Zootaxa 2067: 1–28 (2009)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Molecular phylogeny, classification, and biogeography of West Indian racer snakes of the Tribe Alsophiini (Squamata, Dipsadidae, Xenodontinae)

S. BLAIR HEDGES[1], ARNAUD COULOUX[2], & NICOLAS VIDAL[3,4]

[1]*Department of Biology, 208 Mueller Lab, Pennsylvania State University, University Park, PA 16802-5301 USA. E-mail: sbh1@psu.edu*

[2]*Genoscope. Centre National de Séquençage, 2 rue Gaston Crémieux, CP5706, 91057 Evry Cedex, France www.genoscope.fr*

[3]*UMR 7138, Département Systématique et Evolution, Muséum National d'Histoire Naturelle, CP 26, 57 rue Cuvier, 75005 Paris, France*

[4]*Corresponding author. E-mail : nvidal@mnhn.fr*

Abstract

Most West Indian snakes of the family Dipsadidae belong to the Subfamily Xenodontinae and Tribe Alsophiini. As recognized here, alsophiine snakes are exclusively West Indian and comprise 43 species distributed throughout the region. These snakes are slender and typically fast-moving (active foraging), diurnal species often called racers. For the last four decades, their classification into six genera was based on a study utilizing hemipenial and external morphology and which concluded that their biogeographic history involved multiple colonizations from the mainland. Although subsequent studies have mostly disagreed with that phylogeny and taxonomy, no major changes in the classification have been proposed until now. Here we present a DNA sequence analysis of five mitochondrial genes and one nuclear gene in 35 species and subspecies of alsophiines. Our results are more consistent with geography than previous classifications based on morphology, and support a reclassification of the species of alsophiines into seven named and three new genera: *Alsophis* Fitzinger (Lesser Antilles), *Arrhyton* Günther (Cuba), *Borikenophis* Hedges & Vidal gen. nov. (Puerto Rican Bank and nearby islands), *Caraiba* Zaher et al. (Cuba), *Cubophis* Hedges & Vidal gen. nov. (primarily Cuba but extending throughout the western Caribbean and Bahamas Bank), *Haitiophis* Hedges & Vidal gen. nov. (Hispaniola), *Hypsirhynchus* Günther (Hispaniola and Jamaica), *Ialtris* Cope (Hispaniola), *Magliophis* Zaher et al. (Puerto Rican Bank), and *Uromacer* Duméril & Bibron (Hispaniola). Several subspecies are recognized as full species. Three subtribes are recognized within the tribe Alsophiini Fitzinger: Alsophiina Fitzinger (for *Alsophis, Borikenophis, Caraiba, Cubophis, Haitiophis, Hypsirhynchus, Ialtris,* and *Magliophis*), Arrhytonina Hedges & Vidal subtribus nov. (for *Arrhyton*), and Uromacerina Hedges & Vidal subtribus nov. (for *Uromacer*). Divergence time estimates based on the molecular data indicate a relatively recent (~17–13 million years ago, Ma) origin for alsophiines. A single species apparently dispersed from South America, probably colonizing Hispaniola or Cuba and then later (13–0 Ma) there was dispersal to other islands and subsequent adaptive radiation, mostly in the Pliocene (5.3–1.8 Ma) and Pleistocene (1.8–0.01 Ma). More evidence will be needed to resolve all relationships among the genera and species groups and further details of their biogeographic history.

Key words: Alethinophidia, *Borikenophis,* Caenophidia, Colubroidea, *Cubophis,* cytochrome b, ND4, ND2, RAG2, Serpentes, 16S rRNA, 12S rRNA, West Indies

Introduction

Among snakes (~3150 species), Caenophidia or advanced snakes form a monophyletic group including the great majority (~2620 species) of extant snakes (Vidal 2002; Vidal & Hedges 2002a,b; Vidal *et al.* 2007; Uetz *et al.* 2008). The American caenophidian snake fauna comprises five families: the Viperidae and Elapidae—both displaying a front-fanged venom system—and the Natricidae, Colubridae and Dipsadidae (Vidal & Hedges 2002b; Vidal *et al.* 2007). The latter is one of the largest families of snakes (~700 species),

Accepted by D. Gower: 23 Feb. 2009; published: 8 Apr. 2009

with all living species restricted to the New World (Cadle & Greene 1993; Vidal *et al.* 2000). Dipsadidae are primarily tropical, with most occurring in Central America (Dipsadinae), South America, and the West Indies (Xenodontinae). They vary greatly in body size (10–280 cm) and in ecology. Most species feed on frogs and lizards, but some specialize on snakes, while others feed exclusively on slugs, snails, and earthworms.

The West Indian xenodontines considered here, the Tribe Alsophiini, include six currently recognized, endemic genera (*Antillophis*, *Arrhyton*, *Darlingtonia*, *Hypsirhynchus*, *Ialtris* and *Uromacer*) and most members of the more widespread genus *Alsophis*. Six species belonging to two other genera of xenodontines (*Clelia* and *Liophis*) also occur in the southern Lesser Antilles but are not part of the alsophiine radiation (Vidal *et al.* 2000). Alsophiines include 35–45 species, four of which are possibly extinct (IUCN 2008): *Alsophis antiguae* (Antigua, not including Great Bird Island, see below), *A. ater* (Jamaica), *A. melanichnus* (Hispaniola; Powell & Henderson 1998), and *A. sanctaecrucis* (St. Croix). The current generic arrangement is based largely on the work of Maglio (1970), who concluded that the West Indian species arose through multiple colonizations from the mainland. A study of hemipene variation (Zaher 1999) and several molecular studies (Crother & Hillis 1995; Crother 1999; Vidal *et al.* 2000; Hass *et al.* 2001; Pinou *et al.* 2004) have included more than five West Indian species and all have disagreed with Maglio's (1970) arrangement, although not consistently.

Crother & Hillis' (1995) DNA restriction site study examined 14 species of West Indian alsophiines and two mainland species (*Alsophis elegans* and *Farancia abacura*), analysing the presence or absence of eight DNA restriction sites. A West Indian species (*A. antillensis*) was selected as outgroup based on an allozyme analysis published later (Crother 1999) and the two mainland species were nested (not significantly) among the West Indian species in the resulting majority-rule parsimony tree. However, a strict consensus tree showed a lack of resolution of relationships concerning the position of the two mainland species. Crother's (1999) allozyme study was larger in scope, with 18 West Indian alsophiines and 24 non-West Indian species. Two methods of coding (alleles or loci as characters) were used in parsimony analyses and both resulted in non-monophyly of West Indian alsophiines, although quantitative measures of support were not presented. Aside from two small clusters of West Indian species present in both trees (*Darlingtonia* and the three species of Jamaican *Arrhyton; Uromacer frenatus* and *U. oxyrhynchus*) the two results, based on the two methods of coding, differed considerably. For example, the inclusive clade containing all West Indian species also contained six genera of mainland xenodontines in one tree and 13 genera in the other tree, in different relationships. The two trees also differed from Maglio's (1970) hypothesis of relationships. Specifically, Maglio (1970) suggested that *Darlingtonia* is close to *Arrhyton exiguum*, not the Jamaican *Arrhyton*; that mainland *Rhadinea* is closest to that entire assemblage (*Arrhyton* + *Darlingtonia*); and that *Uromacer* and *Hypsirhynchus* are close relatives. These relationships and most other species relationships proposed by Maglio (1970) were not found in either of the two trees in Crother's (1999) study.

In contrast, DNA sequence analyses (Vidal *et al.* 2000; Pinou *et al.* 2004) and albumin immunological data (Cadle 1984; Hass *et al.* 2001) have consistently supported the monophyly of West Indian alsophiine snakes, albeit without overwhelming quantitative support. Vidal *et al.*'s (2000) sequence analysis included 85 species and two mitochondrial genes and found monophyly of the 24 species included from the West Indies, but with bootstrap support values below 95%. A Bayesian analysis of 87 species also found monophyly of the seven West Indian genera included, although again with support values (posterior probabilities) below 95% (Pinou *et al.* 2004). Cadle's (1984) immunological study of the protein serum albumin found *Philodryas* to be distantly related to *Alsophis* (albumin distance of 46) and not a close relative as hypothesized by Maglio (1970) and Thomas (1997), although few West Indian species were examined. Hass *et al.*'s (2001) immunological study analysed data for 25 species of West Indian alsophiines and seven species from the mainland (genera *Dipsas, Leptodeira, Liophis, Oxyrhopus, Thamnodynastes*, and *Xenodon*). Albumin immunological distances among the West Indian species were low (0–20) whereas those between West Indian and mainland taxa were higher (21–58), supporting monophyly of the West Indian species.

Zaher (1999) examined hemipenial variation among xenodontine snakes, including many from the West Indies. Although he found no shared derived characters linking West Indian alsophiines in a monophyletic

group, his results disagreed with Maglio's (1970) interpretations of species groupings—which were based largely on hemipenial variation—and are more consistent with the molecular phylogenies (see below). For example, Zaher found (as did Vidal *et al.* 2000) that *Alsophis elegans* (South America) is not closely related to species of *Alsophis* from the West Indies and that the species of *Antillophis* on Cuba (*A. andreae*) is closer to Cuban *Alsophis* than to the Hispaniolan species of *Antillophis*. In the latter case he proposed a shared derived character for the Cuban group: an expanded papillate circular area in the lobular crotch of the hemipenes, not present in other xenodontines. In summary, Maglio's (1970) morphological basis for the original proposal of non-monophyly of West Indian alsophiines has been reinterpreted (Zaher 1999) and the immunological and DNA sequence analyses independently support monophyly of the group. Because of the evidence for monophyly of the West Indian species (Vidal *et al.* 2000) we restrict the Tribe Alsophiini to include only this West Indian radiation of the subfamily Xenodontinae.

The type species of *Alsophis* is West Indian (*A. antillensis* Schlegel) and therefore the question arises as to the generic allocation of the non-West Indian species of *Alsophis*, which include the South American species *A. elegans* and the six species occurring in the Galapagos Islands. Thomas (1997) described morphological variation in Galapagos snakes and suggested that two species (*A. slevini* and *A. steindachneri*) are close to some West Indian species (Genus *Antillophis*) and a third species (*Alsophis hoodensis*) is close to species of *Philodryas* in South America. Zaher (1999) disagreed with Thomas (1997), finding a shared derived hemipenial character—an inflated papillate ridge on the medial surface of the lobes—linking Galapagos xenodontines together in a monophyletic group with *Alsophis elegans* and *Saphenophis* Myers. Within this clade, Zaher (1999) found that *A. elegans* and the Galapagos species (i.e., the non-West Indian *Alsophis* sensu Zaher) form a nested monophyletic group based on another shared derived character, the placement of the papillate ridge far medially, "in an almost sulcate position." Furthermore, Zaher (1999) noted that the Galapagos species have "very similar hemipenes" and referred to those species as the "Galapagos radiation," but he did not describe the specific characters uniting the Galapagos species to the exclusion of others within the non-West Indian *Alsophis* clade. Maglio (1970) noted that the dental formula and shape of the premaxillae also linked the Galapagos species that he examined (*Alsophis biserialis*, *A. dorsalis*, and *A. slevini*) in a monophyletic group apart from the West Indian species.

Zaher's (1999) finding, based on hemipenial evidence, that the non-West Indian species of *Alsophis* (*A. elegans* and the Galapagos species) are more closely related to species in the Genus *Saphenopis* than to other species of *Alsophis* led him to conclude that *Alsophis* is "polyphyletic, or at least paraphyletic." This would be true whether or not the South American clade (*A. elegans*, Galapagos species, and *Saphenophis*) was the closest relative of the West Indian clade, something that is presently unknown. Placing *A. elegans* and the Galapagos xenodontines in *Saphenophis* would correct this problem, but those additional species—besides sharing the single hemipenial character—otherwise do not conform to the original definition of the genus *Saphenophis* (Myers 1973).

