 7).

Distribution. *Mitophis* is distributed on the Greater Antillean island of Hispaniola, including the countries of the Dominican Republic and Haiti (Fig. 8).

Etymology. The generic name is masculine and derived from the Greek nouns *mitos* (thread) and *ophis* (snake).

Remarks. Three described species of *Mitophis* were included in the molecular phylogenetic analyses plus one undescribed species from the Dominican Republic. None of the species is sympatric. Four of the five species in the genus are each only known from essentially a single locality and the fifth (*M. pyrites*) is known from several localities in a small area. Even at known localities, it is often difficult to locate individuals. The reason for their unusually sparse distribution and apparent rarity is unknown. Suitable microhabitats have been searched elsewhere on the island, without success, and therefore it is not for lack of search effort. Also, the habitats occupied by these species vary widely, from some of the most xeric habitats known on the island (e.g., localities of *M. asbolepis* and *M. pyrites*) to one of the more mesic areas (locality of *M. calypso*), and from below sea level (undescribed species) to 350–370 m in elevation (*M. asbolepis* and *M. leptepileptus*). A single specimen of *M. leptepileptus*, which is the only species of *Mitophis* known to have three supralabials, was reported to have four supralabials on each side (Thomas *et al.* 1985).

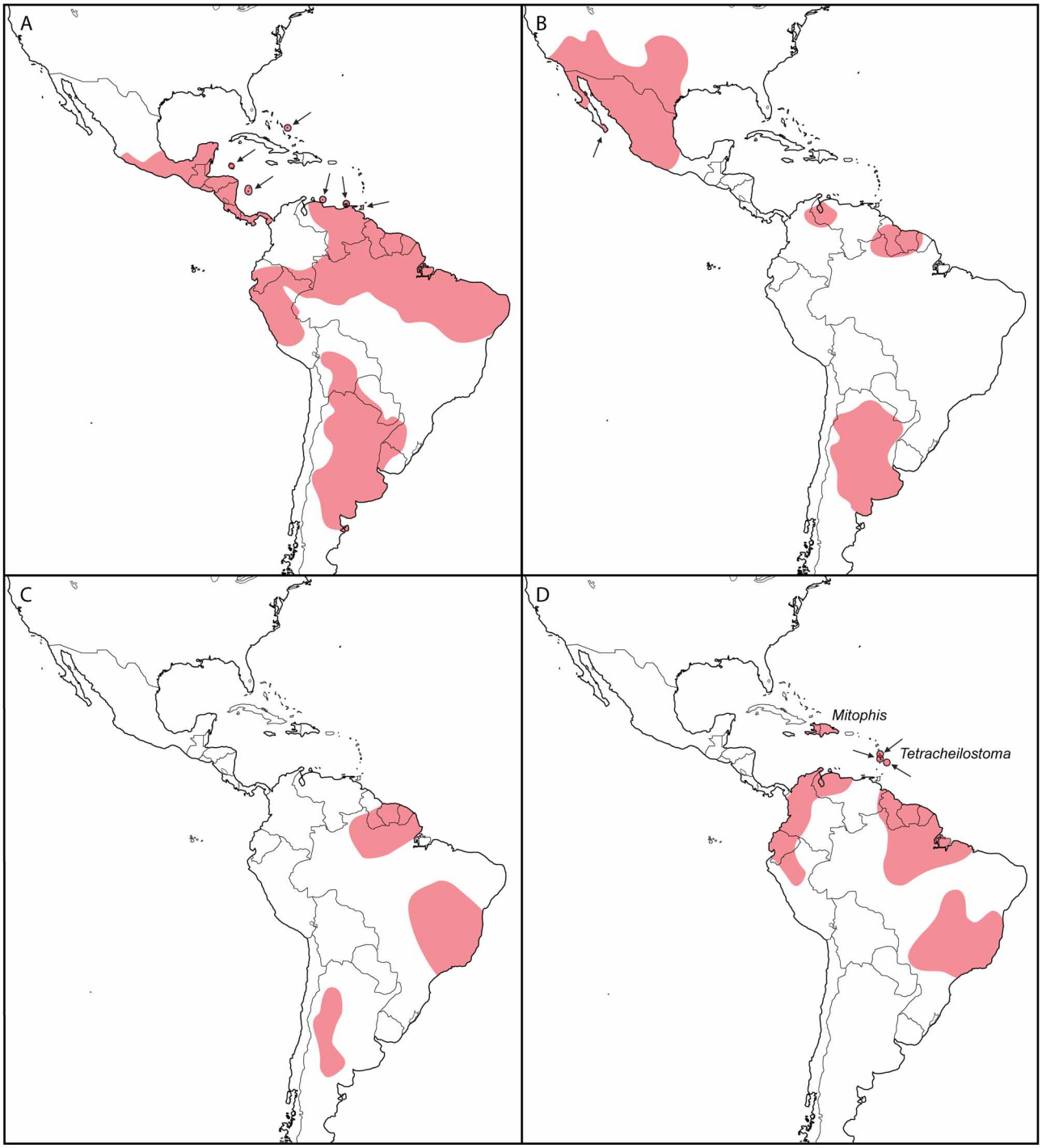


FIGURE 8. Distributions of genera of leptotyphlopid snakes in the New World. (A) *Epictia*. (B) *Rena*. (C) *Siagonodon*. (D) *Tricheilostoma* (South America), *Mitophis* (Hispaniola), and *Tetracheilostoma* (Martinique, Saint Lucia, and Barbados). Some islands close to mainland areas are not indicated; see text for description of distribution.

Genus *Tetracheilostoma* Jan, 1861

Eucephalus Fitzinger, 1843: 24. Type species: *Typhlops bilineatus* Schlegel, 1839, by original description [Preoccupied by *Eucephalus* Laporte, 1834: Coleoptera].
Tetracheilostoma Jan, 1861: 191. Type species: *Typhlops bilineatus* Schlegel, 1839, by monotypy.

Diagnosis. Species of *Tetracheilostoma* have 14 (rarely 16) midbody scale rows, 10–12 midtail scale rows, 170–192 middorsal scale rows, 12–15 subcaudals, four supralabials, moderate anterior supralabials, 104–113 mm maximum adult total length, a body shape of 31–54 (total length/width), a relative tail length of 5.1–7.0 %, a tail shape of 1.4–2.7, striped pattern (dull yellow stripes), dark brown dorsal color, and brown venter (Table 2). They are distinguished from the other genus in this subtribe, *Mitophis*, by having a low number of middorsal scales (170–192 versus 262–414), stouter body (31–54 versus 43–94), and a dark brown dorsum (not a pale brown or unpigmented dorsum). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3); no sequences were included in the nine-gene tree (Fig. 4).

Content. Three described species (Table 1; Fig. 7).

Distribution. *Tetracheilostoma* is distributed on the Lesser Antillean islands of Martinique, Saint Lucia, and Barbados (Fig. 8).

Etymology. The generic name is neuter in gender and derived from the Greek adjective *tetra* (four) and Greek nouns *cheilos* (lip) and *stoma* (mouth), in reference to the presence of four supralabial scales.

Remarks. Two of the three species of *Tetracheilostoma* were recently described, including one from Barbados (*Tetracheilostoma carlae*) that is the smallest known snake (Hedges 2008).

Tribe Rhinoleptini Hedges, Adalsteinsson, & Branch, New Tribe

Type genus. *Rhinoleptus* Orejas-Miranda, Roux-Estève, and Guibé, 1970: 4.

Diagnosis. Members of Rhinoleptini are the only species of the Epictinae that occur in the Old World. They can usually be distinguished from the Tribe Epictini by possession of a small anterior supralabial scale (usually medium or large in Epictini). One species of Rhinoleptini (*Guinea sundewalli*) has a large anterior supralabial and two species out of 56 in Epictini (*Siagonodon cupinensis* and *Rena unguirostris*) have small anterior supralabials (Table 2). The support for this group was 52% BP and 64% PP for the four-gene tree (Fig. 3) and 87% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Two genera and six species (Table 1; Fig. 9).

Distribution. Rhinoleptini is distributed in equatorial Africa, from southern Senegal, Guinea, and Bioko Island in the west to Ethiopia in the east.

Remarks. Rhinoleptini is a primarily West African clade of leptotyphlopids and comprises the Old World members of the Subfamily Epictinae.

Genus *Guinea* Hedges, Adalsteinsson, & Branch, New Genus

Type species. *Stenostoma* (*Tricheilostoma*) *bicolor* Jan, 1860: 1.

Diagnosis. Species of *Guinea* have 14 midbody scale rows, 12 midtail scale rows, 173–288 middorsal scale rows, 6–16 subcaudals, three (two in *G. greenwelli*) supralabials, small anterior supralabials (large in *G. sundewalli*), 112–188 mm maximum adult total length, a body shape of 24–69.2 (total length/width), a relative tail length of 2.4–7.0 %, a tail shape of 1.4–4.3, no striped pattern, a brown dorsum (unpigmented in *G. greenwelli*), and paler brown venter (Table 2). They are distinguished from the other genus in this tribe, *Rhinoleptus*, by having 14 midbody scale rows (versus 16), 12 midtail rows (versus 14), 173–288 middorsal rows (versus 302–546), 6–16 subcaudals (versus 21–28), and a body shape of 24–69.2 (versus 67–77). Only one species was included in the molecular phylogenetic analyses (Figs. 3–4).

Content. Four species (Table 1; Fig. 9).

Distribution. *Guinea* is distributed primarily in rainforests of West Africa, including Guinea, southern Mali, Ivory Coast, Burkina Faso, southwestern Niger, Ghana, Togo, Benin, Nigeria, Cameroon, Bioko Island, southwestern Chad, and Central African Republic (Fig. 11).

Etymology. The generic name is here considered a feminine, Latinized noun referring to the distribution of the genus in the Guinea region, which is a broad area along the southern portion of West Africa (approximately from the country of Guinea to Cameroon). The origin of the word is uncertain but is thought to be derived from either the Susu or Berber languages of Africa, later modified in Portuguese (*Guiné*) and English (*Guinea*).

Remarks. This genus comprises the former *bicolor* Group of "*Leptotyphlops*," most recently discussed by Wallach and Boundy (2005), who noted similarities between it and several species in the New World.

Genus *Rhinoleptus* Orejas-Miranda, Roux-Estève, and Guibé, 1970

Type species. *Typhlops koniagui* Villers, 1956, by monotypy.

Diagnosis. Species in this genus have 16 midbody scale rows, 14 midtail scale rows, 302–546 middorsal scale rows, 21–30 subcaudals, 2–4 supralabials, small anterior supralabials, 160–460 mm maximum adult total length, a body shape of 67–160 (total length/width), a relative tail length of 3.7–10.0 %, a tail shape of 3.5, no striped pattern, a brown dorsum, and brown venter (Table 2). They are distinguished from the other genus in this tribe, *Guinea*, by having 16 midbody scale rows (versus 14), 14 midtail rows (versus 12), 302–546 middorsal rows (versus 173–288), 21–30 subcaudals (versus 6–16), and a body shape of 67–160 (versus 24–69.2). Only one species was included in the molecular phylogenetic analyses (Figs. 3–4).

Content. Two species (Table 1; Fig. 9), although see "Remarks" below.

Distribution. *Rhinoleptus* is distributed in West Africa (*Rhinoleptus koniagui*), including Senegal, and Guinea, and Mali (Trape & Mané 2006); and in East Africa (*Rhinoleptus parkeri*), including Ethiopia (Fig. 11).