Cadle's (1984, 1985) studies included only four species of the Tribe Alsophiini but his results agreed with later studies (Vidal *et al.* 2000; Hass *et al.* 2001) in showing a South American origin for the West Indian clade. This is the most common biogeographic pattern observed for West Indian terrestrial vertebrates (Hedges 1996a, b; Hedges 2001; Hedges 2006). Although Rosen (1975) originally suggested that the Antillean fauna may have arisen by vicariance, and this was debated at length during the 1980s and 1990s, geologic evidence has since suggested that Antillean islands were not continuously emergent until about the late Eocene (~37 million years ago, Ma), negating the possibility of proto-Antillean vicariance in the late Cretaceous (Iturralde-Vinent & MacPhee 1999). Molecular time estimates previously presented for alsophiine snakes (Cadle 1984, 1985; Hedges *et al.* 1992; Hedges 1996b; Hass *et al.* 2001) are consistent with a late Cenozoic arrival in the Antilles by dispersal.

The previous DNA sequence analysis (Vidal *et al.* 2000) used sequences from two mitochondrial genes and relationships among species were not well-resolved. To improve this resolution and further test the current arrangement of genera, based on Maglio (1970), and to reconstruct the biogeographic history of the group, we built an expanded data set. Our expanded data set includes one nuclear gene and five mitochondrial

gene sequences for 35 West Indian species and subspecies in addition to four caenophidian outgroups. The eight West Indian species that we were unable to sample are the four possibly extinct ones mentioned above, and four rare species: one species of the genus *Arrhyton* (*ainictum*), two of the genus *Ialtris* (*agyrtes* and *parishi*), and one of the genus *Alsophis* (*sanctonum*). We present partial data (two genes) for another rare species, *Alsophis anomalus*.

Before proceeding, we first address the status of several taxa in our study that are recognized currently as subspecies. Many subspecies have been recognized for West Indian snakes (Schwartz and Henderson 1991), and careful scrutiny is revealing that some of them warrant recognition as distinct species (e.g., Breuil 2002; Hedges 2002). On the Puerto Rican Bank, three subspecies are recognized for *Arrhyton exiguum* (Cope) and the last reviser (Schwartz 1967) found large morphological differences, including non-overlapping scale counts, between the one occurring throughout Puerto Rico except for the southern coast region—*A. e. stahli* (Stejneger)—and the other two subspecies—*A. e. exiguus* Cope and *A. e. subspadix* Schwartz. We also found a large genetic difference between *A. e. exiguum* and *A. e. stahli* (see below); we did not examine *A. e. subspadix*. For these reasons we recognize *A. stahli* as a distinct species from *A. exiguum*, but retain *A. e. subspadix* as a subspecies of the latter species. Seven subspecies are recognized for the species *Alsophis portoricensis*, which also occurs on the Puerto Rican Bank and satellite islands, as well as Mona Island (Schwartz 1966). We do not revise the status of the six subspecies on the Puerto Rican Bank, in part because we do not have material from all of them and also because some molecular evidence suggests very close relationships (see below); a more complete study of the racers of the Puerto Rican Bank is much needed. However, we recognize the taxon from Mona Island as a distinct species, *Alsophis variegatus* (Schmidt). It was originally described as a full species (Schmidt 1926), is the smallest of the seven taxa, has a distinctive dorsal and ventral pattern, and differences in scalation (Schwartz 1966).

Concerning the Lesser Antilles, we raise the subspecies *Alsophis antiguae sajdaki* Henderson (Great Bird Island, Antigua) to species level, *Alsophis sajdaki*, based on colour pattern differences and non-overlapping ventral scale counts compared with *Alsophis antiguae* Parker from the main island of Antigua (Parker 1933; Lazell 1967; Henderson 1990). We agree with Breuil's (2002) revision of *Alsophis* in the Guadeloupe region, recognizing *Alsophis sanctonum* Barbour as a distinct species from *A. antillensis* (Schlegel), and transferring the subspecies *A. antillensis danforthi* Cochran to *A. sanctonum danforthi*. We raise the three remaining subspecies of *A. antillensis—A. a. antillensis, A. a. manselli* Parker, and *A. a. sibonius* Cope to species: *A. antillensis* (Guadeloupe and Marie Galante), *Alsophis manselli* (Montserrat), and *Alsophis sibonius* (Dominica). They have differences in pattern and scalation and occur on three widely separated islands, and thus are unlikely to intergrade. The taxon on Dominica (*A. sibonius*) was originally described as a distinct species. In the case of the Cayman Islands, we recognize the three subspecies of *Alsophis cantherigerus* (Bibron)—each endemic to one of the three islands—as distinct species: *Alsophis caymanus* Garman (Grand Cayman), *Alsophis fuscicauda* Garman (Cayman Brac), and *Alsophis ruttyi* Grant (Little Cayman). The first two were originally described as distinct species and each of the three taxa can be diagnosed by non-overlapping traits of pattern and scalation (Grant 1940).

Finally, we revisit a taxonomic question left open by Hedges and Garrido (1992) concerning a Cuban species of the genus *Arrhyton*. They investigated the confused history of the name "*Colorhogia redimita*" Cope (1862), of which the type is lost. They noted that the "weight of the evidence" indicates that *Arrhyton landoi* Schwartz is a synonym of *Arrhyton redimitum* Cope, based on details of scalation, pattern, and coloration in the original description. When Schwartz described *A. landoi* he did not consider that it might be a synonym of *A. redimitum* because Grant *et al.* (1959) had earlier concluded that it was a synonym of *A. taeniatum*, based on the supposed rediscovery of the missing holotype. However, Hedges and Garrido (1992) showed that this claim by Grant *et al.* was based on a mix-up of specimens, and that the holotype was not rediscovered and remains missing. In fact, Cope's (1862) original description excludes the possibility that *A. redimitum* is a synonym of *A. taeniatum*; the latter is the only species in Cuba that lacks a loreal (present in Cope's description of *A. redimitum*). Besides *A. landoi*, the only other known species of *Arrhyton* in that region of eastern Cuba is *A. supernum*, a species described by Hedges and Garrido (1992) in the same paper.

But *A. supernum* has a heavily pigmented venter (immaculate in *A. redimitum* and *A. landoi*), a dark brown head lacking a well-defined cap or temporal band (reddish brown cephalic cap and well-defined temporal band present in *A. redimitum* and *A. landoi*), dorsal scales blackish (spotted with brown in *A. redimitum* and *A. landoi*), and a wide lateral stripe that occupies the upper half of the third and most of the fourth scale row (narrow lateral line occupying the middle of the fourth scale row in *A. redimitum* and *A. landoi*). Furthermore, the single prefrontal scale in *A. redimitum* is a variant that occurs most frequently in *A. landoi*, among *Arrhyton* (Hedges and Garrido 1992). The specific name used by Cope, *redimitum*, is derived from the Latin "redimiculum," meaning head band, which aptly describes the distinctive pattern feature of *A. landoi*.

Hedges and Garrido (1992) detailed this evidence from coloration and pattern indicating that *A. redimitum* is a synonym of *A. landoi*, but were reluctant to make that change because some scale counts were missing from Cope's description. As a consequence, some later authors have continued to recognize both *A. redimitum* and *A. landoi* as distinct species (Ruibal 2003; Uetz *et al.* 2008), which was not the intention of Hedges and Garrido (1992). In hindsight, the senior author acknowledges now that the pattern and coloration evidence is sufficiently diagnostic, as noted above. Hence, we place *Arrhyton landoi* Schwartz (1965) in the synonymy of *Arrhyton redimitum* and assign MCZ 42505 (the holotype of *A. landoi*; described in Schwartz, 1965) as the neotype.

While this paper was awaiting publication at *Zootaxa*, and after corrected proofs had been returned on 4th March 2009, a manuscript dealing with similar taxonomic issues was submitted to *Papéis Avulsos de Zoologia* on 6th March 2009 and published unusually rapidly, 14 days later (Zaher et al. 2009). In it, new genera were described that preempted descriptions of taxa in the original version of this article, requiring us to make revisions. The data presented by those authors came from previously published hemipenial data (Zaher 1999) and DNA sequence data that were also mostly previously published. Some 12S and 16S rRNA sequences were new but many of those were from the same species and gene fragments as those used in the study of Vidal et al (2000), available in Genbank, and all of those sequences from West Indian taxa were from Vidal et al. (2000). The majority of the nodes were weakly supported (e.g., 12 of 22 West Indian nodes were supported by MP BP values under 70%). Zaher et al. (2009) used hemipenial data exclusively to diagnose and define West Indian genera and did not refer to scalation or other characters. As we show here with a more comprehensive molecular data set, and with data from scalation and other morphological characters, those taxonomic decisions made by Zaher et al. (2009), in general, are unsupported.

Materials and methods

Data collection. Tissue samples (liver, blood, tail tip, or shed skin) were collected mostly by S.B.H. and associates on expeditions over the last three decades, although several were sent to us by colleagues (see Acknowledgements). The Appendix lists the taxa, localities, and accession numbers of specimens used in the study. DNA extraction was performed as described elsewhere (Winnepenninckx *et al.* 1993), or with the Nucleospin tissue kit from Biotech, or the DNeasy Tissue Kit from Qiagen.

Amplification was performed using the following sets of primers: L2510, 5'-CGC-CTG-TTT-ATC-AAA-AAC-AT-3' (Palumbi *et al.* 1991); L16, 5'-ACG-GCC-GCG-GTA-YCC-TAA-CCG-TG-3' (Vidal *et al.* 2000) and H3056, 5'-CTC-CGG-TCT-GAA-CTC-AGA-TCA-CGT-AGG-3' (Hedges 1994) for the 16SrRNA gene; L12, 5'-CGC-CAA-AYA-ACT-ACG-AG-3' (Vidal *et al.* 2000); H1478, 5'-TGA-CTG-CAG-AGG-GTG-ACG-GGC-GGT-GTG-T-3' (Kocher *et al.* 1989) and H1557, 5'-GTA-CAC-TTA-CCT-TGT-TAC-GAC-TT-3' (Knight & Mindell 1994) for the 12SrRNA gene; ND4, 5'-TGA-CTA-CCA-AAA-GCT-CAT-GTA-GAA-GC-3' (Forstner *et al.* 1995) and LEU, 5'-TAC-TTT-TAC-TTG-GAT-TTG-CAC-CA-3' (Forstner *et al.* 1995) for the ND4 gene; L14724, 5'-TGA-CTT-GAA-GAA-CCA-CCG-TTG-3' (Palumbi *et al.* 1991), L14910, 5' - GACCTGTGATMTGAAAAACCAYCGTTGT- 3' (Burbrink *et al.* 2000), L14919, 5' - AACCACCGTTGTTATTCAACT-3' (Burbrink *et al.* 2000), H16064, 5' - CTTTGGTTTACAAGAACAATGCTTTA-3' (Burbrink *et al.* 2000), H15716, 5' -

TCTGGTTTAATGTGTTG-3' (Burbrink *et al.* 2000) and HVN650, 5'-TAT-GGG-TGG-AAK-GGG-ATT-TT-3' (Vidal & Hedges 2002a) for the cytochrome b gene; L4437b, 5' -CAG-CTA-AAA-AAG-CTA-TCG-GGC-CCA-TAC-C-3' (Kumazawa *et al.* 1996), H5382, 5' -GTG-TGG-GCR-ATT-GAT-GA-3' (de Queiroz *et al.* 2002), and tRNA-trpR, 5' –GGC-TTT-GAA-GGC-TMC-TAG-TTT-3' (de Queiroz *et al.* 2002) for the ND2 gene; L562, 5'-CCT-RAD-GCC-AGA-TAT-GGY-CAT-AC-3' (Vidal and Hedges 2005) and H1306, 5'-GHG-AAY-TCC-TCT-GAR-TCT-TC-3' (Vidal & Hedges 2005) for the RAG2 gene.

Both strands of the PCR products were sequenced using the CEQ cycle sequencing kit (Beckman) in the CEQ-2000 DNA Analysis System (Beckman), the BigDye sequencing kit (Applied Biosystems) in the ABI Prism 3100-Avant Genetic Analyser, at the Genoscope (http://www.genoscope.fr), or at Genoscreen, a private company (http://www.genoscreen.fr).

The two strands obtained for each sequence were combined using the BioEdit Sequence Alignment Editor program (Hall 1999). The 168 sequences generated for this work have been deposited in GenBank under accession numbers FJ416691–FJ416856 and FJ666091–FJ666092 (Appendix). Sequence entry and alignment were performed manually with the MUST2000 software (Philippe 1993). Alignment was straightforward for the cytochrome b, ND4, and RAG2 genes because there were no indels. For the ND2 gene, amino acid translations were used as a guide to produce an alignment including three gaps, each of one codon length. For the 12S and 16S rRNA sequences, ambiguous areas were deleted from analyses. In all further analyses, remaining gaps were treated as missing data. Alignments can be obtained from Nicolas Vidal. Alignments resulted in 287 12S rRNA sites, 361 16S rRNA sites, 609 cytochrome b sites, 678 ND4 sites, 738 ND2 sites, and 714 RAG2 sites.