Etymology. The generic name is masculine and derived from the Greek noun *rhinos* (nose) and Greek adjective *leptos* (thin), in allusion to the unusual rostral scale of *Rhinoleptus koniagui*, with its narrow and pointed anterior tip.

Remarks. We were unable to obtain a tissue sample of *Rhinoleptus parkeri* but assign it here to the genus *Rhinoleptus* because it shares with *R. koniagui* a series of unique or rare traits in the family: an unusually high number of midbody scale rows (16) and midtail scale rows (14), parietals small or undifferentiated, and occipitals undifferentiated. In his description of *parkeri*, Broadley (1999) considered these traits to be ancestral assuming that all other leptotyphlopids (apart from *R. koniagui*) formed a monophyletic group. Wallach (1998) also found that *parkeri* branched early in the tree based largely on visceral characters, and the position of this species was discussed further by Broadley and Wallach (2007). However, considering the phylogenetic relationships obtained in our study (Figs. 3–4) showing that *Rhinoleptus* is not the closest relative of all other leptotyphlopids, those characteristics of *R. parkeri* are now re-evaluated as being derived within Rhinoleptini rather than ancestral among leptotyphlopids.

The specimen of *Rhinoleptus* from West Africa sampled here (Fig. 9B) agrees in many respects with *Rhinoleptus koniagui* (e.g., greatly enlarged rostral, 16 scale rows, oblique orientation of head scales, Villiers 1956). However, it and some other specimens from Senegal lack the distinctive horn on the rostral of *R. koniagui* (Hedges and Trape, unpub. obs.). We conservatively refer it to *Rhinoleptus koniagui* but note that additional material may signal the presence of an additional species of *Rhinoleptus.*

Subfamily Leptotyphlopinae

Type genus. *Leptotyphlops* Fitzinger, 1843: 24.

FIGURE 9. Representatives of the snake Family Leptotyphlopidae from the Old World. (A) *Guinea bicolor* (Mali; Sikasso; Doussoudiana); photograph by Sébastien Trape. (B) *Rhinoleptus koniagui* (Senegal: Tambacounda; Ibel), preserved specimen from Sébastien Trape; photograph by S. Blair Hedges. (C) *Myriopholis boueti* (Sénégal; Dakar; Dakar); photograph by Sébastien Trape. (D) *Myriopholis longicauda* (South Africa: Northern Province; Limpopo); photograph by William R. Branch. (E) *Leptotyphlops distanti* (South Africa: Mpumalanga: near Middleburg); photograph by William R. Branch. (F) *Leptotyphlops incognitus* (South Africa: Mpumalanga: Komati River); photograph by William R. Branch.

Diagnosis. Members of Leptotyphlopinae usually have long, thin tails, with high subcaudal counts: relative tail length is 4.1–18.9 % total length versus 2.1–11.5% in the Epictinae, tail shape is 3.2–11.7 versus 1.3–6.1, and subcaudals number 12–58 versus 6–30 in the Epictinae (Table 2; Fig. 5). All leptotyphlopids possessing more than two supralabials, more than 14 midbody scale rows, stripes, and bold colors (e.g., reds and yellows)

are in the Epictinae rather than this subfamily. The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3) and 100% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Three tribes, four genera, and 54 species (Table 1; Figs. 9–10).

Distribution. Leptotyphlopinae is distributed throughout Africa (north and south of the Sahara Desert) as well as on nearby islands (Bazaruto archipelago, Pemba, Manda, Lamu, and Socotra), the Arabian Peninsula, and in southwest Asia (Turkey, Iran, Pakistan, and northwest India).

Remarks. We divide this subfamily into three tribes. Two are well-defined, include 51 of the 54 species, and correspond to the former *longicaudus* Group of "*Leptotyphlops*" on one hand (a primarily northeast Africa-Arabia clade) and the former *nigricans*, *rostratus*, and *scutifrons* groups of "*Leptotyphlops*" on the other hand (a primarily southern African clade). The remaining three species, corresponding to the former *reticulatus* Group of "*Leptotyphlops*," are placed here in a third tribe (A primarily East African clade); no molecular data were available for this tribe. A few characters previously used to define species groups, such as the fusion of skull bones and of the frontal and rostral scales (Broadley & Wallach 2007), show homoplasy among the genera of Leptotyphlopinae recognized here and therefore are excluded from diagnoses of taxa. Nonetheless combinations of those characters may still prove to be diagnostic for restricted clades of species. Hedges (2008) noted that Old World species of *Leptotyphlops* have a more pronounced sexual dimorphism in body size, averaging ~1.3 (total length of average adult female/total length of average adult male), compared with New World species (~1.1). However, data are available for only nine species of New World Epictinae and three species of Leptotyphlopinae (Bailey 1946; Zug 1977; Thomas *et al.* 1985; Broadley 1996; Webb *et al.* 2000; Passos *et al.* 2005, 2006), and therefore more sampling is needed before this trend can be considered diagnostic of the two subfamilies.

Tribe Epacrophini Hedges, Adalsteinsson, & Branch, New Tribe

Genus *Epacrophis* Hedges, Adalsteinsson, & Branch, New Genus

Type species. *Glauconia reticulata* Boulenger, 1906: 441.

Diagnosis. Species of *Epacrophis* and Epacrophini have 14 midbody scale rows, 10 midtail scale rows, 180–248 middorsal scale rows, 18–32 subcaudals, two supralabials, a moderate-sized anterior supralabial, 143–201 mm maximum adult total length, a body shape of 30–57 (total length/width), a relative tail length of 7.9–10.9 %, a tail shape of 3.2–5.7, no striped pattern, and usually a brown dorsum and white venter (Table 2). Epacrophini can be distinguished from the two other tribes in the subfamily Leptotyphlopinae by the presence of a moderate-sized anterior supralabial (versus absent or small in other species of Leptotyphlopinae, except *L. howelli*) and a stout apical spine on the tip of the tail (Broadley & Wallach 2007; Wallach 1996). No species were included in the molecular phylogenetic analyses.

Content. One genus and three species (Table 1; Fig. 9).

Distribution. Epacrophini is distributed in East Africa (Kenya and Somalia) and nearby islands (Manda and Lamu) (Fig. 11).

Etymology. The generic name is masculine and derived from the Greek adjective *epakros* (pointed at the end) and Greek noun *ophis* (snake), in allusion to the distinctive thorny spine at the tip of the tail in species of this genus.

Remarks. This tribe comprises the former *reticulatus* Group of "*Leptotyphlops*," most recently defined by Broadley and Wallach (2007).

Tribe Myriopholini Hedges, Adalsteinsson, & Branch, New Tribe

Genus *Myriopholis* Hedges, Adalsteinsson, & Branch, New Genus

Ramphostoma Jan in Jan and Sordelli, 1860. Type species *Stenostoma macrorhynchum* Jan, 1860, by monotypy. [Preoccupied by *Ramphostoma* Wagler (1830: 353) as corrected from *Rhamphostoma* by Wagler (1830: 141): Crocodilia.]

Rhamphostoma Boulenger, 1893: 59. [Replacement name for *Ramphostoma* Jan, 1861. Preoccupied by *Rhamphostoma* Agassiz, 1847, an unjustified emendation of *Ramphostoma* Wagler, 1830: Crocodilia.]

Type species. *Stenostoma longicaudum* Peters, 1854:621.

Diagnosis. Species of Myriopholini and *Myriopholis* have 14 midbody scale rows, 10–12 midtail scale rows, 165–558 middorsal scale rows, 25–58 subcaudals, two supralabials (three in *M. dissimilis*), a small anterior supralabial (moderate in *M. narirostris*), 103–293 mm maximum adult total length, a body shape of 27–138 (total length/width), a relative tail length of 5.7–18.9 %, a tail shape of 5.0–11.7, no striped pattern, and usually a pale brown dorsum and white venter (Table 2). Members of this genus and tribe can be distinguished from the two other tribes in the subfamily Leptotyphlopinae by the presence of a higher average number of middorsal scales (165–558 versus 171–387) and subcaudals (25–58 versus 12–44). Also, members of the tribe usually have a white venter and semilunate cloacal shield whereas members of the Tribe Leptotyphlopini usually have a brown or pale brown venter and a heart-shaped or subtriangular cloacal shield (see fig. 2 in Broadley & Wallach, 2007). Members of the Tribe Myriopholini also can be distinguished from the Tribe Epacrophini by the presence of a small anterior supralabial (moderate in size in Epacrophini). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3) and 100% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. One genus and 24 species (Table 1; Fig. 9).

Distribution. The tribe (and genus) is distributed throughout Africa (north and south of the Sahara Desert), the Arabian Peninsula and Socotra Island, and in southwest Asia (Turkey, Iran, Pakistan, and northwest India). Most species are distributed in the northern portion of sub-Saharan Africa, including West Africa, Central Africa, and East Africa (Fig. 11).

Etymology. The generic name is feminine and derived from the Greek adjective *myrios* (many, countless) and Greek noun *pholis* (scale), in allusion to the high number of middorsal and subcaudal scales typical of species in this genus.

Remarks. This tribe comprises the former *longicaudus* Group of "*Leptotyphlops*," most recently discussed and defined by Broadley and Wallach (2007). Those authors were unable to allocate the species "*L.*" *dissimilis* to a species group; it is known only from a single specimen now destroyed. We tentatively place it here in *Myriopholis* because it agrees with other species in that genus in number of subcaudals (29–30), relative tail length (8.7), body shape (42; low but consistent with a small individual), and midtail scales (10) (Bocage 1886). The presence of three supralabials sets it apart, but it is possible that it represents a derived or arberrant condition within the genus. Also, the locality (Sudan) is consistent with being a member of *Myriopholis*. McDiarmid *et al.* (1999) recognized "*L.*" *hamulirostris* as a distinct species but we follow Hahn & Wallach (1998) in placing that name in the synonymy of *Myriopholis macrorhyncha*. Rösler & Wranik (2006) discussed the four species isolated on Socotra Island: *Myriopholis wilsoni*, *M. filiformis*, *M. macrura*, and *M.* sp. They are provisionally assigned to *Myriopholis*, although their isolation on this Gondwana fragment may indicate deeper divergence.

The lower bound (103 mm) of the maximum adult total length in *Myriopholis* corresponds to *M. tanae*, known only from adult males, which are always smaller than females among leptotyphlopids, and considerably so among species in the subfamily Leptotyphlopinae (Hedges 2008). Also, the single known specimens of *M. yemenicus* (91 mm, total length) and *M. dissimilis* (104 mm, total length) are not known to be adults. Aside from these three species, the next smallest species of *Myriopholis* is *M. albiventer* (128 mm maximum adult total length).

FIGURE 10. Representatives of the snake Family Leptotyphlopidae from the Old World (continued). (A) *Namibiana labialis* (Namibia); photograph by Johan Marais. (B) *Namibiana occidentalis* (Namibia, 5 km W Sesfontein); photograph by William R. Branch.

Tribe Leptotyphlopini, New Tribe

Type genus. *Leptotyphlops* Fitzinger, 1843: 24.