Phylogenetic analysis. We built phylogenies using Maximum Likelihood (ML) and Bayesian methods of inference. We used a natricid (genus *Xenochrophis*), a heterodontine (genus *Heterodon*), a dipsadine (genus *Leptodeira*), and a xenodontine from mainland South America (genus *Helicops*) as outgroups. ML analyses were performed with RAxML 7.0.4 (Stamatakis 2006; Stamatakis *et al.* 2008), and Bayesian analyses were performed with MrBayes 3.1 (Ronquist & Huelsenbeck 2003). We used eight data partitions in the analyses: 12S rRNA, 16S rRNA, each of the three codon positions of the mitochondrial protein-coding genes, and each of the three codon positions of the nuclear RAG-2 gene. Bayesian analyses were performed by running 5,000,000 generations in four chains, saving the current tree every 100 generations, with a GTR model as inferred by Modeltest using the AIC criterion (Posada & Crandall 1998) applied to each partition. The last 48,000 trees were used to construct a 50% majority rule consensus tree. For the ML analysis, we used the same eight partitions and performed 1000 bootstrap replicates.

Divergence time estimation. Bayesian timing analyses were conducted with Multidivtime T3 (Thorne & Kishino 2002; Yang & Yoder 2003) using the topology obtained from the Bayesian analysis and the same eight data partitions. PAML 3.14 (Yang 1997) was used to estimate model parameters. Bayesian credibility intervals (CI), which are posterior probability intervals analogous to the confidence interval in frequentist statistics, were calculated for time estimates. Fossil calibrations were not available because there are no pre-Pleistocene fossils of Alsophiini. Also, the oldest known dipsadid (14–12 Ma) is *Paleoheterodon arcuatus* from Sansan, France (Augé & Rage 2000), which is much younger than molecular estimates of the divergence of the family lineage from its closest relative, 40–33 Ma (Wiens *et al.* 2006; Burbrink & Pyron 2008; Vidal *et al.* 2009). Instead we used three geologic calibrations, all establishing maximum times. These correspond to the emergence of Jamaica 10 Ma (Donovan 2002; Mitchell 2004) constraining the earliest split among the three Jamaican species, the emergence of the South Island of Hispaniola 10 Ma (Iturralde-Vinent & MacPhee 1999) constraining the divergence of two South Island endemics (*Darlingtonia haetiana* and *Ialtris dorsalis*), and the earliest emergence of continuous land in the West Indies 37.2 Ma (Iturralde-Vinent & MacPhee 1999) constraining the earliest divergence of West Indian alsophiines. Because all three geologic calibrations were maximums, at least one minimum calibration was needed to avoid a bias towards underestimation of divergence time. Therefore we included a single minimum calibration from a molecular time estimate for the divergence of North and Middle American dipsadids versus South American dipsadids (22.6 Ma; 30.2–16.0, credibility interval). It came from a study involving nine nuclear genes in all major snake groups, with

geologic and fossil calibrations (Vidal *et al.* 2009). We used the low extreme (16.0 Ma) of the Bayesian credibility interval for the calibration. Analyses were run with and without this calibration point.

For the ingroup root (rttm) prior, which corresponded to the same node as the minimum calibration, we used the mean (22.6 Ma) of the molecular time estimate (Vidal *et al.* 2009). For the prior (bigtime) designating a value larger than any expected posterior, we used the Mesozoic-Cenozoic boundary (66 Ma). The molecular time estimate for the divergence of the dipsadid lineage from the pseudoxenodontid lineages, 32.9 Ma (42.6–24.7 Ma; Vidal *et al.* 2009) is consistent (i.e., intermediate between) the rttm and bigtime priors. Other priors followed recommendations accompanying the software. Analyses were run for 1,100,000 generations, with a sample frequency of 100 after a burn-in of 100,000 generations. The use of only 100,000 generations resulted in time estimates within approximately 0.5% of the times using 1,100,000 generations.

Results

Phylogenetic relationships. Our alignment resulted in 3387 sites. The ML and Bayesian results are almost identical (in the ML tree, not shown, *Uromacer* and the Cuban species of *Arrhyton* are each monophyletic and cluster together (BP value: 59%); *Arrhyton procerum* and *A. tanyplectum* are sister-groups (BP value: 52%); and the clade formed by *Arrhyton exiguum* and *A. stahli* is the sister-group to all alsophiines excluding *Uromacer* and Cuban species of *Arrhyton* (BP: 49%)). Both analyses support the monophyly of alsophiines in the context of the outgroups (Fig. 1). Three strongly supported clades are found, each with 100% BP and PP values: *Uromacer*, the Cuban species of *Arrhyton*, and a large assemblage of mostly species of *Alsophis*, but including species currently classified in other genera and thus rendering *Alsophis* paraphyletic. The non-Cuban members of the genus *Arrhyton* are not monophyletic because Puerto-Rican species are not closely related to the Jamaican species that cluster (BP 97%, PP 100%) with a Hispaniolan clade formed by the genus *Hypsirhynchus* and *Antillophis parvifrons*. The genus *Antillophis* is not monophyletic because *Antillophis andreae* (Cuba) clusters with species of the genus *Alsophis* from Cuba, Bahamas and Caymans (BP 97%, PP 100%). Furthermore, species of the genus *Alsophis* from the Lesser Antilles form a clade (BP 100%, PP 100%) that is not the closest relative of the species of the genus *Alsophis* from Puerto Rico. Finally, *Ialtris* and *Darlingtonia*, both from Hispaniola, form a clade (BP 96%, PP 100%). A tissue sample of a road-killed specimen of the rare *Alsophis anomalus*, from Hispaniola, was available and sequences from two of the six genes (12S and 16S rRNA) were obtained. Phylogenetic analyses (not shown) of each gene and the two combined all placed *Alsophis anomalus* as the closest relative of *Antillophis andreae* from Cuba, although with moderate support (ML BP 70%, PP 91% in the combined analysis).

Taxonomic implications. The results have taxonomic implications for the diagnosis and content of tribes, subtribes, genera, and species groups within the Tribe Alsophiini of the Subfamily Xenodontinae (Family Dipsadidae). Our proposed classification is presented in Table 1. The type species of the genus *Arrhyton* is *A. taeniatum* from Cuba, so Cuban members of that genus (a clade) retain that generic name and we propose no generic change for species of *Uromacer*. For the large, well-supported clade that includes all alsophiine species except *Uromacer* and *Arrhyton*—recognized here as a subtribe (see below)—there are seven strongly supported clades (Fig. 1) totaling 32 species (Table 1). We recognize each of these as a distinct genus. In doing so, five take available generic names whereas two others are newly named. We also place *Alsophis anomalus* in a new genus. Although the monophyly of all genera of alsophiines (with more than one species) is supported by DNA sequence evidence (Fig. 1) with ML bootstrap and Bayesian posterior probabilities > 95%, each is further supported by morphological evidence, which we summarize in the following accounts of the tribe, subtribes, and genera of alsophiine snakes.

TABLE 1. Classification of West Indian xenodontine snakes, Tribe Alsophiini. The arrangement used in this study is compared with that in previous classifications (Maglio 1970; Schwartz & Henderson 1991; Powell *et al.* 1996).

This study	Previous classification
Alsophis antillensis (Schlegel) (*antillensis* Group)	*Alsophis antillensis antillensis*
Alsophis manselli Parker (*antillensis* Group)	*Alsophis antillensis manselli*
Alsophis sanctonum danforthi Cochran (*antillensis* Group)	*Alsophis sanctonum danforthi*
Alsophis sanctonum sanctonum Barbour (*antillensis* Group)	*Alsophis sanctonum sanctonum*
Alsophis sibonius Cope (*antillensis* Group)	*Alsophis antillensis sibonius*
Alsophis antiguae Parker (*rufiventris* Group)	*Alsophis antiguae antiguae*
Alsophis rijgersmaei Cope (*rufiventris* Group)	*Alsophis rijgersmaei*
Alsophis rufiventris (Duméril, Bibron, & Duméril) (*rufiventris* Group)	*Alsophis rufiventris*
Alsophis sajdaki Henderson (*rufiventris* Group)	*Alsophis antiguae sajdaki*
Arrhyton dolichura Werner (*dolichura* Group)	*Arrhyton dolichura* (*dolichura* Group)
Arrhyton procerum Hedges & Garrido (*dolichura* Group)	*Arrhyton procerum* (*dolichura* Group)
Arrhyton tanyplectum Schwartz & Garrido (*dolichura* Group)	*Arrhyton tanyplectum* (*dolichura* Group)
Arrhyton taeniatum Günther (*taeniatum* Group)	*Arrhyton taeniatum* (*taeniatum* Group)
Arrhyton ainictum Schwartz & Garrido (*vittatum* Group)	*Arrhyton ainictum* (*vittatum* Group)
Arrhyton redimitum (Cope) (*vittatum* Group)	*Arrhyton landoi* (*vittatum* Group)
Arrhyton supernum Hedges & Garrido (*vittatum* Group)	*Arrhyton supernum* (*vittatum* Group)
Arrhyton vittatum (Gundlach) (*vittatum* Group)	*Arrhyton vittatum* (*vittatum* Group)
Borikenophis portoricensis anegadae (Barbour)	*Alsophis portoricensis anegadae*
Borikenophis portoricensis aphantus (Schwartz)	*Alsophis portoricensis aphantus*
Borikenophis portoricensis nicholsi (Grant)	*Alsophis portoricensis nicholsi*
Borikenophis portoricensis portoricensis (Reinhardt & Lütken)	*Alsophis portoricensis portoricensis*
Borikenophis portoricensis prymnus (Schwartz)	*Alsophis portoricensis prymnus*
Borikenophis portoricensis richardi (Grant)	*Alsophis portoricensis richardi*
Borikenophis sanctaecrucis (Cope)	*Alsophis sanctaecrucis*
Borikenophis variegatus (Schmidt)	*Alsophis portoricensis variegatus*
Caraiba andreae andreae (Reinhardt & Lütken)	*Antillophis andreae andreae*
Caraiba andreae melopyrrha (Thomas & Garrido) (*andreae* Group)	*Antillophis andreae melopyrrha*
Caraiba andreae morenoi (Garrido)	*Antillophis andreae morenoi*
Caraiba andreae nebulatus (Barbour)	*Antillophis andreae nebulatus*
Caraiba andreae orientalis (Barbour & Ramsden)	*Antillophis andreae orientalis*
Caraiba andreae peninsulae (Schwartz & Thomas)	*Antillophis andreae peninsulae*
Cubophis cantherigerus cantherigerus (Bibron)	*Alsophis cantherigerus cantherigerus*
Cubophis cantherigerus adspersus (Gundlach & Peters)	*Alsophis cantherigerus adspersus*
Cubophis cantherigerus brooksi (Barbour)	*Alsophis cantherigerus brooksi*
*Cubophis cantherigerus pepe*i (Schwartz & Thomas)	*Alsophis cantherigerus pepei*
Cubophis cantherigerus schwartzi (Lando and Williams)	*Alsophis cantherigerus schwartzi*

to be continued.