Diagnosis. Members of this tribe are distinguished from the other tribes of the Subfamily Leptotyphlopinae in having a brown or pale brown (rather than white) venter. Also they are distinguished from the Tribe Myriopholini by having few middorsal scales, on average (171–387 versus 165–558), and from the Tribe Epacrophini by having a small or absent (rather than moderate) first supralabial scale (Table 2). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3) and 100% BP and 100% PP for the nine-gene tree (Fig. 4).

Content. Two genera and 27 species (Table 1).

Distribution. The tribe is distributed throughout South Africa, extending as far north as the Democratic Republic of the Congo in the west and Somalia in the east; including Pemba Island (Tanzania) and the Bazaruto archipelago off of Mozambique.

Remarks. This tribe comprises the former *nigricans*, *rostratus*, and *scutifrons* groups of "*Leptotyphlops*," most recently defined (Broadley & Broadley 1999; Broadley & Wallach 2007) by the fusion of the rostral and frontal scales as found in the *scutifrons* and *rostratus* groups (unfused in the *nigricans* Group and in other leptotyphlopids). However, the molecular phylogeny (Fig. 3) shows that the *nigricans* Group (here represented by *L. kafubi* and *L. nigricans*) is polyphyletic or paraphyletic with respect to the *scutifrons* Group, thus indicating that the fused state evolved more than one time, or evolved once and reverted to the unfused state in some species. For this reason we do not recognize species groups but instead recognize one genus (*Leptotyphlops*) for the combined members of the former *nigricans* and *scutifrons* species Groups and a second genus (described below) for the former members of the *rostratus* Group.

Genus *Leptotyphlops* Fitzinger, 1843

Glauconia Gray, 1845: 139. Type species: *Typhlops nigricans* Schlegel, 1839, by monotypy.
Type species. *Typhlops nigricans* Schlegel, 1839, by original designation.

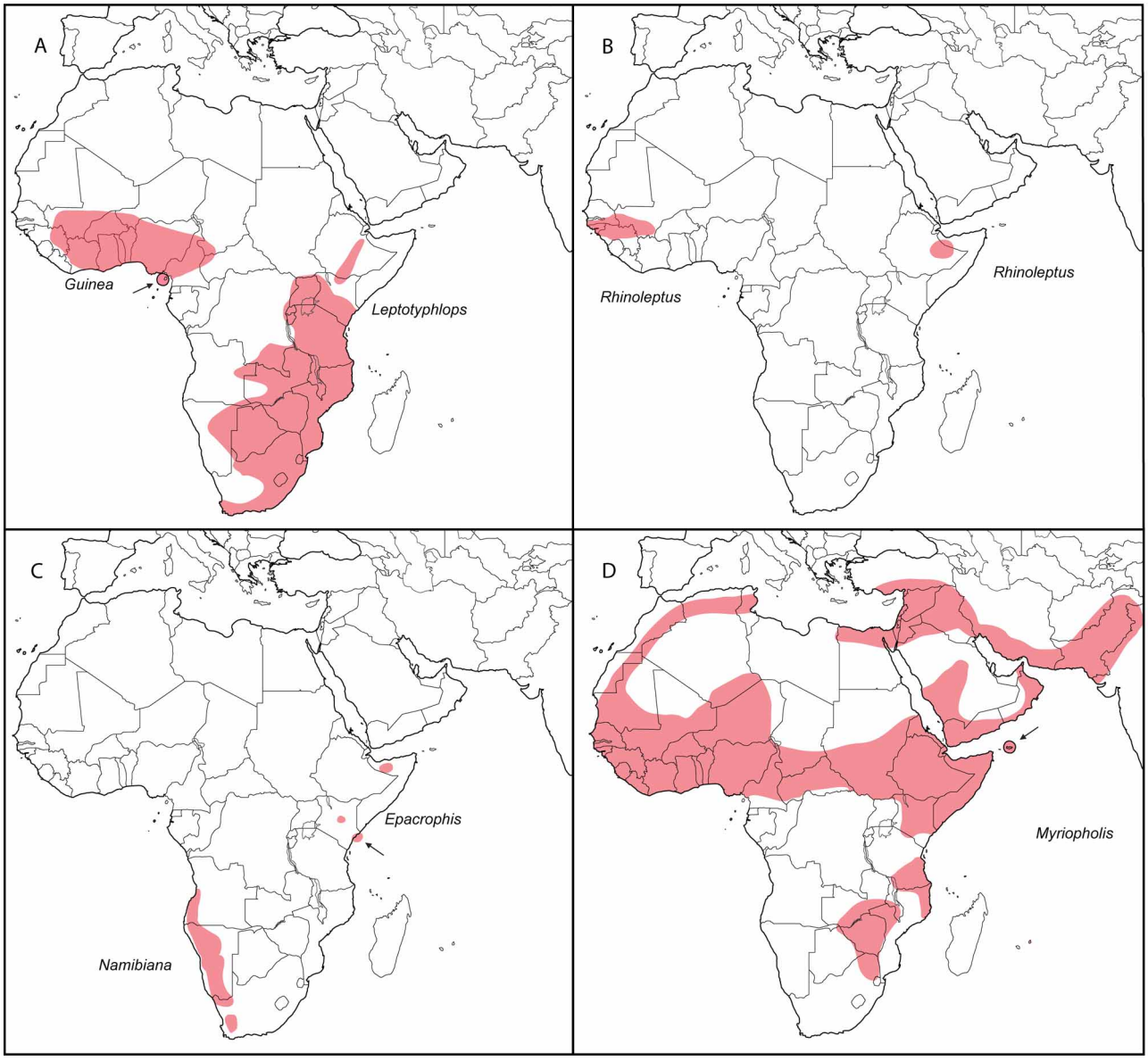


FIGURE 11. Distributions of genera of leptotyphlopid snakes in the Old World. (A) *Guinea* and *Leptotyphlops*. (B) *Rhinoleptus*. (C) *Epacrophis* and *Namibiana*. (D) *Myriopholis*.

Diagnosis. Species of *Leptotyphlops* have 14 midbody scale rows, 10–12 midtail scale rows, 171–322 middorsal scale rows, 18–44 subcaudals, two supralabials, a small anterior supralabial (moderate in *L. howelli*), 126–292 mm maximum adult total length, a body shape of 36–106 (total length/width), a relative tail length of 5.1–13.7 %, a tail shape of 3.4–9.2, no striped pattern, and usually a dark brown or brown dorsum and venter (Table 2). Members of *Leptotyphlops* can be distinguished from the other genus in the Tribe Leptotyphlopini (described below) by having a heart-shaped or subtriangular (rather than semilunate) cloacal shield, a lower number (on average) of middorsal scales (171–322 versus 241–387), and a less attenuate body shape (36–106 versus 45–142). The support for this group was 100% BP and 100% PP for the four-gene tree (Fig. 3) and 100% BP and 100% PP for the nine-gene tree (Fig. 4).

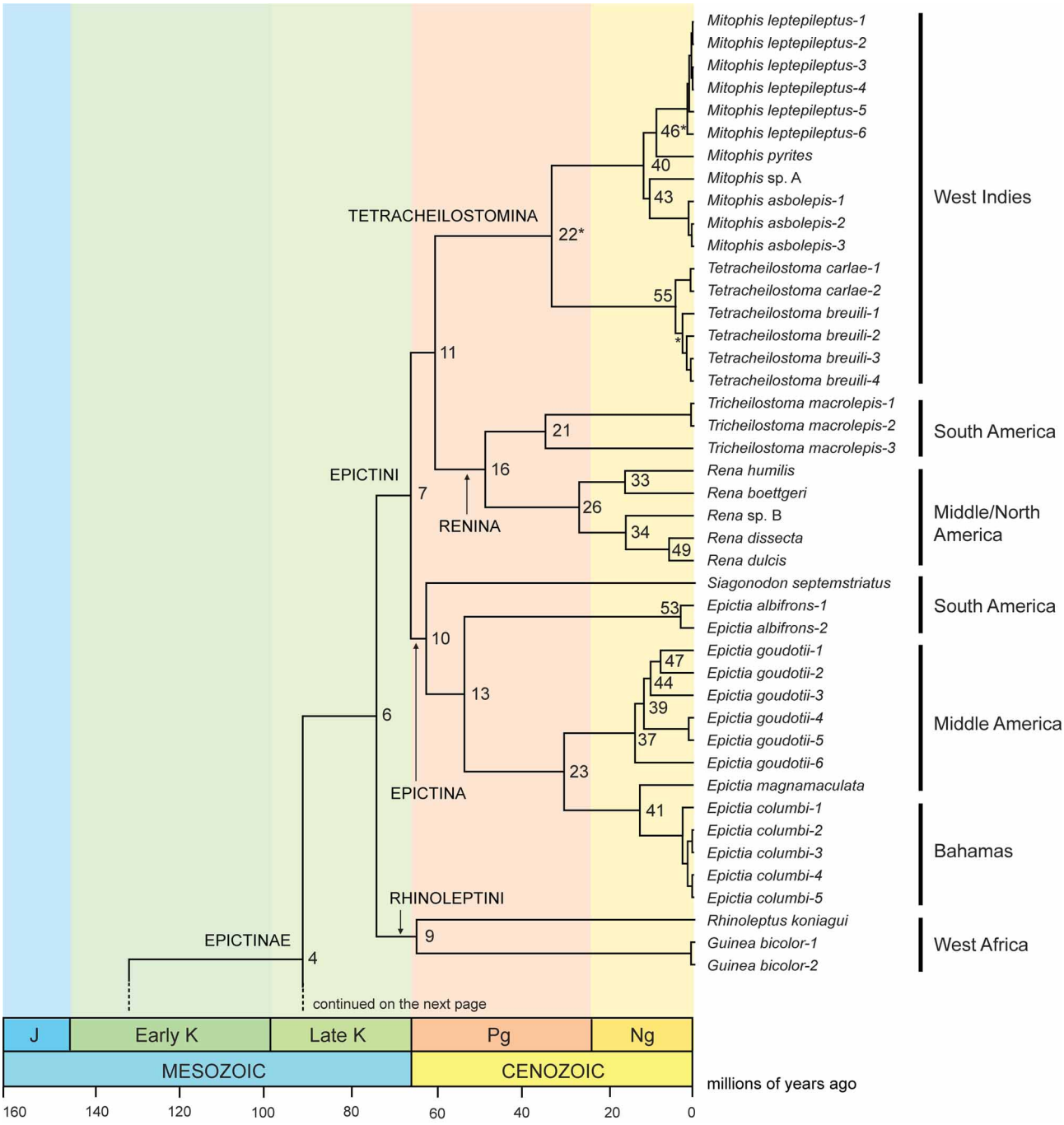
Content. Twenty-two species (Table 1; Fig. 9).

Distribution. *Leptotyphlops* is distributed throughout South Africa, extending as far north as the Democratic Republic of the Congo in the west and Somalia in the east, including Pemba Island off Tanzania and the Bazaruto archipelago off of Mozambique (Fig. 11).

Etymology. The generic name is masculine and derived from the Greek adjective *leptos* (thin) and Greek noun *typhlops* (blind), in allusion to the attenuate body shape and reduced vision of these snakes.

Remarks. This genus comprises the former *nigricans* and *scutifrons* groups of *Leptotyphlops*, most recently defined by Broadley and Wallach (2007). See "Remarks" above under the Subfamily Leptotyphlopinae and Tribe Leptotyphlopini regarding diagnostic characters used in the past for these species groups, and the reason for abandoning them.