TABLE 1. (continued)

This study	Previous classification
Cubophis caymanus (Garman)	*Alsophis cantherigerus caymanus*
Cubophis fuscicauda (Garman)	*Alsophis cantherigerus fuscicauda*
Cubophis ruttyi (Grant)	*Alsophis cantherigerus ruttyi*
Cubophis vudii aterrimus (Barbour & Shreve)	*Alsophis vudii aterrimus*
Cubophis vudii picticeps (Conant)	*Alsophis vudii picticeps*
Cubophis vudii raineyi (Barbour & Shreve)	*Alsophis vudii raineyi*
Cubophis vudii utowanae (Barbour & Shreve)	*Alsophis vudii utowanae*
Cubophis vudii vudii (Cope)	*Alsophis vudii vudii*
Haitiophis anomalus (Peters)	*Alsophis anomalus*
Hypsirhynchus ater (Gosse) (*ater* Group)	*Alsophis ater*
Hypsirhynchus callilaemus (Gosse) (*callilaemus* Group)	*Arrhyton callilaemum*
Hypsirhynchus funereus (Cope) (*callilaemus* Group)	*Arrhyton funereum*
Hypsirhynchus polylepis (Buden) (*callilaemus* Group)	*Arrhyton polylepis*
Hypsirhynchus ferox exedrus Schwartz (*ferox* Group)	*Hypsirhynchus ferox exedrus*
Hypsirhynchus ferox ferox Günther (*ferox* Group)	*Hypsirhynchus ferox ferox*
Hypsirhynchus ferox paracrousis Schwartz (*ferox* Group)	*Hypsirhynchus ferox paracrousis*
Hypsirhynchus scalaris Cope (*ferox* Group)	*Hypsirhynchus scalaris*
Hypsirhynchus melanichnus (*melanichnus* Group) (Cope)	*Alsophis melanichnus*
Hypsirhynchus parvifrons alleni (Dunn) (*parvifrons* Group)	*Antillophis parvifrons alleni*
Hypsirhynchus parvifrons lincolni Cochran (*parvifrons* Group)	*Antillophis parvifrons lincolni*
Hypsirhynchus parvifrons niger Dunn (*parvifrons* Group)	*Antillophis parvifrons niger*
Hypsirhynchus parvifrons paraniger (Thomas & Schwartz) (*parvifrons* Group)	*Antillophis parvifrons paraniger*
Hypsirhynchus parvifrons parvifrons (Cope) (*parvifrons* Group)	*Antillophis parvifrons parvifrons*
Hypsirhynchus parvifrons protenus (Jan) (*parvifrons* Group)	*Antillophis parvifrons protenus*
Hypsirhynchus parvifrons rosamondae (Cochran) (*parvifrons* Group)	*Antillophis parvifrons rosamondae*
Hypsirhynchus parvifrons stygius (Thomas & Schwartz) (*parvifrons* Group)	*Antillophis parvifrons stygius*
Hypsirhynchus parvifrons tortuganus (Dunn) (*parvifrons* Group)	*Antillophis parvifrons tortuganus*
Ialtris haetianus haetianus (Cochran) (*haetianus* Group)	*Darlingtonia haetiana haetiana*
Ialtris haetianus perfector (Schwartz & Thomas) (*haetianus* Group)	*Darlingtonia haetiana perfector*
Ialtris haetianus vaticinatus (Schwartz) (*haetianus* Group)	*Darlingtonia haetiana vaticinatus*
Ialtris agyrtes Schwartz & Rossman (*dorsalis* Group)	*Ialtris agyrtes*
Ialtris dorsalis (Günther) (*dorsalis* Group)	*Ialtris dorsalis*
Ialtris parishi Cochran (*dorsalis* Group)	*Ialtris parishi*
Magliophis exiguus exiguus (Cope)	*Arrhyton exiguum exiguum*
Magliophis exiguus subspadix (Schwartz)	*Arrhyton exiguum subspadix*
Magliophis stahli (Stejneger)	*Arrhyton exiguum stahli*

to be continued.

TABLE 1. (continued)

This study	Previous classification
Uromacer catesbyi catesbyi (Schlegel) (*catesbyi* Group)	*Uromacer catesbyi catesbyi*
Uromacer catesbyi cereolineatus Schwartz (*catesbyi* Group)	*Uromacer catesbyi cereolineatus*
Uromacer catesbyi frondicolor Schwartz *(catesbyi* Group)	*Uromacer catesbyi frondicolor*
Uromacer catesbyi hariolatus Schwartz (*catesbyi* Group)	*Uromacer catesbyi hariolatus*
Uromacer catesbyi inchausteguii Schwartz (*catesbyi* Group)	*Uromacer catesbyi inchausteguii*
Uromacer catesbyi insulaevaccarum Schwartz (*catesbyi* Group)	*Uromacer catesbyi insulaevaccarum*
Uromacer catesbyi pampineus Schwartz (*catesbyi* Group)	*Uromacer catesbyi pampineus*
Uromacer catesbyi scandax Dunn (*catesbyi* Group)	*Uromacer catesbyi scandax*
Uromacer frenatus chlorauges Schwartz (*oxyrhychus* Group)	*Uromacer frenatus chlorauges*
Uromacer frenatus dorsalis Dunn (*oxyrhychus* Group)	*Uromacer frenatus dorsalis*
Uromacer frenatus frenatus (Günther) (*oxyrhychus* Group)	*Uromacer frenatus frenatus*
Uromacer frenatus wetmorei Cochran (*oxyrhychus* Group)	*Uromacer frenatus wetmorei*
Uromacer oxyrhynchus Duméril & Bibron (*oxyrhychus* Group)	*Uromacer oxyrhynchus*

Tribe Alsophiini Fitzinger, 1843

Type genus. *Alsophis* Fitzinger, 1843:26.

Diagnosis. Genera in this tribe have slender bodies, smooth scales, 17–23 midbody scale rows, 107–220 ventrals, 40–224 subcaudals, 0–3 apical scale pits, 6–9 upper labials, 7–11 lower labials, 8–23 total maxillary teeth, and 10–35 dentary teeth (Table 2). All are considered racer snakes, which refers to their habitus (slender, with smooth scales) and behavior (swift-moving, active foragers). They share with other xenodontine snakes a derived hemipenial character: enlarged lateral spines and two distinctly ornamented regions on the lobes (Zaher 1999). No hemipenial character unambiguously supports monophyly of the tribe, but most alsophiines have a reduced number of ornamentations on the asulcate surface of the lobes (Zaher 1999). Evidence for the monophyly of the tribe comes from albumin immunological data (Hass *et al.* 2001) and DNA sequence data (Vidal *et al.* 2000).

Content. Three subtribes, 10 genera, and 43 species (85 species + subspecies) are included in the tribe (Table 1).

Distribution. The tribe is distributed throughout the West Indies (Fig. 2).

Remarks. Fitzinger (1843) used the family name "Alsophes" and Dowling (1975) recognized the tribe Alsophiini, but in both cases these names were used for a considerably more inclusive group than is recognized here. Three subtribes are introduced here to recognize three well-supported clades defined in the molecular phylogeny (Fig. 1).

Subtribe Alsophiina Fitzinger, 1843

Type genus. *Alsophis* Fitzinger, 1843:26

Diagnosis. Genera in this subtribe have 17–23 midbody scale rows, 123–220 ventrals, 40–162 subcaudals, 0–3 apical scale pits, 7–8 upper labials, 8–10 lower labials, 13–23 total maxillary teeth, and 17–35 dentary teeth (Table 2). The subtribe lacks green body pigmentation (thus distinguishing it from the subtribe Uromacerina), and has a high number (17–35) of dentary teeth (thus distinguishing it from the subtribe Arrhytonina). Evidence for the monophyly of this subtribe comes from DNA sequence data (Fig. 1) in which the six included genera form a clade with 100% BP and 100% PP support.

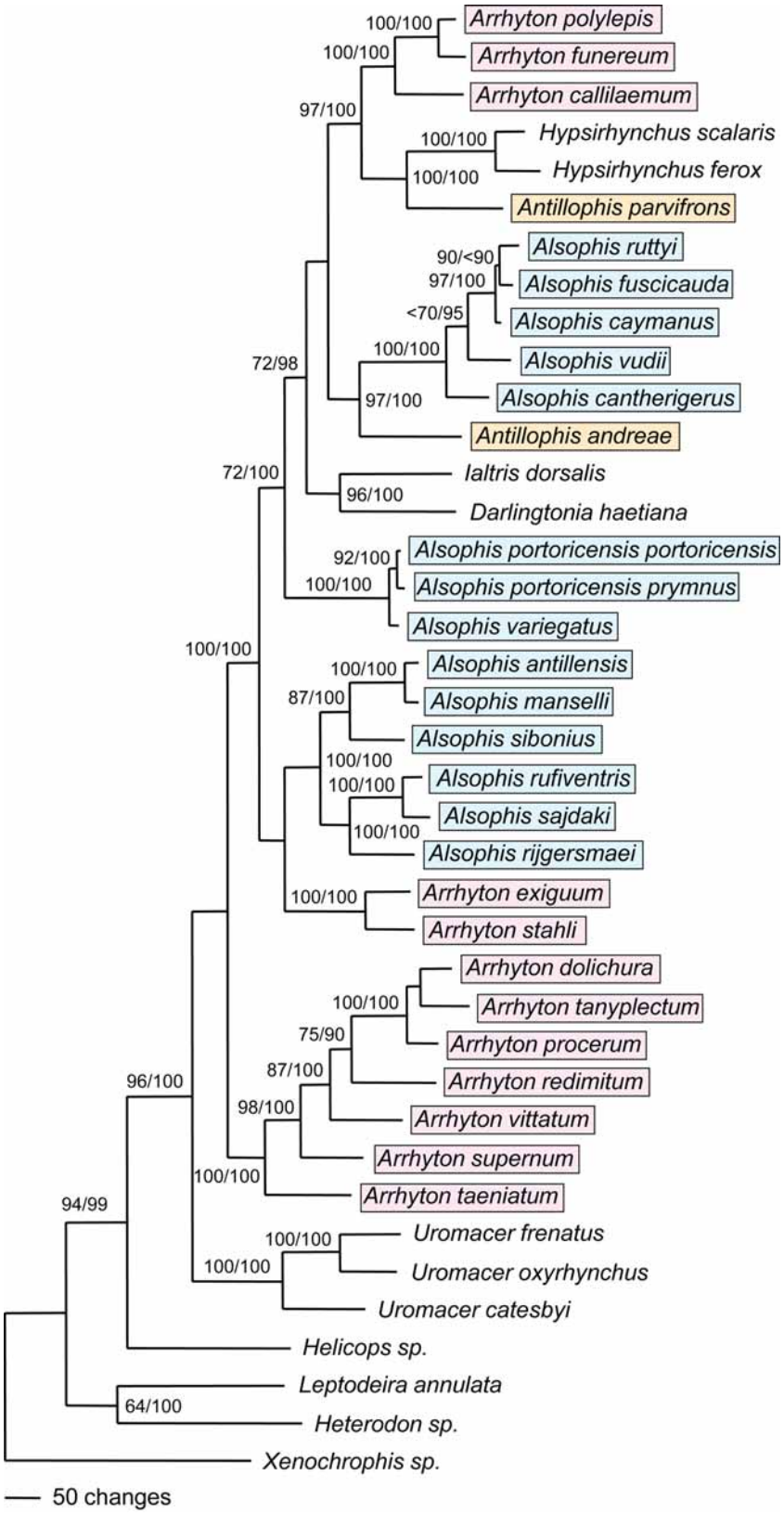

FIGURE 1. A phylogeny of Alsophiini. Bayesian tree obtained from the combined data set of six genes (RAG2, 12S & 16S rRNA, cytochrome b, ND2 and ND4; 3387 sites). *Alsophis portoricensis portoricensis* and *A. p. anegadae* have identical sequences at all genes sampled, and therefore the latter taxon is not shown. Values are ML bootstrap values above 70% followed by Bayesian posterior probabilities above 90%. The generic taxonomy in this tree reflects usage prior to this study and shows paraphyly and polyphyly of *Alsophis* (blue), *Arrhyton* (purple), and *Antillophis* (orange). See Table 1 and Figure 4 for the new classification proposed here.

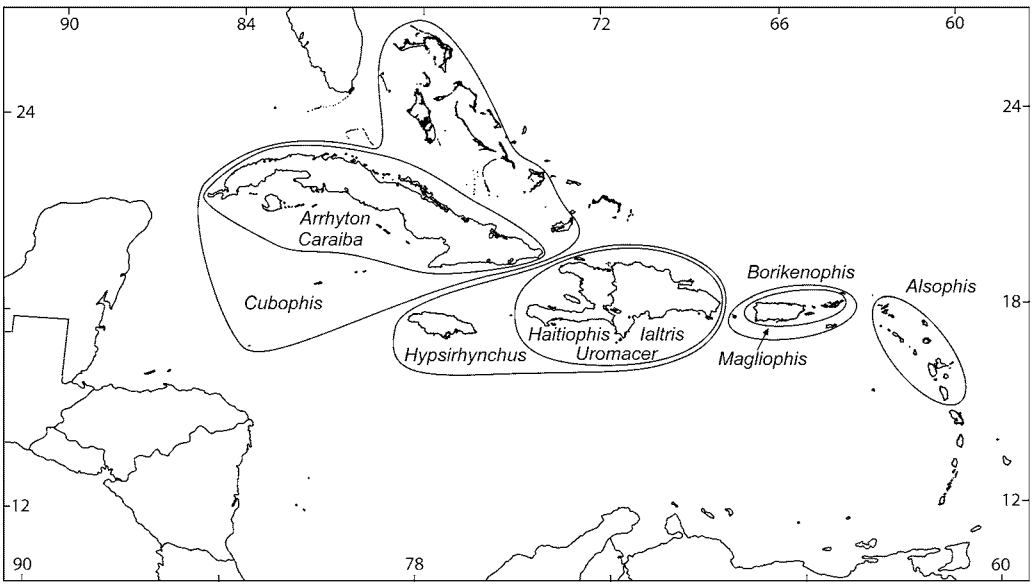

FIGURE 2. Map showing the West Indies (including the southern tip of Florida above, Central America to the west, and the northern edge of South America below) and the distributions of the genera of the Tribe Alsophiini, Subfamily Xenodontinae, Family Dipsadidae.

TABLE 2. Morphological variation in the genera of alsophiine snakes (SVL = snout-vent length), from Barbour & Ramsden (1919), Boulenger (1893), Breuil (2002), Cochran (1941), Cope (1862), Dunn (1932), Grant (1940), Hedges & Garrido (1992), R. W. Henderson (personal communication), Lynn & Grant (1940), Powell & Henderson (1994), Schwartz (1967, 1970, 1971), Schwartz & Henderson (1991), Schwartz & Rossman (1976), and Schwartz & Thomas (1965). Tooth counts are from Maglio (1970) and do not include all species; maxillary teeth include the two teeth separated from the rest by the diastema. Rare variants of midbody and labial counts not included. For characters that sometimes show sexual dimorphism, male (m) and female (f) ranges are shown, if known.

Taxon	Maximum SVL (mm)	Ventrals	Subcaudals	Midbody scale rows	Upper labials	Lower labials	Apical scale pits	Maxillary teeth	Dentary teeth
Alsophis	m: 810 f: 1080	184–220	m: 112–138 f: 94–132	19–23	8	10	2	18–21	21–26
Arrhyton	m: 396 f: 448	m: 107–187 f: 108–189	m: 52–140 f: 52–136	17	6–7	7–9	1	8–17	10–17
Borikenophis	1025	m: 163–184 f: 166–198	m: 114–143 f: 106–145	17–19	8	10	1–3	16–21	22–35
Caraiba	m: 593 f: 850	m: 131–157 f: 132–153	m: 95–120 f: 90–116	17	8	9	1	20–23	25–28
Cubophis	m: 937 f: 1280	m: 161–181 f: 159–187	m: 108–133 f: 101–120	17	8	10	2	14	18–19
Haitiophis	m: 1470 f: 2000	207–215	113–130	21	8	10	2	14	18–19
Hypsirhynchus	m: 830 f?: 850	m: 123–189 f: 128–182	m: 73–151 f: 62–138	17–19	7-8	9–10	1–2	13–21	18–27
Ialtris	m: 905 f: 990	m: 132–191 f: 133–192	m: 45–115 f: 40–109	19	7	8–9	0, 2	18–19	20–24
Magliophis	m: 428 f: 438	m: 137–165 f: 138–161	m: 77–102 f: 71–96	19	8	9	0	15–18	19–23
Uromacer	1500	m: 157–212 f: 155–204	m: 168–224 f: 159–215	17–19	8–9	10–11	0	15–20	20–28

Content. Eight genera (*Alsophis, Borikenophis, Caraiba,Cubophis, Haitiophis, Hypsirhynchus, Ialtris*, and *Magliophis*) and 32 species (64 species + subspecies) are included in the subtribe (Table 1).

Distribution. The subtribe is distributed throughout the West Indies (Fig. 2).

Remarks. This large subtribe includes a diverse radiation of West Indian terrestrial racers, excluding the arboreal genus *Uromacer* (Subtribe Uromacerina) and the radiation of small, ground-dwelling species in Cuba, Genus *Arrhyton* (Subtribe Arrhytonina). The relationships of genera within this subtribe are poorly resolved, although there is moderate support (72% BP, 98% PP) for a clade of five genera occurring in the western Caribbean, on Cuba, Hispaniola, Jamaica, and nearby areas (*Caraiba, Cubophis*, *Haitiophis*, *Hypsirhynchus*, and *Ialtris*), and for a group (72% BP, 100 % PP) comprising this clade plus *Borikenophis* (Fig. 1).

Genus *Alsophis* Fitzinger, 1843

Type species. *Psammophis antillensis* Schlegel, 1837:214.

Diagnosis. Species in this genus have 19–23 midbody scale rows, 184–220 ventrals, 94–138 subcaudals, two apical scale pits, eight upper labials, 10 lower labials, 18–21 maxillary teeth, and 21–26 dentary teeth (Table 2). *Alsophis* differs in at least one of these characters from all alsophiine genera except *Borikenophis* and *Hypsirhynchus*. *Alsophis* differs almost completely from *Hypsirhynchus* in ventrals (184–220 versus 123–189 in *Hypsirhynchus*). It differs from most *Borikenophis* (163–187), except for *B. sanctaecrucis* (191–198), in having a higher number of ventrals (184–220).

Content. Eight species (nine species + subspecies) are included in the genus (Table 1).

Distribution. The genus is distributed in the northern Lesser Antilles (Fig. 2).

Remarks. Species of *Alsophis* are moderate-sized (1080 mm, maximum SVL) racers (Fig. 3A). They are all endemic to islands in the northern Lesser Antilles, from Anguilla to Dominica (Fig. 2). These northern islands are sometimes referred to as the "Leeward" islands. Within the genus, two well-supported geographic groups are present (Figs. 1 and 4) for which we propose species groups. The *rufiventris* Group comprises species from the northernmost Leeward islands of Anguilla to Antigua (*A. antiguae, A. rijgersmaei, A. rufiventris*, and *A. sajdaki*). Within this group, we lacked *A. antiguae* which is possibly extinct (Henderson *et al*. 1996), but it is closest to *A. sajdaki*, morphologically. The *rufiventris* Group is also supported by a hemipenial character (Zaher 1999). The *antillensis* Group comprises species from Montserrat to Dominica (*A. antillensis, A. manselli, A. sanctonum*, and *A. sibonius*), the southern Leeward islands. We did not sample *A. sanctonum*, but it shares a unique hemipenial character with *A. sibonius* (Zaher 1999), and we assume the two species to be closely related. A comprehensive review of the morphology of Lesser Antillean alsophiines is needed.

Genus *Borikenophis* Hedges & Vidal, New Genus

Type species. *Alsophis portoricensis* Reinhardt & Lütken 1862:221.

Diagnosis. Species in this genus have 17–19 midbody scale rows, 163–198 ventrals, 106–145 subcaudals, 1–3 apical scale pits, eight upper labials, 10 lower labial, 16-21 maxillary teeth, and 22-35 dentary teeth (Table 2). *Borikenophis* differs in at least one of these characters from all other alsophiine genera except *Alsophis* and *Hypsirhynchus*. Except for *B. sanctaecrucis* (191–198 ventrals), it differs from most *Alsophis* in having a lower number of ventrals (163–187 versus 184–220 in *Alsophis*). Most *Hypsirhynchus* have 19 midbody scales rows (*H. ater* and *H. melanichnus* have 17 rows) whereas most *Borikenophis* have 17 rows (those populations from the Virgin Islands usually have 19 rows).

Content. Three species (eight species + subspecies) are included in the genus (Table 1).

Distribution. Species of *Borikenophis* are distributed throughout the Puerto Rican Bank, and on the nearby islands of Mona, Desecheo, and Saint Croix (Fig. 2).

Etymology. The generic name refers to its distribution centered on the Puerto Rican Bank; Boriken is the Taino word for Puerto Rico.

Remarks. Species of *Borikenophis* are moderate-sized (1025 mm, maximum SVL) racers (Fig. 3B) and they occur sympatrically with the smaller racers of the Genus *Magliophis*. Six subspecies are recognized for *Borikenophis portoricensis*. The species from St. Croix, *B. sanctaecrucis*, is possibly extinct (Henderson & Powell 1996) and was not included in this study, but it has been considered a close relative of *B. portoricensis* based on color pattern and scalation (Schwartz 1966). Although we found *B. p. portoricensis* and *B. p. anegadae* to have identical sequences at all genes sampled, the two subspecies are not particularly close morphologically, with different midbody scale row counts (17 versus 19, respectively). Therefore, to resolve geographic variation in the species *B. portoricensis*, sequences of additional, more variable, genes will be needed. Zaher et al. (2009) included *B. portoricensis* together with various other West Indian species in the resurrected genus *Ocyophis* Cope, but our data (Figs. 1 and 4) contradict that decision as the genera *Borikenophis*, *Cubophis* and *Haitiophis* (the latter not sampled by Zaher et al.) do not form a monophyletic group (see Remarks in *Hypsirhynchus*).

Genus *Caraiba* Zaher et al., 2009

Type species. *Liophis andreae* Reinhardt & Lütken, 1862:214.

Diagnosis. The species in this genus has 17 midbody scale rows, 131–157 ventrals, 90–120 subcaudals, 1 apical scale pit, 8 upper labials, 9 lower labials, 20–23 total maxillary teeth, and 25–28 dentary teeth (Table 2). *Caraiba* differs in at least one of these characters from all other alsophiine genera except *Hypsirhynchus*. From that genus it differs in having a hemipene with enlarged papillate body calyces in the basal region and medial surface of the lobes (Zaher 1999).

Content. One species (six species + subspecies) is included in the genus (Table 1).

Distribution. The genus is distributed on Cuba, including Isla de Juventud (Fig. 2).

Remarks. The single species of *Caraiba* is a moderate-sized species of racer, occurring sympatrically with smaller and larger genera of racers on Cuba. The finding here (Figs. 1 and 4) that "*Antillophis*" *andreae* (Cuba) groups with large Cuban racers of another genus (see below) and that "*Antillophis*" *parvifrons* (Hispaniola) groups with Hispaniolan species (*Hypsirhynchus*) is also supported by morphology: the former species (Cuba) have 17 midbody scale rows whereas the latter species (Hispaniola) have 19 midbody scale rows. Myers (1973) also had reservations about Maglio's (1970) recognition of *Antillophis* based on morphology. Zaher et al. (2009) described *Caraiba* for the single species, based only on its hemipenial differences.

Genus *Cubophis* Hedges & Vidal, New Genus

Type species. *Coluber cantherigerus* Bibron, 1840:27.

Diagnosis. Species in this genus have 17 midbody scale rows, 159–187 ventrals, 101–133 subcaudals, 2 apical scale pits, 8 upper labials, 10 lower labials, 13–17 total maxillary teeth, and 17–21 dentary teeth (Table 2). *Cubophis* differs in at least one of these characters from all other alsophiine genera except *Hypsirhynchus*. It differs from *Hypsirhynchus* in hemipenial characters such as the presence of enlarged papillate body calyces in the basal region and medial surface of the lobes (Zaher 1999).

Content. Five species (13 species + subspecies) are included in the genus (Table 1).

Distribution. The genus is distributed in the western Caribbean: Cuba, the Cayman Islands, Bahamas, Turks and Caicos Islands, and Swan Islands (Fig. 2).

Etymology. The generic name refers to its distribution, centered on Cuba and nearby islands.