We sampled nine of the 22 described species in the genus as recognized here. Among these, three deeply-branching clades are evident: Central Africa (*Leptotyphlops kafubi*), East Africa (*L. merkeri*, *L. nigroterminus*, and *L. pitmani*), and South Africa (all other species). The geographic concordance of these phylogenetic groups suggests that other species from the three regions will join the respective groups when sampled. However, they may not, and there is not yet clear morphological support for these three clades. Thus we refrain from recognizing species groups within *Leptotyphlops* until additional species are sampled genetically. *Leptotyphlops merkeri* and *L. pitmani* were most recently treated as northern races of *L. scutifrons*



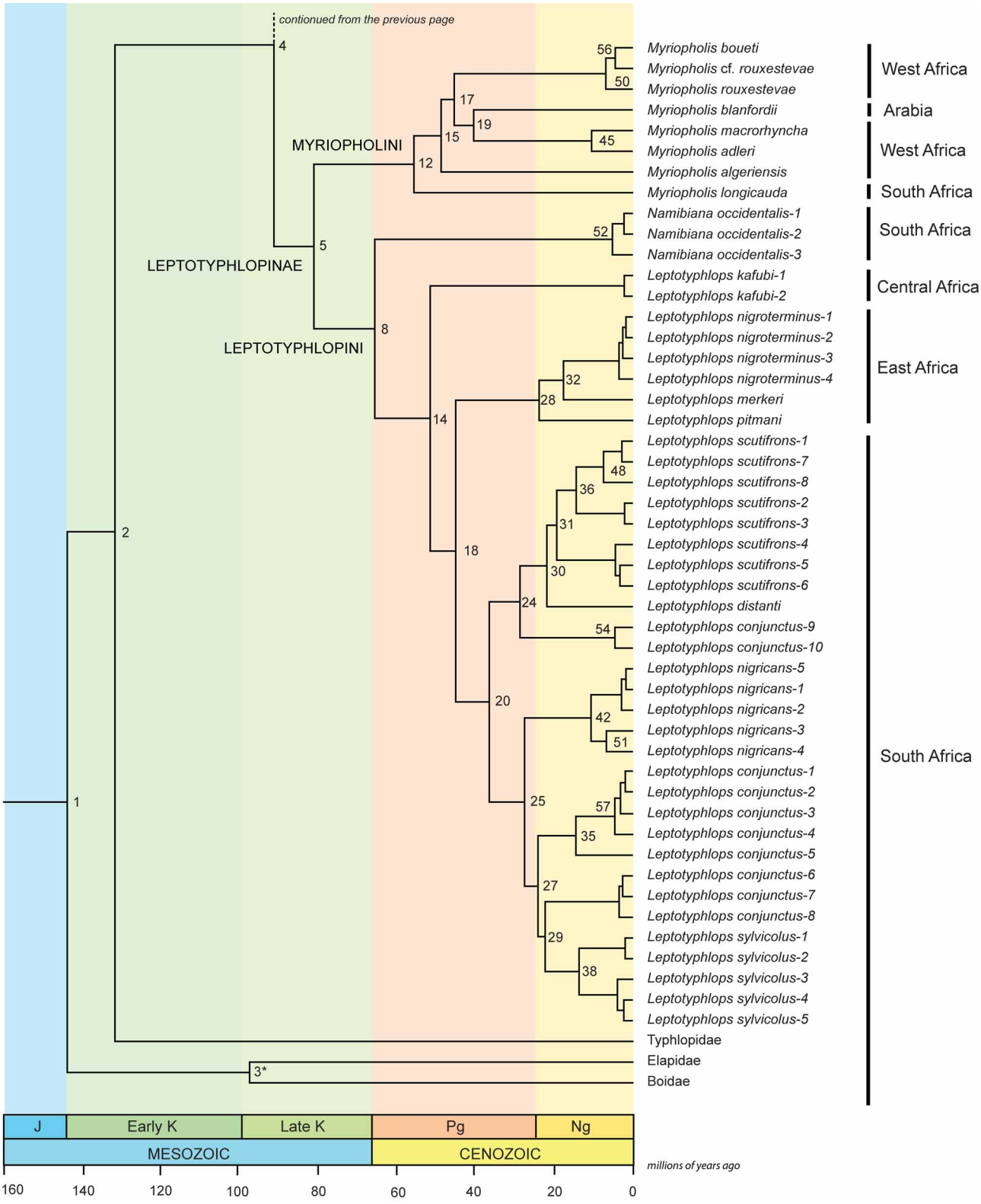


FIGURE 12. A timetree of the Family Leptotyphlopidae. Divergence times and credibility/confidence intervals are shown in Table 3. Ng=Neogene; Pg=Paleogene; J=Jurassic; and K=Cretaceous. The taxonomy in this tree reflects the new classification proposed here and detailed in Table 1; only species and higher taxa sampled with molecular data are shown here.

(Broadley & Wallach 2007), whilst *L. kafubi* was included in the *nigricans* Group and *L. nigroterminus* in the *scutifrons* Group (Broadley & Wallach 2007). None of these arrangements are supported by molecular data. The relationships between the deeply divergent *L. kafubi* and other East African leptotyphlopids previously synonymized or associated with South Africa *L. nigricans*—i.e. *L. emini, L. howelli, L. pembae, L. macrops, L. monticolus, L. mbanjensis, L. keniensis,* and *L. aethiopicus* (Broadley & Wallach 2007)— requires further study. The species *L. pungwensis* was not included in the size range for total length because the single known specimen (90 mm) is a juvenile.

An additional complication is the large sequence divergence observed among samples assigned to the same species, such as *L. conjunctus, L. nigricans, L. scutifrons,* and *L. sylvicolus* (Fig. 3). Based on levels of sequence divergence among other valid species in the phylogeny, at least 12 unrecognized species would appear to be present among samples assigned to those four species alone. The fact that one species (*L. conjunctus*) is polyphyletic (Fig. 3) further supports the presence of cryptic species. While we accept that *L. incognitus* is a valid species (Broadley & Broadley 1999), we lack genetic material from the type locality (Umtali, Zimbabwe) and are therefore unable at this time to correctly assign any of our material of *L. conjunctus* or *L. scutifrons* to this taxon. This problem requires further study utilizing additional morphological and molecular data, especially from type localities (Branch and Hedges in prep.); we suggest that each of these species be referred to as a "complex."

Genus *Namibiana* Hedges, Adalsteinsson, & Branch, New Genus

Type species. *Leptotyphlops occidentalis* FitzSimons, 1962: 239.

Diagnosis. Species of *Namibiana* have 14 midbody scale rows, 10–12 midtail scale rows, 241–387 middorsal scale rows, 12–41 subcaudals, 1–2 supralabials, anterior supralabial absent or small scale present, 192–322 mm maximum adult total length, a body shape of 45–142 (total length/width), a relative tail length of 4.1–10.8 %, a tail shape of 3.8–7.8, no striped pattern, and usually a brown dorsum and pale brown venter (Table 2). Members of *Namibiana* can be distinguished from the other genus in the Tribe Leptotyphlopini (*Leptotyphlops*) by having a semilunate (rather than heart-shaped or subtriangular) cloacal shield (except *N. gracilior*), a higher number (on average) of middorsal scales (241–387 versus 171–322), and a more attenuate body shape (ratio of total length divided by width at midbody, 45–142 versus 36–106). *Namibiana occidentalis*, reaching a total length of 322 mm (Bauer 1988), is the largest member of the Leptotyphlopinae. Only one species was included in the molecular phylogenetic analyses (Figs. 3–4).

Content. Five species (Table 1; Fig. 10).

Distribution. The genus is distributed in Southwest Africa, including South Africa, Namibia, and Angola (Fig. 11).

Etymology. The generic name is a feminine noun derived from the name (*Namib*) given to that region of southwest Africa by the indigenous people (the Nama), used in allusion to the distribution of species in this genus.

Remarks. This genus comprises the former *rostratus* Group of "*Leptotyphlops*," most recently defined by Broadley and Wallach (2007). See "Remarks" above under the Subfamily Leptotyphlopinae and Tribe Leptotyphlopini regarding diagnostic characters used for species groups.

Timetree of leptotyphlopid snakes. The results of time estimation analyses using the two rttm values, 159.9 Ma and 102.3 Ma, were similar, with point estimates for most nodes varying by less than two percent. For this reason, we averaged the times and credibility bounds, using the two rttm values, for each node. Additionally, corresponding time estimates from both data sets were similar, with most varying by < 5%, and therefore they were averaged as well. Only the time tree from the mitochondrial RNA-gene data set is shown (Fig. 12), but many divergence time estimates in Table 3 represent the average of divergence times estimated from that data set and the RNA+nuclear gene data set (denoted by bold node numbers).

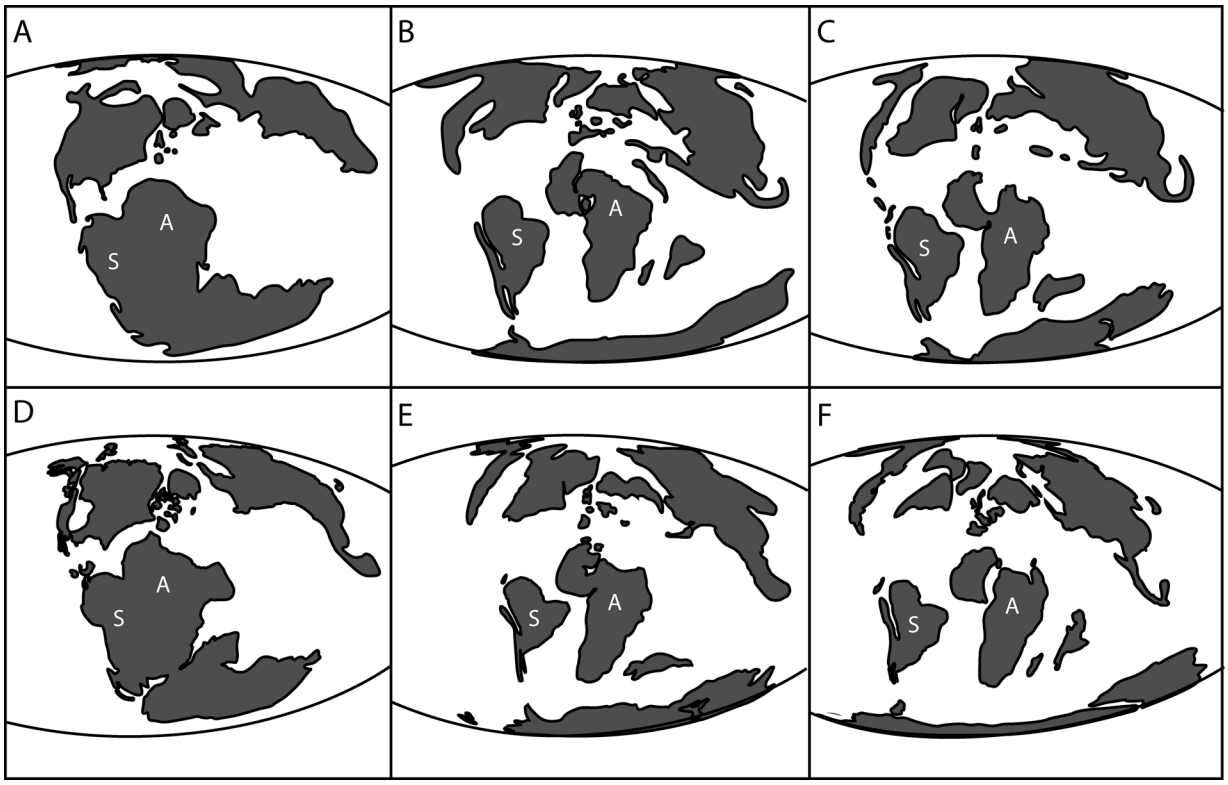


FIGURE 13. The position of continents at three periods in Earth history, based on two models. The Scotese (2009) model: (A) Late Jurassic (152 Ma), (B) mid-Cretaceous (94 Ma), (C) Mesozoic-Cenozoic boundary (66 Ma). The Smith *et al.* (1994) model: (D) Late Jurassic (153 Ma), (E) mid-Cretaceous (95 Ma), (F) Late Cretaceous (70 Ma). S=South America, A=Africa.

Leptotyphlopidae diverged from Typhlopidae in the early Cretaceous (~139 Ma; 165–119 Ma, Bayesian credibility interval). A slightly older divergence (151.9 Ma; 163–137 Ma) was found in a recent study (Vidal *et al.* 2009) using nine nuclear genes and a larger number (eight versus two here) of calibration points. The two subfamilies, Epictinae and Leptotyphlopinae, diverged from one another 92 Ma (113–75 Ma). In both subfamilies, divergences among the tribes occurred in the Late Cretaceous (100–67 Ma) whereas divergences among the subtribes and genera occurred in the Paleogene (67–23 Ma).

Divergences among morphologically distinct and previously recognized species were as recent as 3.8 Ma (*Myriopholis boueti* and *M. rouxestevae*), and 3.1 Ma (*Tetracheilostoma breuili* and *T. carlae*). Divergence times among individuals from the same population (e.g., in *Epictia columbi*, *Mitophis asbolepis*, *M. leptepileptus*, and *Tetracheilostoma breuili*), and among populations of some species (e.g., *Guinea bicolor* and two populations of *Epictia goudotii*) were so low (< 1 Ma) as to be not measurable with precision. In contrast, divergences among other populations were deeper: *Epictia goudotii* (16.3–9.2 Ma), *Leptotyphlops conjunctus* (28.4–18.1 Ma), *Leptotyphlops nigricans* (14.1–7.4 Ma), *Leptotyphlops scutifrons* (23.1–8.1 Ma), *Leptotyphlops sylvicolus* (17.5 Ma), and *Namibiana occidentalis* (6.5 Ma). Using the divergence of *T. breuili* and *T. carlae* (3.1 Ma) for comparison, as many as 18 unrecognized species are present in our limited genetic data set alone. However, determining the actual number of species present, and assigning names, will necessarily require study of specimens from type localities and other relevant material.

The separate analyses that excluded the 94 Ma fossil calibration resulted in time estimates (as above, averaging estimates from the mitochondrial RNA gene data set and the RNA + nuclear gene data set), for the two key nodes, that were entirely in the Cretaceous and similar to those that included that calibration point. As described above in the Methods, estimates were obtained using three alternate calibrations for the typhlopid/leptotyphlopid divergence: 163, 158, and 137 Ma. The resulting time estimates for the divergence of Epictinae

and Leptotyphlopinae were 106.8 Ma (124–92 Ma), 104.3 Ma (121–90 Ma), and 92.9 Ma (108–81 Ma), respectively. The time estimates for the divergence of Epictini and Rhinoleptini were 88.2 Ma (105–74 Ma), 86.4 Ma (103–73 Ma), and 77.7 Ma (92–66 Ma), respectively. These were similar, but slightly older than, estimates we obtained for those two nodes using the 94 Ma calibration: 92 Ma (113–75 Ma) and 78 Ma (98–63 Ma), respectively (Table 3).

TABLE 3. Divergence times (Ma) and their Bayesian credibility intervals (CI) among leptotyphlopid snakes based on the three-gene analysis (12S rRNA, tRNA-Valine, and 16S rRNA). Tree nodes refer to those numbered in Fig.12. Nodes in bold are those where time estimates and 95% credibility interval values represent averages of analyses using the three-gene and nine-gene data sets (see text).

Node	Time	CI	Node	Time	CI
1	148.4	174–129	30	26.0	49–15
2	139.4	165–119	31	23.1	45–13
3	98.6	111–94	32	20.8	40–11
4	92.3	113–75	33	17.3	29–11
5	81.4	102–64	34	16.9	28–11
6	78.1	98–63	35	18.1	38–9.2
7	69.1	91–54	36	17.6	37–9.1
8	63.2	83–48	37	16.3	32–9.1
9	69.5	90–54	38	17.5	38–8.7
10	64.5	82–51	39	13.7	27–7.6
11	62.8	82–49	40	12.7	16–10
12	53.2	72–40	41	13.6	31–6.5
13	53.6	70–41	42	14.1	34–6.4
14	46.8	66–34	43	10.6	14–7.9
15	46.7	65–34	44	11.8	23–6.6
16	50.4	67–38	45	8.7	16–5.0
17	44.1	62–32	46	9.1	10–7.3
18	40.8	59–29	47	9.2	18–4.9
19	39.4	56–28	48	8.1	22–3.4
20	33.5	51–23	49	6.4	12–3.4
21	36.4	52–26	50	4.8	12–3.2
22	33.9	37–28	51	7.4	21–2.9
23	33.7	54–22	52	6.5	24–2.1
24	33.2	58–20	53	4.9	17–1.6
25	24.6	40–16	54	4.5	15–1.6
26	28.1	42–19	55	3.1	5.4–1.6
27	28.4	52–17	56	3.8	10.9–1.6
28	27.7	51–16	57	3.9	14.0–1.0
29	26.5	50–15			

Discussion

Phylogenetic relationships within the Leptotyphlopidae. Wallach's (1998) analysis of morphological data for species groups resulted in a close relationship of the former *scutifrons* and *nigricans* groups, which was supported here. However, there are few other points of agreement in the two studies. Wallach found a monophyletic "*Leptotyphlops*," whereas we found *Rhinoleptus* to be nested within "*Leptotyphlops*." Wallach (1998) found that the New World taxa were not monophyletic whereas we found them to be monophyletic. Wallach (1998) found that the *bicolor* Group was part of a monophyletic Old World Clade (excluding *Rhinoleptus* and "*L.*" *parkeri*) whereas we found *bicolor* instead to be the closest relative of *Rhinoleptus*. Also, the relationships of species groups differed in the two analyses. The reason for the differences is unclear, although it may be attributed to a lack of higher-level phylogenetic signal in the visceral anatomy traits which otherwise have performed well in species-level identifications (Broadley & Wallach 2007; Wallach 1998). Despite this discordance in one suite of morphological traits (visceral anatomy), our molecular phylogenies (Fig. 3) showed considerable agreement with classical morphological characters used to construct species groups, such as scalation, body proportions, and coloration (Table 2). For example, the tail proportion and subcaudal scale count differences between the two subfamilies (Fig. 5), albeit overlapping, are remarkable in that they agree even in the placement of the African genera *Rhinoleptus* and *Guinea* in the otherwise New World Subfamily Epictinae. Although it is likely that some species not sampled genetically are misplaced in our classification, we expect that most revisions in the future will likely involve clarifying relationships of species within genera, and defining new species groups and new genera as many new taxa are described.

Biogeography. Snakes probably arose on Gondwana, considering that scolecophidians have a Gondwanan distribution and the early history of alethinophidians has been tied to West Gondwana (Vidal *et al.* 2007; Vidal *et al.* 2009). However, the relationships of the three families of scolecophidians are poorly known, and the presumed close relationship of typhlopids and anomalepidids has not yet been confirmed with molecular evidence (Vidal *et al.* 2009; Wiens *et al.* 2008), complicating biogeographic inferences.

The virtual absence of a fossil record for the Family Leptotyphlopidae eliminates that otherwise useful source of information on biogeographic history. Based on its current distribution, the family appears to have evolved on West Gondwana (South America and Africa) subsequent to the separation of that land mass from East Gondwana (India, Madagascar, Australia, and Antarctica) during the Jurassic and Early Cretaceous (~160–120 Ma) (Ali & Aitchison 2008; Scotese 2009). It is possible, but far from substantiated, that typhlopids occupied East Gondwana and that their divergence from leptotyphlopids was this vicariant event. The time estimates for the divergence of typhlopids and leptotyphlopids, noted above (~150–140 Ma), add support to that scenario. Such a model infers later dispersal of typhlopids to most other continents during the Late Cretaceous and/or Cenozoic. Anomalepidids may have arisen on West Gondwana where they are now located in South America. Unfortunately the earliest divergence time estimate among living lineages of leptotyphlopids, 92 Ma (113–75 Ma) (Table 3), occurred after the breakup of West Gondwana, and therefore there is no evidence recorded of the early history of this family lineage (the first 40–50 million years) which would assist in reconstructing its biogeographic history.

The breakup of West Gondwana began around 133 Ma (Ogg *et al.* 2004) and continued until South America and Africa were completely separated (Fig. 13). The time of this complete separation has been estimated by a diversity of authorities to be ~105–100 Ma (Ogg *et al.* 2004; Pitman III *et al.* 1993; Scotese 2009; Smith *et al.* 1994), although one study (Nishihara *et al.* 2009) proposed an earlier date of 120 Ma. The molecular time estimate for the first major split within Leptotyphlopidae, between Epictinae and Leptotyphlopinae, was 92 Ma (113–75 Ma), which is younger but statistically indistinguishable from the geologic separation of the continents. This raises the possibility that the subfamilial divergence was caused by the separation of South America and Africa. Other groups of vertebrates that have been timed with molecular clocks and thought to have been similarly affected by this continental breakup event are placental mammals (Hedges *et al.* 1996; Murphy *et al.* 2007), alethinophidian snakes (Vidal *et al.* 2007; Vidal *et al.* 2009), and lungfishes (Heinicke *et al.* 2009). However, for leptotyphlopid snakes it would require a subsequent dispersal

from South America to Africa leading to the ancestor of Rhinoleptini (*Rhinoleptus* + *Guinea*). The molecular time estimate for that dispersal is 78 Ma (98–63 Ma).

Alternatively, the same relationships and divergence times could be explained by an "Early Dispersal" scenario involving a single transatlantic dispersal of the ancestor of Epictinae from Africa to South America at 78 Ma (98–63 Ma). Besides being simpler, this second scenario also is consistent with ocean current flow, which would have been more likely to facilitate an east-to-west dispersal than the reverse. East-to-west dispersal has been indicated for all other groups of terrestrial vertebrates thought to have dispersed across the Atlantic, including primates (Kumar & Hedges 1998), hystricognath rodents (Honeycutt 2009), bats (Eick *et al*. 2005), geckos (Carranza *et al*. 2000; Weiss & Hedges 2007), skinks (Whiting *et al*. 2006), and amphisbaenians (Vidal *et al*. 2008). If leptotyphlopids dispersed in this manner, it would be the earliest proposed transatlantic dispersal, occurring at a time when the two continents were much closer together. The existence of leptotyphlopids on islands that were never connected to continents (e.g., *Epictia columbi* in the Bahamas, the genus *Mitophis* on Hispaniola, the genus *Tetracheilostoma* in the Lesser Antilles) indicates that they are capable of dispersal over ocean waters, perhaps on rafts of vegetation or volcanic pumice, or within floating logs. Regardless of which scenario occurred (Vicariance or Early Dispersal), the relationships and divergence times (Figs, 3–4, 12) reveal that the breakup of South America and Africa had a great influence on the evolution of leptotyphlopid snakes, allowing two major lineages (Epictinae and Leptotyphlopinae) to evolve in isolation for at least 80 Ma.