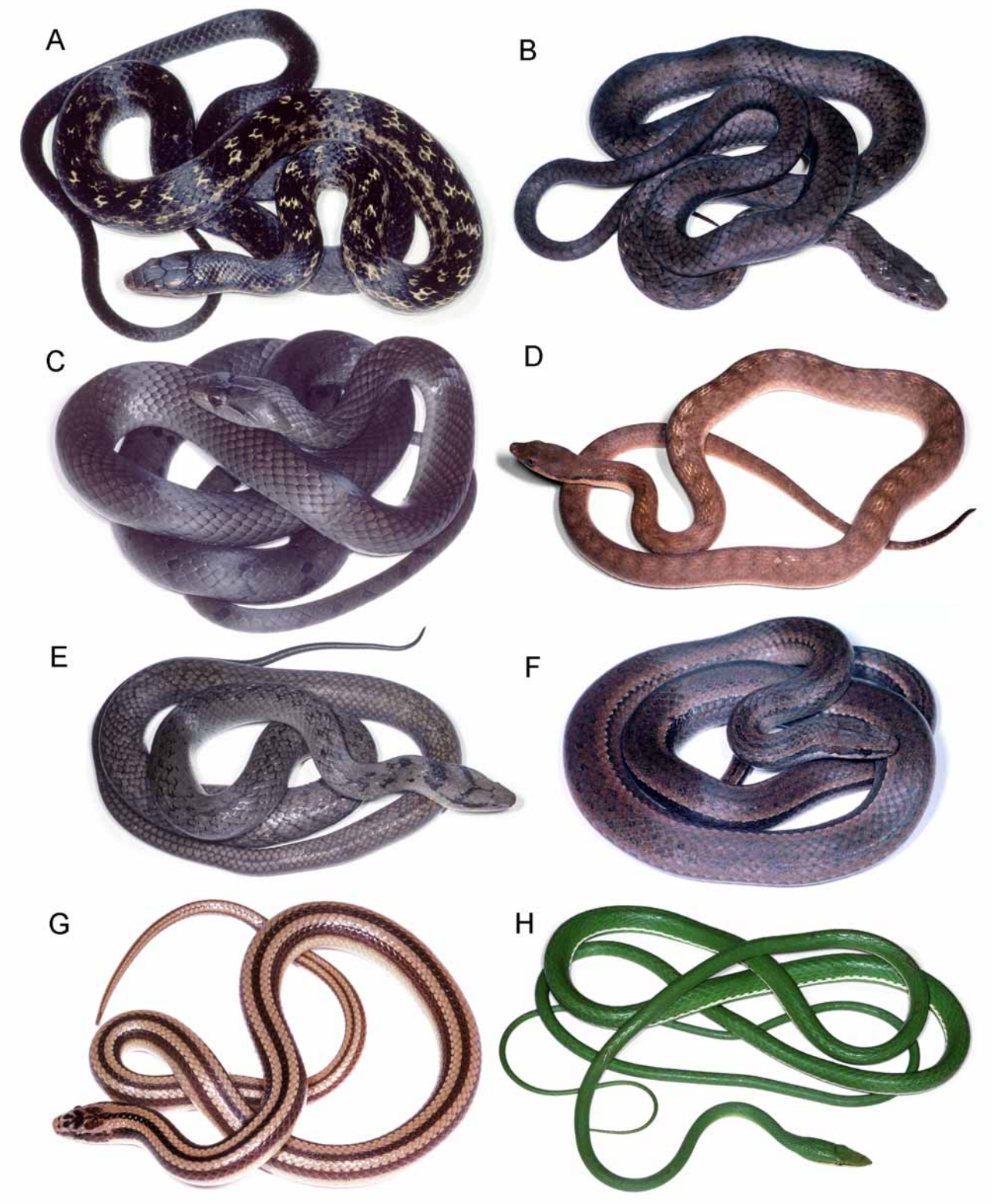

FIGURE 3. Representatives of genera of the snake Tribe Alsophiini (Dipsadidae: Xenonodontinae). Subtribe Alsophiina: *Alsophis manselli* (Woodlands Spring, Montserrat), *Borikenophis portoricensis* (1.5 km W. Playa de Tamarindo, Puerto Rico), *Cubophis cantherigerus* (2.0 km W Viñales, Pinar del Rio, Cuba), *Hypsirhynchus ferox* (Barahona, Barahona, Dominican Republic), *Ialtris dorsalis* (3 km N Bois Sec, Grand'Anse, Haiti), and *Magliophis stahli* (1.9 km NE Vista Alegre, Puerto Rico). Subtribe Arrhytonina: *Arrhyton taeniatum* (0.2 km WE Windmill Beach, Guantanamo Bay Naval Station, Cuba). Subtribe Uromacerina: *Uromacer oxyrhynchus* (4.4 km W Canada Honda, La Altagracia, Dominican Republic). Photos by S. B. Hedges.

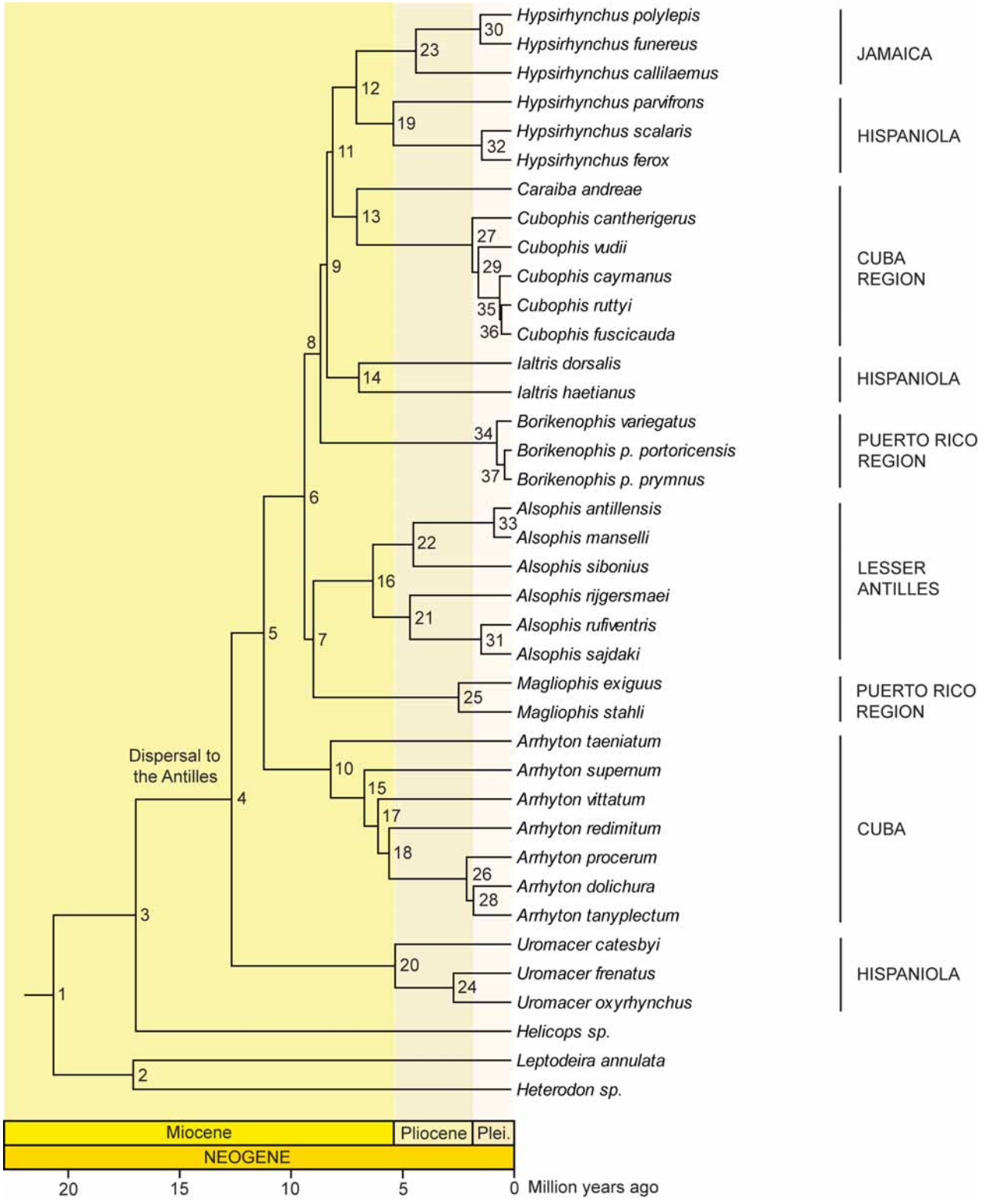

FIGURE 4. A timetree of Alsophiini. Divergence times and credibility/confidence intervals are shown in Table 3. Plei = Pleistocene. The generic taxonomy in this tree reflects the new classification proposed here and detailed in Table 1.

Remarks. Species of *Cubophis* (Fig. 3C) are large species of racers which occur sympatrically with small (*Arrhyton*) and moderate-sized (*Caraiba*) species of racers on Cuba. Our finding that the Cayman Island taxa are most closely related to *Cubophis vudii* supports their elevation from subspecies of *Cubophis cantherigerus*

to full species. Zaher et al. (2009) classified all of these species together with *Borikenophis portoricensis* and other West Indian species in *Ocyophis* Cope, but our results (Figs. 1 and 4) contradict that decision (see Remarks in *Hypsirhynchus*)

Genus *Haitiophis* Hedges & Vidal, New Genus

Type species. *Zamenis anomalus* Peters, 1863:282.

Diagnosis. The single species in this genus has 21 midbody scale rows, 207–215 ventrals, 113–130 subcaudals, 2 apical scale pits, 8 upper labials, 10 lower labials, 14 total maxillary teeth, and 18–19 dentary teeth (Table 2). *Haitiophis* differs from all other genera except *Alsophis* in its high number (21) of midbody scales, and from *Alsophis* in its low number of total maxillary teeth (14 versus 18–21) and dentary teeth (18–19 versus 21–26).

Content. One species, *Haitiophis anomalus*, is included in the genus (Table 1).

Distribution. The genus is distributed in Hispaniola, including Ile de la Tortue (Haiti) and Isla Beata (Dominican Republic) (Fig. 2).

Etymology. The generic name is derived from the Taino word Haiti (meaning high mountains) for the entire island now called Hispaniola and refers to the distribution of the genus.

Remarks. The single species of *Haitiophis* is one of the largest snakes in the family Dipsadidae, reaching 2.8 meters in total length and 2.0 meters in SVL (Powell & Henderson 1998; Thomas et al. 2007) and past morphological studies have had difficulty in determining its relationship to other alsophiine species (Maglio 1970; Zaher 1999). Our molecular evidence from the 12S and 16S rRNA genes associates *H. anomalus* with *Caraiba* and *Cubophis*, but more data are needed to place it in the phylogeny with confidence. Maglio (1970) also noted that the species is closer to a Cuban species (*Cubophis cantherigerus*) than any other in the West Indies—in having similar vomer, postorbital, and supratemporal bones. We classify it here in a separate genus because it differs considerably in scalation from either *Caraiba* or *Cubophis*. Zaher et al. (2009) classified this species with *Borikenophis portoricensis* and other West Indian species including *Cubophis vudii* and *Cubophis cantherigerus* in *Ocyophis* Cope, but our results (Figs. 1 and 4) refute that classification (see Remarks in *Hypsirhynchus*).

Genus *Hypsirhynchus* Günther, 1858

Type species. *Hypsirhynchus ferox* Günther 1858:49.

Diagnosis. Species in this genus have 17–19 midbody scale rows, 123–189 ventrals, 62–151 subcaudals, 1–2 apical scale pits, 7–8 upper labials, 9–10 lower labials, 13–21 total maxillary teeth, and 18–27 dentary teeth (Table 2). *Hypsirhynchus* differs in at least one of these characters from *Arrhyton*, *Haitiophis*, *Magliophis*, and *Uromacer*. *Alsophis* differs almost completely from *Hypsirhynchus* in ventrals (184–220 versus 123–189 in *Hypsirhynchus*). *Cubophis* differs from *Hypsirhynchus* in possessing a unique hemipenial character: enlarged papillate body calyces in the basal region and medial surface of the lobes (Zaher 1999). Most *Hypsirhynchus* have 19 midbody scales rows (*H. ater* and *H. melanichnus* have 17 rows) whereas most *Borikenophis* have 17 rows (those populations from the Virgin Islands usually have 19 rows). *Caraiba* differs from *Hypsirhynchus* in having a unique hemipenis (Zaher et al. 2009). In most *Ialtris*, maxillary teeth are grooved whereas in *Hypsirhynchus* (as in other alsophiines) they are ungrooved (Maglio 1970); in *I. haetianus* they are ungrooved. Also, most *Hypsirhynchus* have eight upper labials whereas *Ialtris* has seven upper labials; the small Jamaican *Hypsirhynchus* (*H. callilaemus*, *H. funereus*, and *H. polylepis*) have seven upper labials.

Content. Eight species (18 species + subspecies) are included in the genus (Table 1).

Distribution. The genus is distributed on Hispaniola and Jamaica (Fig. 2).