If the Early Dispersal model is correct, the last common ancestor of living leptotyphlopid snakes would have lived in Africa ~92 Ma, soon after the geologic breakup with South America (Figs. 12–13). (According to the Vicariance model, that ancestor would have lived on West Gondwana.) Because the last common ancestor of Rhinoleptini lived in West Africa and the common ancestor of Leptotyphlopinae likely lived in South Africa (the deepest-branching lineages sampled of Myriopholini and Leptotyphlopini are South African, or South and East African), the subfamilial divergence may have been a vicariant event: the isolation of West Africa from South and East Africa. This was a major division that has been recorded in reconstructions of the paleogeographic history of Africa, and was in large part affected by high sea levels in the mid-Cretaceous (Ali & Aitchison 2008; Cox & Moore 2005; Hallam 1994; Nishihara *et al*. 2009; Reyment & Dingle 1987; Scotese 2009; Smith *et al*. 1994). At the time of the transatlantic dispersal (~78 Ma) of the common ancestor of Epictini and Rhinoleptini, West Africa still would have been isolated, or nearly isolated, from southern and eastern Africa based on either the Smith *et al*. or Scotese models (Fig. 13) and it would have been the closest portion of Africa to South America (as it is today). The only other Cretaceous divergence separated the Myriopholini from the Leptotyphlopini, ~84 Ma (109–64 Ma). Presumably that split occurred in South Africa based on the distribution of the deepest-branching members of both tribes.

Further evolution of leptotyphlopids in the Old World began with early divergences in the late Cretaceous 69–68 Ma (CI: 96–49 Ma) leading to the origin of the two genera of Leptotyphlopini and the two genera of Rhinoleptini (Fig. 12). The timetree indicates a deep structure within *Leptotyphlops*, showing divergences throughout the Cenozoic. Undoubtedly, the number of known species in this genus (Table 1) is a gross underestimate. Within the other large genus, *Myriopholis*, the deepest-branching species sampled was *M. longicauda* from South and East Africa. Morphological data further support its position deep in the tree (Broadley & Wallach 2007). However, all other species occur in East and West Africa, Arabia, and Southwest Asia. Assuming the group originated in South (or East) Africa, its presence in these other regions would have happened subsequent to the divergence of *M. longicauda* and other species of *Myriopholis*, 60 Ma (84–42 Ma). The divergence of *M. blanfordii* (endemic to Arabia and Southwest Africa) from African species 44 Ma (67–29 Ma) raises the possibility of an early dispersal out of Africa. However, more Old World species must be sampled genetically before these tentative conclusions can be substantiated. Socotra is a neglected Gondwanan fragment of the Afro-Arabian plate that became isolated during Eocene-Oligocene (41–31 Ma) rifting in the Red Sea and Gulf of Aden region. The endemic Socotran chameleon (*Chamaeleo monachus*) is a deeply-branching species within the *Chamaeleo chamaeleon* complex, and tectonic events associated with the formation of Socotra are believed to have played a role in the evolution of the complex (Macey *et al*. 2008).

Whether similar vicariance played a role in cladogenesis of the endemic Socotran leptotyphlopids (*M. filiformis*, *M. macrura*, and *M. wilsoni*) is unknown.

The evolution of leptotyphlopids in the New World began with early divergences in the late Cretaceous and early Cenozoic 69–34 Ma (CI: 91–28 Ma) leading to the origin of the three subtribes and six genera of Epictinae (Fig. 12). A clustering of divergences near the Mesozoic-Cenozoic boundary (66 Ma) also is seen in molecular clock analyses of other groups (Delsuc *et al.* 2004; Hedges & Vidal 2009; Nilsson *et al.* 2003; Pereira & Baker 2008; Roelants *et al.* 2007) and might be related to ecological changes following the asteroid impact in that region (Neotropics) and subsequent mass extinction event. Without a larger number of species sampled it is difficult to reconstruct the biogeographic history of this subfamily except to note some general patterns. One of interest is that divergences among species in southern North America and Middle America occurred as early as 34 Ma (54–22 Ma) in Epictina and 28 Ma (42–19 Ma) in Renina. This indicates that leptotyphlopids dispersed (likely across ocean waters) northward from South America to those land areas prior to the emergence of the Isthmus of Panama. Such dispersal would have been facilitated by ocean currents moving westward across the north coast of South America in the general direction of Middle America and southern North America, and possibly facilitated ("island-hopping") by the emergence of some proto-Antillean islands (Hedges 2001; 2006; Iturralde-Vinent & MacPhee 1999).

The West Indian subtribe Tetracheilostomina diverged from its closest relative 63 Ma (CI: 49–82 Ma). None of the West Indian islands was permanently established then (Iturralde-Vinent & MacPhee 1999), so this speciation event probably occurred on the mainland, followed by a single dispersal to the West Indies prior to the first intra-Antillean split at 34 Ma (37–28 Ma) (Fig. 12). The Bahamian species *Epictia columbi* arose by dispersal from Middle America subsequent to 14 Ma (31–7 Ma). This would have been facilitated by ocean currents which flow in a northerly direction around western Cuba, past the southern tip of Florida, to the Bahamas (Hedges 2001; 2006; Iturralde-Vinent & MacPhee 1999).

Conservation. Tropical forest habitat is declining nearly everywhere, and the most threatened species are often those that have small distributions in areas of declining habitat (Mittermeier *et al.* 2005). For these reasons, the discovery here that many species of these fossorial snakes are unrecognized is significant for conservation. The significance derives from the fact that most species of leptotyphlopids are allopatric (Broadley & Broadley 1999; Broadley & Wallach 2007), and thus when a single wide-ranging species (e.g., *Epictia goudotii*, *Leptotyphlops scutifrons*) is found to be a complex of multiple species, the ranges of each species is invariably much smaller than the original composite distribution. For example, until last year, the species *Tetracheilostoma bilineatum* was thought to occur on three islands in the Lesser Antilles: Martinique, Saint Lucia, and Barbados. With the discovery that populations on each island constitute separate endemic species (Hedges 2008), the rarity of the Barbados populations (only five specimens of *T. carlae* are known in museums) takes on new meaning. Similarly, *Leptotyphlops sylvicolus* is currently considered to occupy a number of isolated, heavily-impacted coastal forests in the KwaZulu-Transkei region, South Africa (Broadley & Broadley 1999). However, our demonstration of deep genetic divergence within this species complex indicates the presence of a number of undescribed species that will almost certainly have more restricted ranges and be of significant conservation concern. Thus a greater precision in the taxonomy and distribution of the organisms confers (at least in this case) a greater priority for conservation.

Unfortunately, taxonomic revisions at the species level, such as in Hedges' (2008) study of Antillean snakes, require both genetic sampling and detailed and labor-intensive comparison of museum specimens, which may take years to accomplish in any group of organisms, especially one such as leptotyphlopid snakes which are studied by a very small number of researchers. In particular, comparing unnamed with named taxa is one of the most time-consuming tasks of a systematist. Fortunately, higher-level taxonomic revisions can greatly reduce the number of comparisons needed to diagnose species (by defining smaller monophyletic groups). Therefore, we anticipate that the higher-level taxonomic revisions proposed here, and the demonstration of hidden diversity within certain wide-ranging species, will facilitate the much needed species revisions so critical for conservation efforts.

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Appendix 1

List of taxa used for this study including museum catalog number, geographic origin, and DNA sequence accession numbers. In cases where museum catalog number is not known, tissue catalog number is indicated. Abbreviations are: AMB (Aaron M. Bauer, Villanova University, USA; vouchers deposited in CAS and MCZ), AMNH (American Museum of Natural History, USA), CAS (California Academy of Sciences, USA), ENEPI (Escuela Nacional de Estudios Profesionales Iztacala, DF, Mexico), LSUMZ (Louisiana State University, Museum of Zoology, USA), MB and MBUR (Marius Burger, SARCA Project, South Africa; vouchers deposited in PEM), MCZF (Museum of Comparative Zoology Field Series, Harvard University, USA), MZFC (Museo de Zoologia Facultad de Ciencias, UNAM, DF, Mexico), PEM (Port Elizabeth Museum, South Africa), ROM (Royal Ontario Museum, Toronto, Canada), SBH (S. Blair Hedges, Pennsylvania State University, USA; vouchers deposited in USNM), TR (Sébastien Trape, Montpellier University, France), and USNM (National Museum of Natural History, Washington, D.C., USA). Nearly all sequences used in this study are new; they have been deposited in GenBank under accession numbers GQ468987–GQ469284. Some sequences of outgroup taxa were taken from Genbank and are so indicated below. Sequence accession numbers are listed after the locality, in the following gene order: 12SrRNA+tRNA+16SrRNA, cytochrome b, amelogenin, BDNF, C-*mos*, NT3, and RAG1 (n/a = not applicable = gene not sequenced). If only two accession numbers are listed they correspond to 12SrRNA+tRNA+16SrRNA and cytochrome b.