Remarks. Species of *Hypsirhynchus* (Fig. 3D) are small and moderate-sized (850 mm, maximum SVL) racers. Members of the Genus *Hypsirhynchus* included in our analysis (Figs. 1 and 4) were previously placed in three genera: "*Arrhyton*" (Jamaica), and "*Antillophis*" and *Hypsirhynchus* (Hispaniola). Here, the species formerly placed in those genera are assigned to three species groups in the Genus *Hypsirhynchus*: the *callilaemus* Group (*H. callilaemus*, *H. funereus*, and *H. polylepis*) occurring in Jamaica, the *ferox* Group (*H. ferox* and *H. scalaris*) occurring in Hispaniola, and the *parvifrons* Group (*H. parvifrons*) also occurring in Hispaniola. Members of the *callilaemus* Group have seven upper labials and nine lower labials compared with eight and 10–11 (respectively) present in other members of the genus. Members of the group also share two unique hemipenial characters (Zaher 1999), and their monophyly suggests an island radiation on Jamaica. The *ferox* Group can be distinguished from the *parvifrons* Group by its fewer subcaudals (71–93 versus 100–138, respectively). Hemipenial morphology does not suggest a relationship between the *callilaemus* Group and any other West Indian group. Instead, Zaher (1999) found unique characters uniting *Hypsirhynchus ferox*, *Haitiophis anomalus*, and *Borikenophis portoricensis*, and other characters uniting *Hypsirhynchus parvifrons*, *Ialtris haetianus*, and "*Arrhyton*" *exiguum*.

Hypsirhynchus ater from Jamaica has not been seen in about 80 years or more (Henderson 1992; Henderson & Powell 1996). Another related species, *H. capistratus*, was described from Jamaica at the same time that *H. ater* was described (Gosse 1851), but it was synonymized with *H. ater* by Boulenger (1893). Although we do not recognize *H. capistratus* here, the original description suggests that *H. capistratus* could be a valid species; additional study is needed. No tissue samples were available from any of these taxa, but morphological data suggest some tentative assignments to genus. *Hypsirhynchus ater* (and *H. capistratus*, if a valid species) lacks a loreal scale, an uncommon character (the absence of the scale) in the Subtribe Alsophiina that occurs in a few species of the genera *Hypsirhynchus* (*H. callilaemus* of Jamaica, and *H. ferox* and *H. scalaris* of Hispaniola), *Ialtris* (*I. haetianus* of Hispaniola) and *Magliophis* (*M. exiguus* of the Puerto Rican Bank). Although Zaher (1999) could not associate *H. ater* with any West Indian xenodontine based on hemipenial morphology, Maglio (1970) noted skull bone similarities with *H. ferox*.

Cochran (1941) noted that *Hypsirhynchus melanichnus* differs from species in the eastern Caribbean (genera *Alsophis* and *Borikenophis*) in lacking a furrow on the side of the head at the upper border of the upper labials. In scale counts it differs from the genera *Ialtris* and *Magliophis* in having 17 midbody scale rows (not 19 rows), and from the Genus *Borikenophis* in having 102 subcaudals (not 106–145). *Hypsirhynchus melanichnus* also has relatively large posterior upper labials compared with *Borikenophis portoricensis*, and is closer in that sense to the Genus *Hypsirhynchus*. Considering all of the morphological evidence, and while recognizing it is not strong, we tentatively assign *H. melanichnus* to the Genus *Hypsirhynchus*. In terms of biogeography, such an assignment also makes sense because other species of the genus are distributed in Hispaniola.

Recently, Zaher et al. (2009) resurrected *Ocyophis* Cope for *Hypsirhynchus ater* (type species) and included *Hypsirhynchus melanichnus*, *Haitiophis anomalus*, *Cubophis cantherigerus*, *C. vudii*, and *Borikenophis portoricensis* in the genus. Such a grouping is unsupported in our expanded molecular data set (Figs. 1 and 4). Therefore we place *Ocyophis* in the synonymy of *Hypsirhynchus*. Zaher et al. (2009) also named *Schwartzophis* for the three small Jamaican species of *Hypsirhynchus* (our *callilaemus* Group). However, while those three species have long been known to form a group, we consider it unnecessary to recognize every small cluster of species as a separate genus. Also, in this case the decision was premature because the larger Jamaican racer (*Hypsirhynchus ater*) may be part of that radiation (see above) and it carries an older generic name (*Ocyophis*) that would take priority. Therefore, we also place *Schwartzophis* in the synonymy of *Hypsirhynchus*.

Genus *Ialtris* Cope, 1862

Type species. *Philodryas dorsalis* Günther, 1858:126.

Diagnosis. Species in this genus have 19 midbody scale rows, 132–192 ventrals, 40–115 subcaudals, zero or two apical scale pits, seven upper labials, 8–9 lower labials, 18–19 total maxillary teeth, and 20–24 dentary teeth (Table 2). *Ialtris* differs in at least one of these characters from all other alsophiine genera except *Hypsirhynchus*. In most *Ialtris*, maxillary teeth are grooved whereas in *Hypsirhynchus* (as in other alsophiines) they are ungrooved; in *I. haetianus* they are ungrooved. Also, most *Hypsirhynchus* have eight upper labials whereas *Ialtris* has seven upper labials; the small Jamaican *Hypsirhynchus* (*H. callilaemus*, *H. funereus*, and *H. polylepis*) have seven upper labials (Table 2).

Content. Four species (six species + subspecies) are included in the genus (Table 1).

Distribution. The genus is distributed on Hispaniola (Fig. 2).

Remarks. *Ialtris* (Fig. 3E) includes the former Genus *Darlingtonia* with its single species (*A. haetianus*) and three subspecies (the *haetianus* Group) and the three species in the genus *Ialtris* (the *dorsalis* Group) (Table 1). Besides the strong molecular support for the monophyly of this genus, there is some morphological support as well. All four species of the Genus *Ialtris* have seven upper labials, a rare number found only in the three species of the *callilaemus* group (Jamaica) of the genus *Hypsirhynchus*, among other members of the Subtribe Alsophiina (which otherwise have eight). Also, two species of the genus *Ialtris* (*A. agyrtes* and *A. haetianus*) lack apical scale pits; such pits are present in the genera *Alsophis*, *Borikenophis*, and *Cubophis*, and absent in the Genus *Magliophis*. Thus, the Genus *Ialtris* is separable from all other genera of Alsophiina except *Hypsirhynchus*. Relationships among the genera of the Subtribe Alsophiina are not well-resolved (Fig. 1), and it might be that these two genera (*Ialtris* and *Hypsirhynchus*) occurring on Hispaniola are closest relatives.

Genus *Magliophis* Zaher et al., 2009

Type species. *Dromicus exiguus* Cope, 1862 [1863]:79.

Diagnosis. Species in this genus have 19 midbody scale rows, 137–165 ventrals, 71–102 subcaudals, no apical scale pits, eight upper labials, and nine lower labials (Table 2). *Magliophis* differs from each of the other alsophiine genera in at least one of those characters.

Content. Two species (three species + subspecies) are included in the genus (Table 1).

Distribution. Species of *Magliophis* are distributed throughout the Puerto Rican Bank (Fig. 2).

Remarks. Species of *Magliophis* (Fig. 3F) are small racers (438 mm, maximum snout-vent length, SVL) that occur sympatrically with the larger racers of the Genus *Borikenophis* on the Puerto Rican Bank. The two included species were previously placed in the Genus *Arrhyton*. The phylogenetic trees (Figs. 1 and 4) show that *Magliophis stahli* is quite divergent from *M. exiguus*, which agrees with morphology (Schwartz 1967) and supports its recognition as a distinct species rather than subspecies. Zaher et al. (2009) described this genus based on hemipenial characters in the species *M. exiguus*. Oddly, that species was omitted from their molecular phylogeny even though it was present in the data set of Vidal et al (2000), and corresponding sequences were available in GenBank.

Subtribe Arrhytonina Hedges & Vidal, New Subtribe

Type genus. *Arrhyton* Günther, 1858:244.

Diagnosis. The single genus in this subtribe has 17 midbody scale rows, 107–189 ventrals, 52–140 subcaudals, one apical scale pits, 6–7 upper labials, 7–9 lower labials, 15-20 total maxillary teeth, and 20-28 dentary teeth (Table 2). It can be distinguished from the other two subtribes in the Tribe Alsophiini by its low

number of dentary teeth (10–17 versus 17–35 in Alsophiina and Uromacerina) and a derived hemipenial character: the medial papillate crest extends from the lobular crotch to the edge of the capitulum on each lobe, and forms a Y-shaped structure on the distal region of the body (Zaher 1999).

Content. A single genus, *Arrhyton*.

Distribution. The subtribe is distributed throughout Cuba (Fig. 2).

Remarks. This subtribe represents a radiation of small, ground-dwelling species in Cuba.

Genus *Arrhyton* Günther, 1858

Type species. *Arrhyton taeniatum* Günther, 1858:244.

Diagnosis. See diagnosis for the subtribe Arrhytonina.

Content. Eight species are included in the genus (Table 1).

Distribution. The genus is distributed throughout Cuba (Fig. 2).

Remarks. Species of *Arrhyton* (Fig. 3G) are small (448 mm, maximum SVL) racers. An informal classification of Cuban *Arrhyton* was based on color pattern and scalation, especially ventral and subcaudal counts (Schwartz & Garrido 1981; Hedges & Garrido 1992). The most distinct species, morphologically, is *A. taeniatum*, because it lacks a loreal scale, has an enlarged rostral (presumably related to semi-fossorial habits), and has a boldly striped pattern. It was placed in its own species group (*taeniatum* Group) and the sequence evidence (Figs. 1 and 4), although missing *A. ainictum*, shows it to be the sister group of all other species of *Arrhyton*. The three species having high ventral scale counts and long tails (*A. dolichura*, *A. procerum*, and *A. tanyplectum*), were placed together in the *dolichura* Group, also supported by DNA evidence (Fig. 1). The remaining species, with lower ventral counts and relatively short tails, were placed in a separate group, the *vittatum* Group, though this is resolved (without maximal support) as paraphyletic in our phylogeny.

Subtribe Uromacerina Hedges & Vidal, New Subtribe

Type genus. *Uromacer* Duméril & Bibron, 1853:478.

Diagnosis. The single genus in this subtribe has 17–19 midbody scale rows, 155–212 ventrals, 159–224 subcaudals, no apical scale pits, 8–9 upper labials, 10–11 lower labials,15–20 total maxillary teeth, and 20–28 dentary teeth (Table 2). It can be distinguished from the other two subtribes in the Tribe Alsophiini by the presence of green body pigmentation.

Content. A single genus, *Uromacer.*

Distribution. The subtribe is distributed in Cuba (Fig. 2).

Remarks. This subtribe is named after the Genus *Uromacer* and should not be confused with *Uromacerina*, a genus of xenodontine snake that occurs in South America.

Genus *Uromacer* Duméril & Bibron, 1853

Type species. *Uromacer oxyrhynchus* Duméril and Bibron, 1853:722.

Diagnosis. See diagnosis for the subtribe Uromacerina.

Content. Three species (13 species + subspecies) are included in the genus (Table 1).

Distribution. The genus occurs on Hispaniola (Fig. 2).

Remarks. *Uromacer* (Fig. 3H) is known only from Hispaniola and includes three species (Table 1; Fig. 2). All are arboreal, and they are the only West Indian alsophiines occupying an arboreal niche. As is typical of arboreal species, they are slender-bodied, and two of the species (*U. frenatus* and *U. oxyrhynchus*) are more slender than *U. catesbyi* and feed exclusively on lizards; *U. catesbyi* feeds on lizards and frogs (Henderson

1984; Henderson *et al.* 1987). As expected, *U. frenatus* and *U. oxyrhynchus* are closest relatives (Figs. 1 and 4); we place them here in the *oxyrhynchus* Group and place *U. catesbyi* in the *catesbyi* Group. All three species have green on their bodies, as concealing coloration, consistent with many arboreal species of snakes. There is considerable geographic variation in morphology within at least two of the species (*U. catesbyi* and *U. frenatus*) which has led to the recognition of 12 subspecies (Table 1) (Cochran 1941; Horn 1969; Schwartz 1970, 1976), some of which may prove to be distinct species.