Epictia albifrons-1 (ROM 22487; Guyana, Baramita; GQ469224, GQ469097, GQ468997, GQ469180, GQ469065, GQ469020, GQ469043); *Epictia albifrons*-2 (ROM 20503; Guyana, Kurpukari; GQ469223, GQ469096); *Epictia columbi*-1 (USNM 576215; Bahamas, San Salvador, Little Fortune Hill, NE Corner; GQ469212, GQ469089); *Epictia columbi*-2 (Bahamas, San Salvador, Little Fortune Hill, NE Corner; GQ469211, GQ469090, GQ468995, GQ469178, GQ469063, GQ469018, GQ469041); *Epictia columbi*-3 (SBH 192979; Bahamas, San Salvador, Little Fortune Hill, NE Corner; GQ469213, GQ469091); *Epictia columbi*-4 (SBH 192980; Bahamas, San Salvador, Little Fortune Hill, NE Corner; GQ469214, GQ469092); *Epictia columbi*-5 (SBH 192981; Bahamas, San Salvador, Little Fortune Hill, NE Corner; GQ469215, GQ469093); *Epictia goudotii*-1 (UTA R-54554; Mexico, Michoacán; GQ469220, GQ469121); *Epictia*-2 (UTA R-53657; Mexico, Oaxaca; GQ469217, GQ469123); *Epictia goudotii*-3 (UTA R-57498; Mexico, Oaxaca; GQ469221, GQ469122); *Epictia goudotii*-4 (UTA R-42208; Guatemala, Huehuetenango; GQ469218, GQ469117); *Epictia goudotii*-5 (ENEPI 6752; Mexico, Oaxaca, San Isidro Manteca, 16°28'41"N, 96°3'7"W; GQ469222, GQ469124); *Epictia goudotii*-6 (UTA R-52658; Mexico, Veracruz, Municipio Catemaco, vicinity of La Victoria; GQ469219, GQ469119); *Epictia magnamaculata* (SBH 172915; Honduras, Isla de Utila; GQ469216, GQ469094); *Guinea bicolor*-1 (TR 2219; Togo, Fazao, 8°41'N, 0°46'E; GQ469234, GQ469153); *Guinea bicolor*-2 (TR 01-N; Niger, Niamey Airport, 13°31'N, 2°7'E; GQ469233, GQ469152, GQ468992, GQ469175, GQ469060, GQ469016, GQ469038); *Leptotyphlops conjunctus*-1 (PEM R17410; South Africa, KwaZulu-Natal, Mkhuze Game Reserve, Mixed Bushveld; GQ469280, GQ469159, GQ468996, GQ469179, GQ469064, GQ469019, GQ469042); *Leptotyphlops conjunctus*-2 (PEM R18157; South Africa, KwaZulu-Natal Province, Lebombo, Manyiseni region, 26°56’10”S, 31°59’58”E; GQ469279, GQ469149); *Leptotyphlops conjunctus*-3 (PEM R 5913; South Africa, KwaZulu-Natal, Lebombo Mountains; GQ469273, GQ469103, GQ469001, GQ469184, GQ469069, GQ469023, GQ469046); *Leptotyphlops conjunctus*-4 (PEM R17531; South Africa, KwaZulu-Natal, Phinda PGR; GQ469281, GQ469136); *Leptotyphlops conjunctus*-5 (PEM R17418; South Africa, KwaZulu-Natal Province, Mkhuze Game Reserve, Mixed Bushveld; GQ469277, GQ469160); *Leptotyphlops conjunctus*-6 (MBUR 00107; South Africa, Mpumalanga Province, approximately 40 km S Lydenburg; GQ469274, GQ469143); *Leptotyphlops conjunctus*-7 (PEM R18152; South Africa, Mpumalanga Province, approx 40km W Nelspruit in mountains; GQ469276, GQ469145); *Leptotyphlops conjunctus*-8 (PEM R18153; South Africa, Mpumalanga Province, approximately 40 km W Nelspruit; GQ469275, GQ469144); *Leptotyphlops conjunctus*-9 (PEM R17420; South Africa, KwaZulu-Natal Province, Mkhuze Game Reserve, Lebombo Foothills; GQ469262, GQ469161); *Leptotyphlops conjunctus*-10 (PEM R18149; South Africa, KwaZulu-Natal Province, Lebombo, Manyiseni region; GQ469261, GQ469167); *Leptotyphlops distanti* (PEM R18150; South Africa, Mpumalanga, Phalaborwa; GQ469271, GQ469162, GQ468998, GQ469181, GQ469066, GQ469021, GQ469044); *Leptotyphlops kafubi*-1 (PEM R17439; Democratic Republic of the Congo, HautKatanga Province, Kalakundi, 10°38’07.7”N, 25°55’54.9”E; GQ469253, GQ469165, GQ469000, GQ469183, GQ469068, n/a, n/a); *Leptotyphlops kafubi*-2 (PEM R17441; Democratic Republic of the Congo, HautKatanga Province, Kalakundi, 10°39'43.6"S, 25°55'35.8"E; GQ469254, GQ469166); *Leptotyphlops merkeri* (PEM R17862; Kenya, Taita Hills, Sagalla; GQ469260, GQ469164); *Leptotyphlops nigricans*-1 (PEM R 12556; South Africa, Western Cape Province, Cape Hangklip, Caledon; GQ469235, GQ469128); *Leptotyphlops nigricans*-2 (CAS 207002, South Africa, Western Cape Province, Cape Hangklip, Caledon; GQ469237, GQ469129); *Leptotyphlops nigricans*-3 (PEM R17392; South Africa, Sardinia Bay, Port Elizabeth; GQ469239, GQ469102); *Leptotyphlops nigricans*-4 (MCZF 38479; South Africa, Eastern Cape Prov., Grahamstown commonage; GQ469238, GQ469130); *Leptotyphlops nigricans*-5 (CAS 207001;

South Africa, Western Cape Province, Caledon, Cape Hangklip; GQ469236, GQ469134); *Leptotyphlops nigroterminus*-1 (PEM R17330; Tanzania, NW Serengeti, Klein's Camp Lodge area, Loliondo Game Controlled Area, 01°50'05.8"S, 35°14' 46.3"E; GQ469256, GQ469139); *Leptotyphlops nigroterminus*-2 (PEM R17348; Tanzania, NW Serengeti, Klein's Camp Lodge area, Loliondo Game Controlled Area, 01°50'05.8"S, 35°14' 46.3"E; GQ469259, GQ469142); *Leptotyphlops nigroterminus*-3 (PEM R17347; Tanzania, NW Serengeti, Klein's Camp Lodge area, Loliondo Game Controlled Area, 01°50'05.8"S, 35°14' 46.3"E; GQ469258, GQ469141); *Leptotyphlops nigroterminus*-4 (PEM R17346; Tanzania, NW Serengeti, Klein's Camp Lodge area, Loliondo Game Controlled Area, 01°50'05.8"S, 35°14' 46.3"E; GQ469257, GQ469140, GQ469005, GQ469188, GQ469073, GQ469027, GQ469050); *Leptotyphlops pitmani* (PEM R5577; Rwanda, L'Akagera National Park, between Gabiro and the Tanzanian border, 1°25'32.9"S, 30°29'31.7"E; GQ469255, GQ469163); *Leptotyphlops scutifrons*-1 (PEM R17393; South Africa, NW Province, near Dithakong, 65k NE Kuruman, 27°07'49"S, 23°59'42"E; GQ469264, GQ469135); *Leptotyphlops scutifrons*-2 (MB 393; South Africa, Limpopo Province, Blouberg; GQ469267, GQ469138); *Leptotyphlops scutifrons*-3 (MB 327; South Africa, Limpopo Province, Blouberg; GQ469266, GQ469137); *Leptotyphlops scutifrons*-4 (MCZ R184538; South Africa, Limpopo Province, 33.1 km S Kgama on gravel road to Molimolle, 24°19'58"S, 28°23'05" E; GQ469270, GQ469127); *Leptotyphlops scutifrons*-5 (MCZ R184522; South Africa, Limpopo Province, Kgama, Tshukudu Lodge area, 24°04'02"S, 28°26'16"E; GQ469268, GQ469125); *Leptotyphlops scutifrons*-6 (CAS 234220; South Africa, Limpopo Province, Farm Fancy (23°52'38"S, 27°38'49"E); GQ469269, GQ469126); *Leptotyphlops scutifrons*-7 (MB 20939; South Africa, Northern Cape Province, Fm Black Ridge, E of Langeberge, NEE of Groblershoop, near Upington, 28°50'07"S, 22°34'21"E; GQ469263, GQ469169); *Leptotyphlops scutifrons*-8 (PEM R181151; South Africa, Limpopo Province, E of Tsipise, 22°37'46"S, 30°24'42"E; GQ469265, GQ469148); *Leptotyphlops sylvicolus*-1 (PEM R17343a; South Africa, KwaZulu-Natal Province, Xilonde Transect; GQ469284, GQ469101); *Leptotyphlops sylvicolus*-2 (PEM R17343b; South Africa, KwaZulu-Natal Province, Xilonde Transect, 1 km S of Mozambique border; GQ469272, GQ469150, GQ469009, GQ469192, GQ469077, GQ469031, GQ469054); *Leptotyphlops sylvicolus*-3 (PEM R18156; South Africa, Eastern Cape Province, Matatiele Dist, Fever Village, 79 km SW Cedarville, Transkei, 30°32'08"S, 28°49'38"E; GQ469278, GQ469168); *Leptotyphlops sylvicolus*-4 (PEM R18154; South Africa, Eastern Cape Province, Matatiele Dist, Fever Village, 79 km SW Cedarville, Transkei, 30°32'08"S, 28°49'38"E; GQ469282, GQ469146); *Leptotyphlops sylvicolus*-5 (PEM R18155; South Africa, Eastern Cape Province, Matatiele Dist, Fever Village, 79 km SW Cedarville, Transkei 30°32'08"S, 28°49'38"E; GQ469283, GQ469147); *Mitophis asbolepis*-1 (SBH 160213; Dominican Republic, Barahona, Canoa, 0.3 km S, 13.5 km E; GQ469210, GQ469088, GQ468991, GQ469174, GQ469059, GQ469015, GQ469037); *Mitophis asbolepis*-2 (SBH 160212; Dominican Republic, Barahona, Canoa, 0.3 km S, 13.5 km E; GQ469209, GQ469087); *Mitophis asbolepis*-3 (SBH 160211; Dominican Republic, Barahona, 1517 Canoa, 0.3 km S, 13.5 km E; GQ469208, GQ469086); *Mitophis leptepileptus*-1 (USNM 576216; Haiti, l'Quest, Soliette, N of Fond Verrettes, along border with Dominican Republic; GQ469201, GQ469085); *Mitophis leptepileptus*-2 (USNM 576217; Haiti, l'Quest, Soliette, N of Fond Verrettes, along border with Dominican Republic; GQ469198, GQ469082); *Mitophis leptepileptus*-3 (SBH 103603; Haiti, l'Quest, Soliette, N of Fond Verrettes, along border with Dominican Republic; GQ469200, GQ469084); *Mitophis leptepileptus*-4 (USNM 576218; Haiti, l'Quest, Soliette, N of Fond Verrettes, along border with Dominican Republic; GQ469199, GQ469083); *Mitophis leptepileptus*-5 (USNM 564820; Haiti, l'Quest, Soliette, N of Fond Verrettes, along border with Dominican Republic; GQ469197, GQ469081, GQ469002, GQ469185, GQ469070, GQ469024, GQ469047); *Mitophis leptepileptus*-6 (SBH 103599; Haiti, l'Quest, Soliette, N of Fond Verrettes, along border with Dominican Republic; GQ469196, GQ469080); *Mitophis pyrites* (SBH 102591; Dominican Republic, Pedernales, 6.4 km SW of Las Mercedes; GQ469194, GQ469079, GQ468987, GQ469170 GQ469056, GQ469011, GQ469033); *Mitophis* sp. A (= "L. sp. A") (SBH 266699; Dominican Republic, Independencia, La Zurza; GQ469195 GQ469095, GQ468988, GQ469171, GQ469057, GQ469012, GQ469034); *Myriopholis adleri* (TR 7750; Senegal, Bandafassi, 12°32'N, 12°19'W; GQ469246, GQ469155, GQ468989, GQ469172, GQ469058, GQ469013, GQ469035); *Myriopholis algeriensis* (TR 115; Mauritania, Rachid, 18°48'N, 11°41'W; GQ469243, GQ469151, GQ468990, GQ469173, n/a, GQ469014, GQ469036); *Myriopholis blanfordii* (MVZ 236621; Yemen, Lahij, Bir Nasr Farm, 3 km SW Sabir; GQ469241, GQ469104, GQ468993, GQ469176, GQ469061, n/a, GQ469039); *Myriopholis boueti* (TR 3305; Mali, Bouyanga, 14°30'N, 9°39'W; GQ469248, GQ469157, GQ468994, GQ469177, GQ469062, GQ469017, GQ469040); *Myriopholis longicauda* (MCZ R184447; South Africa, Limpopo Province, near Waterport, 22°42'19"S, 29°49'40"E; GQ469244, GQ469131, GQ469003, GQ469186, GQ469071, GQ469025, GQ469048); *Myriopholis macrorhyncha* (LSUMZ H-20102; Ghana, Northern region, 2.5 km SW Buipe; GQ469245, GQ469115, GQ469004, GQ469187, GQ469072, GQ469026, GQ469049); *Myriopholis* cf. *rouxestevae* (TR 3286; Mali, Sebekourani, 12°12'N, 8°42'W; GQ469249, GQ469154); *Myriopholis rouxestevae* (TR 7760; Senegal, Ibel, 12°31'N, 12°23'W; GQ469247, GQ469156, GQ469007, GQ469190, GQ469075, GQ469029, GQ469052); *Namibiana occidentalis*-1 (PEM R11915; South Africa, Northern Cape Province, Hellskloof Gate, Richtersveldt National Park, Namaqualand, 28°15'38"S, 16°56'18"E; GQ469251, GQ469133, GQ469006, GQ469189, GQ469074, GQ469028, GQ469051); *Namibiana occidentalis*-2 (PEM R11906; South Africa, Northern Cape

Province, 3.2 km from Koebus, Richtersveldt National Park, Namaqualand, 28°25'31"S, 17°00'06"E; GQ469250, GQ469132); *Namibiana occidentalis*-3 (AMNH-AMCC 105532; Namibia; GQ469252, GQ469100); *Rena boettgeri* (MVZ 190030; Mexico, Baja California, 3.8 mi N via Mexico Hwy. 1, San Pedro; NC005961); *Rena dissectus* (LSUMZ H-9314; USA, Arizona, Chochise County, 2.2 km by road SW Portal; GQ469230, GQ469112); *Rena dulcis* (MVZ 230602; USA, Texas, Crane County, 2.4 km W of junction with Farm Road 1601; GQ469229, GQ469105, GQ468999, GQ469182, GQ469067, GQ469022, GQ469045); *Rena humilis* (ROM 45259; Mexico, Baja California Norte, Vizcaino; GQ469228, GQ469098); *Rena* sp. B (= "L. sp. B") (MZFC 17047; Mexico, Jalisco; GQ469231, GQ469120); *Rhinoleptus koniagui* (TR 7757; Senegal, Ibel; GQ469242, GQ469158, GQ469010, GQ469193, GQ469078, GQ469032, GQ469055); *Siagonodon septemstriatus* (LSUMZ H-12312; Brazil, Roraima, Fazenda Nova Esperanca, 47km W BR-174 on BR-210; GQ469232, GQ469116, GQ469008, GQ469191, GQ469076, GQ469030, GQ469053); *Tetracheilostoma breuili*-1 (USNM 564813; St. Lucia, Anse Galet, 5 m elevation, 13° 56.080'N, 61° 02.950'W; GQ469203, GQ469109); *Tetracheilostoma breuili*-2 (USNM 564812; St. Lucia, Maria Major Island, slope on N side, 60 m elevation, 13° 43.430'N, 60° 55.897'W; GQ469205, GQ469108); *Tetracheilostoma breuili*-3 (USNM 564817; St. Lucia, 1.6 km N Praslin, 40 m elevation, 13° 52.875'N, 60° 53.418'W; GQ469207, GQ469111); *Tetracheilostoma breuili*-4 (USNM 564816; St. Lucia, 1.6 km N Praslin, 40 m elevation, 13° 52.875'N, 60° 53.418'W; GQ469206, GQ469110); *Tetracheilostoma carlae*-1 (USNM 564818; Barbados, Bonwell, 280 m elevation, 13° 11.196'N, 59° 32.445'W; GQ469202, GQ469106); *Tetracheilostoma carlae*-2 (USNM 564819; Barbados, Bonwell, 280 m elevation, 13° 11.196'N, 59° 32.445'W; GQ469204, GQ469107); *Tricheilostoma macrolepis*-1 (LSUMZ H-14220; Brazil, Para, Agropecuaria Treviso LTDA, ca 101 km S and 18 km E Santarem, 3°8'47.2"S, 54°50'32.3"W; GQ469227, GQ469113); *Tricheilostoma macrolepis*-2 (LSUMZ H-14449; Brazil, Para, Agropecuaria Treviso LTDA, ca 101 km S and 18 km E Santarem, 3°8'18.6"S, 54°50'29.6"W; GQ469226, GQ469114); *Tricheilostoma macrolepis*-3 (ROM 28367; Guyana, Paramakatoi; GQ469225, GQ469099).

Non-leptotyphlopid samples (all from Genbank, except one *Ramphotyphlops braminus*): *Boa constrictor* (12S, tRNAval,16S, cytb: NC_007398; amelogenin: FJ434054; BDNF: FJ433975; C-mos: AF544676; NT3: AY988047; RAG1: AY487351); *Dendroaspis angusticeps* (amelogenin: EF144002; BDNF: FJ433988; C-mos: AF544735; NT3: FJ434089; RAG1: AY487395); *Heloderma suspectum* (12S, tRNAval,16S, cytb: NC_008776; amelogenin: FJ434034; BDNF: FJ433955; C-mos: AY487348; NT3: FJ434061; RAG1: AY487352); *Naja naja* (12S, tRNAval,16S, cytb: NC_010225); *Python regius* (12S, tRNAval,16S, cytb: NC_007399); *Python reticulatus* (amelogenin: FJ434048; BDNF: FJ433969; C-mos: AF544675; NT3: FJ434074; RAG1: AY487396); *Ramphotyphlops braminus* (UTA R-53537; Mexico, Guerrero, Carretera federal Chipancingo-Acapulco, km 35, near the turn to Acahuizotla, 948m; 12S, tRNAval,16S, cytb: GQ469240, GQ469118); *Ramphotyphlops braminus* (amelogenin: FJ434048, BDNF: FJ433959; C-mos: AF544717; NT3: FJ434065; RAG1: AY487410).

Appendix 2. Primers used in the DNA sequencing. SBH = laboratory of S. Blair Hedges; NV = Nicolas Vidal (pers. comm.).

Gene	Primer name	Sequence (5' -3')	Reference
12S	12L2	5'-AAAGCAWRGCACTGAARATGCTWAGATG-3'	SBH
12S	12L31	5'-AAAGTSTTGGTCCTRAACCT-3'	SBH
12S	12L16	5'-AAAGCATGGCACTGAAGATGCCAAGAYGG-3'	SBH
12S	12H3	5'-CTAGAGGAGCCTGTTCTYTAATCGATKKCCRCG-3'	SBH
12S	12L17	5'-CAAACTAGGATTAGATACCCTACTATGC-3'	SBH
12S	12L24	5'-CAAACTRGGATTAGATACCCYACTAT-3'	SBH
12S	12L5	5'-GATTAGATACCCCACTATGC-3'	SBH
12S	12H11	5'-CACTTTCCAGTACGCTTACCATGTTACG-3'	SBH
12S	12H40	5'-CGTAACATGGTAAGCGTACTGGAAAGTG-3'	SBH
12S	12H10	5'-AAGTCGTAACAYGGTAARYGYACYGGAARGTG-3'	SBH
12S	12H4	5'-CGYACACACCGCCCGTCACCCT-3'	SBH
12S	12L3	5'-TGARGCRCGYACACACCGCCCGTCACCCTC-3'	SBH
12S	12L7	5'-GAAGGWGGATTTAGYAGTAAA-3'	SBH
12S	12L14	5'-ACTAAWACGTCAGGTCAAGGTGYAGC-3'	SBH
12S	12L23	5'-CTATATACCGCCGTCGRAAGTTCA-3'	SBH
12S	12L13	5'-AAAGAAGAGGAAAGTCGTAACATGGTA-3'	SBH
16S	16L3	5'-AGCAAAGAYYAAMCCTYGTACCTTTTGCAT-3'	SBH
16S	16L26	5'-GTRCCGYAAGGGAMYAATGAAA-3'	SBH
16S	16H22	5'-GTAGGCCYTAAAGCAGCCAYCAAWAA-3'	SBH
16S	16H27	5'-GTRGRCCTYTAARCMGCCAMCAAAAAYA-3'	SBH
16S	16H21	5'-GTACCTHTTGCATCATGGTYYAGCDAG-3'	SBH
16S	16L44	5'-CCCGAAACCRRGTGAGCTAC-3'	SBH
16S	16L10	5'-AGTGGGCCTAAAAGCAGCCA-3'	SBH
16S	16L20	5'-TGAAAASCCWAMCGARCYTGRTGATAGCTG-3'	SBH
16S	16L16	5'-AACCCKTCTCTGTKGCAAAAGAGTGRGA-3'	SBH
16S	16H24	5'-ACGGCCGCGGTAYMCTAACCGTGCGAAGGTA-3'	SBH
16S	16H17	5'-GCWRRRGGRKATGTTTTTGGTAAACA-3'	SBH
16S	16L39	5'-CTGTTTACCAAAAACATAGCCTTTAG-3'	SBH
16S	16H1	5'-CCTACGTGATCTGAGTTCAGACCGGAG-3'	SBH
Cytb	S1L	5'-GAAAAACCGCYRTTGTWWTTCAACTA-3'	SBH
Cytb	Ltyph3L	5'-CATATATCGGACAAACTCTTGTCA-3'	SBH
Cytb	Ltyph5L	5'-GCCACMGTMATCACYAAYCT-3'	SBH
Cytb	H16064	5'-CTTTGGTTTACAAGAACAATGCTTTA-3'	SBH
Cytb	Ltyph4R	5'-GTGTTAATGTGGCGTTGTTTACTGA-3'	SBH
Cytb	Ltyph2R	5'-AGYTTGTTTGGGATKGCTCGTAGRAT-3'	SBH
Cytb	Ltyph6R	5'-AGAAYCGKGTTARDGTGGCGT-3'	SBH
Amelogenin	LAMSQ	5'-ATGGGAGGATGGATGCACCA-3'	NV
Amelogenin	LAM2N	5'-TATCCACGTTATGGCTATGAACC-3'	(Vidal & Hedges 2005)
Amelogenin	HAMSQ	5'-TGGCCATGRTTCAAGAGGYGTAT-3'	NV
BDNF	F	5'-GACCATCCTTTTCCTKACTATGGTTATTTCATACTT-3'	(Noonan & Chippindale 2006)

BDNF	R	5'-CTATCTTCCCCTTTTAATGGTCAGTGTACAAAC-3'	(Noonan & Chippindale 2006)
C-*mos*	F4	5'-AATGHACRTCCMTGYAGYAGCCCTTTGGTCTGT-3'	NV
C-*mos*	G74	5'-TGAGCATCCAAAGTCTCCAATC-3'	(Saint *et al.* 1998)
NT3	F1	5'-ATGTCCATCTTGTTTTATGTGATATTT-3'	(Townsend *et al.* 2008)
NT3	F3	5'-ATATTTCTGGCTTTTCTCTGTGGC-3'	(Noonan & Chippindale 2006)
NT3	R1	5'-ACRAGTTTRTTGTTYTCTGAAGTC-3'	(Townsend *et al.* 2008)
NT3	R4	5'-GCGTTTCATAAAAATATTGTTTGACCGG-3'	(Noonan & Chippindale 2006)
RAG-1	L2408	5'-TGCACTGTGACATTGGCAA-3'	(Vidal & Hedges 2004)
RAG-1	Ltyph2L	5'-AGAGAATTAATGGACCTTTA-3'	SBH
RAG-1	H2920	5'-GCCATTCATTTTYCGAA-3'	(Vidal & Hedges 2004)
RAG-1	Ltyph1R	5'-ATCTCCATACTGGTTTCATC-3'	SBH