Timescale of alsophiine snake evolution. A timetree of alsophiine snakes using the four calibrations shows a relatively recent origin for the West Indian clade (Fig. 4), between 16.8 (23.2–12.4) Ma and 12.5 (17.4–8.92) Ma. Divergences among species or groups of species within the clade range from 12.5 (17.4–8.92) Ma to 0.41 (0.71–0.20) Ma (Table 3). Eighteen of the alsophiine taxa included in the figure (species and subspecies) diverged from their closest relatives within the Pleistocene (1.81–0.01 Ma), another nine taxa diverged from their closest relatives within the Pliocene (5.33–1.81 Ma), and the remaining eight diverged from their closest relatives within the Miocene (23.0–5.33 Ma). Lineages leading to the three subtribes arose early and approximately at the same time, between 12.5 (17.4–8.92) Ma and 11.1 (15.4–7.91) Ma.

TABLE 3. Divergence times (Ma) and their confidence/credibility intervals (CI) among Alsophiini (Serpentes, Dipsadidae, Xenodontinae). Tree nodes refer to those numbered in Fig. 4.

Node	Time	CI	Node	Time	CI	Node	Time	CI
1	20.5	28.2–16.2	14	6.80	9.62–4.53	27	1.72	2.68–1.03
2	16.9	24.4–12.3	15	6.55	9.49–4.52	28	1.67	2.61–1.02
3	16.8	23.2–12.4	16	6.16	8.83–4.31	29	1.45	2.27–0.84
4	12.5	17.4–8.92	17	5.95	8.65–4.05	30	1.36	2.16–0.79
5	11.1	15.4–7.91	18	5.45	7.75–3.73	31	1.31	2.16–0.74
6	9.24	12.8–6.56	19	5.25	7.69–3.34	32	1.29	2.16–0.65
7	8.84	12.3–6.25	20	5.17	7.66–3.36	33	0.74	1.36–0.34
8	8.52	11.9–5.90	21	4.50	6.57–2.91	34	0.62	1.16–0.30
9	8.23	11.5–5.75	22	4.36	6.17–2.90	35	0.49	0.85–0.25
10	8.05	11.4–5.53	23	4.25	6.14–2.79	36	0.41	0.71–0.20
11	7.97	11.2–5.61	24	2.55	4.05–1.47	37	0.27	0.54–0.09
12	6.91	9.87–4.73	25	2.33	3.61–1.39			
13	6.88	9.90–4.78	26	1.98	3.03–1.27			

To examine the influence of the various priors, analyses were done without selected calibrations and altering the rttm prior. After removing the molecular-based, secondary calibration point, leaving only the three geologic calibrations, the divergence time estimates dropped by an average of 8.4%. Removing the 37.2 Ma maximum geologic calibration resulted in an average change of only 0.8% in time estimates. Lowering the ingroup-root (rttm) prior by 12% to 20 Ma lowered divergence times an average of only 2.1% whereas increasing the rttm prior by about the same amount to 25 Ma resulted in an average increase in time estimates of only 0.6%. These results indicate that, as expected, the calibration priors have a larger influence on the posterior time estimates than the rttm prior, but that the differences in either case are relatively minor, especially considering the large credibility intervals.

Discussion

Phylogenetic relationships. The additional taxa and gene sequence data in this study compared with the earlier DNA sequence study of Vidal *et al.* (2000) resulted in better resolution of relationships among West Indian alsophiine snakes. It revealed that *Alsophis*, *Antillophis*, and *Arrhyton* were all three paraphyletic or polyphyletic, thus requiring a major revision of the generic classification of Maglio (1970). The nine major lineages of Alsophiini, recognized here as genera, have each strong (>95%) BP and PP support, although some of the relationships among the genera remain unresolved. One node joining seven of the genera (Subtribe Alsophiina) has strong support (100% BP and PP) and two other nodes have moderate support (72% BP, 98–100% PP). These moderately supported nodes join (A) the Cuban and Hispaniolan genera *Caraiba*, *Cubophis*, *Haitiophis* (partial data), *Hypsirhynchus*, and *Ialtris* in a clade, and (B) that clade with the Genus *Borikenophis.* In contrast, the conclusions and taxonomy of the recent study by Zaher et al. (2009) are largely unsupported. For example, their resurrected genus *Ocyophis* includes a diverse array of species here placed significantly in different parts of the tree and in four genera. Also, we find no reason to retain the genera *Antillophis* and *Darlingtonia*, which were recognized by Zaher et al. (2009).

These new phylogenetic results also shed light on ecological differences among species. One noticeable pattern is the size stratification of species in the Greater Antilles, mostly from intra-island diversification (adaptive radiation). On Cuba, there are small (*Arrhyton*), moderate-sized (*Caraiba*), and large (*Cubophis*) species of racers. On Jamaica there are small and large species of *Hypsirhynchus.* On Hispaniola there is one very large species (*Haitiophis anomalus*), small and large species of *Hypsirhynchus*, and small and large species of *Ialtris*. Finally, on the Puerto Rican Bank there are small racers (*Magliophis*) and larger racers (*Borikenophis*). Now, with a general phylogenetic framework, and with additional, detailed, ecological and phylogenetic work (e.g., Henderson & Sajdak 1996), it should be possible to better understand the ecological and evolutionary origin of this body size stratification and the adaptive radiation of alsophiines in general.

Biogeography. The divergence time estimate here for earliest colonization of the West Indies by alsophiine snakes, 16.8 (23.2–12.4) Ma, rejects models of Caribbean snake biogeography that espouse proto-Antillean vicariance (~70 Ma) (Rosen 1975) or a mid-Cenozoic land-bridge (~33 Ma) (Iturralde-Vinent & MacPhee 1999). Instead, they indicate that the group radiated subsequent to dispersal over ocean water at a time when there were no connections to the mainland (Hedges *et al.* 1992; Hedges 2001; Hedges 2006). Because the closest relatives of alsophiines are in South America (Vidal *et al.* 2000) they must have arrived by dispersal. Unfortunately, the relationships of the genera of alsophiines are not resolved sufficiently in this study to assist in reconstructing their historical biogeography except in some general terms.

The most surprising biogeographic pattern to emerge is the close correspondence between the relationships of species and geography (Fig. 2). This is considerably different from the previous concept of West Indian xenodontine phylogeny (Maglio 1970), which proposed multiple dispersals (instead of one) from the mainland, and widely distributed genera (e.g., *Alsophis*, *Arrhyton*, and *Antillophis*) in the West Indies. The new phylogeny and classification reveals that those previous groupings were based at least partly on morphological convergences, and that most—but not all—evolutionary radiation has occurred within islands or island banks rather than between islands. Also, most (18 of 35) of the taxa studied diverged relatively recently, in the Pleistocene, when glacial cycles were causing major changes in sea level and climate, potentially facilitating isolation and speciation.

Because two of the three subtribes (Alsophiina and Uromacerina) contain Cuban and Hispaniolan species and the third subtribe (Arrhytonina) is Cuban, this suggests that the initial colonization and diversification occurred on Cuba or Hispaniola. The origin of the Jamaican *Hypsirynchus* from Hispaniola is consistent with the east-to-west current flow. However, colonization of the Puerto Rican Bank and, especially, the northern Lesser Antilles, is not consistent with current flow. The Isthmus of Panama was open prior to ~3 Ma, and some early current patterns were different (Iturralde-Vinent and MacPhee 1999; Hedges 2006), but the general east-to-west pattern was still present before ~3 Ma. The colonization of the northern Lesser Antilles by Greater Antillean alsophiines, anole lizards, teiid lizards (Hower & Hedges 2003), and frogs (Heinicke *et*

al. 2007) is therefore a conundrum. Certainly, instances of low sea level, such as occurred at the end of the Miocene (~5–6 Ma), and subsequently during intervals in the Pliocene and Pleistocene, would have facilitated dispersal over land that connected some islands, but it is unclear whether all of the islands in the northern Lesser Antilles would have been interconnected. Alternatively, that distribution pattern could be explained by different current patterns at times in the past. As timetrees from more groups of Antillean organisms become available, it should be possible to better understand distributional patterns like this one that are currently unexpected.

Acknowledgements

This work was funded by the Service de Systématique moléculaire, Institut de Systématique to N.V., by grants from the U.S. National Science Foundation to S.B.H., and by the Consortium National de Recherche en Génomique, Genoscope. S.B.H. thanks the representatives of the various governments involved in the West Indies for permission to collect and export specimens, and the many persons who assisted him in the field, especially Richard Thomas. Some additional tissues were provided by Michel Breuil, Karim Daoues, Robert Henderson, Ulrich Kuch, Miguel Landestoy, James Lazell, Luke Mahler, Anita Malhotra, Robert Powell, Olivier Pauwels, and Yann Surget-Groba. Colin McCarthy and Robert Henderson assisted S.B.H. in evaluation of the taxonomic status of some species, and Patrick David assisted with nomenclatural issues. Permission to use the vertebrate animals in this study was provided by the Institutional Animal Care and Use Committee (#24460) of Pennsylvania State University.

References

Augé, M. & Rage, J.-C. (2000) Les Squamates (Reptilia) du Miocène moyen de Sansan. *Mémoires du Muséum National d'Histoire Naturelle*, 183, 263–313.

Barbour, T., & Ramsden, C.T. (1919) The Herpetology of Cuba. *Memoirs of the Museum of Comparative Zoology*, 47, 71–213.

Bibron, G. (1840) Plate 27. *In*: de la Sagra, R., *Historia física, politica y natural de la Isla de Cuba*. Arthus Bertrand, Paris.

Boulenger, G.A. (1893) *Catalogue of snakes in the British Museum (Natural History). Vol. 1*, Longmans and Company, London, 448 pp.

Breuil, M. (2002) *Histoire naturelle des amphibiens et reptiles terrestres de l'archipel Guadeloupéen*. Muséum National d'Histoire Naturelle, Paris, 339 pp.

Burbrink, F.T. & Pyron, R.A. (2008) The taming of the skew: Estimating proper confidence intervals for divergence dates. *Systematic Biology*, 57, 317–328.

Burbrink, F.T., Lawson, R. & Slowinski, J.B. (2000) Mitochondrial DNA phylogeography of the polytypic North American ratsnake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution*, 54, 2107–2118.

Cadle, J.E. (1984) Molecular systematics of xenodontine colubrid snakes: I. South American xenodontines. *Herpetologica*, 40, 8–20.

Cadle, J.E. (1985) The Neotropical colubrid snake fauna: lineage components and biogeography. *Systematic Zoology*, 34, 1–20.

Cadle, J.E. & Greene, H.W. (1993) Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. *In*: Ricklefs, R.E. & Schluter, D. (Eds.), *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, pp. 281–293.

Carlquist, S. (1965) *Island life. A natural history of the islands of the World*. Natural History Press, Garden City, New York, 451 pp.

Cochran, D.M. (1941) The herpetology of Hispaniola. *Bulletin of the U.S. National Museum*, 177, 1–398.

Cope, E.D. (1862 [1863]) Synopsis of the species of *Holcosus* and *Ameiva*, with diagnoses of new West Indian and South American Colubridae. *Proceedings of the Academy of Natural Sciences*, Philadelphia, 14, 60–82.

Crother, B.I. (1999) Phylogenetic relationships among West Indian xenodontine snakes (Serpentes; Colubridae) with comments on the phylogeny of some mainland xenodontines. *Contemporary Herpetology*, 1999, 1–21. Available: http://www.contemporaryherpetology.org/ch/1999/2/index.htm

Crother, B.I. & Hillis, D.M. (1995) Nuclear ribosomal DNA restriction sites, phylogenetic information, and the phylogeny of some xenodontine (Colubridae) snakes. *Journal of Herpetology*, 29, 316–320.
De Queiroz, A., Lawson, R. & Lemos-Espinal, J.A. (2002) Phylogenetic relationships of North American garter snakes (*Thamnophis*) based on four mitochondrial genes: how much DNA sequence is enough? *Molecular Phylogenetics and Evolution*, 22, 315–329.
Donovan, S.K. (2002) A karst of thousands: Jamaica's limestone scenery. *Geology Today*, 18, 143–151.
Dowling, H.G. (1975) A provisional classification of snakes. *In*: Dowling, H. G. (Ed.), *1974 yearbook of herpetology.* Herpetological Information Search Systems, The American Museum of Natural History, New York, pp. 167–170.
Duméril, A.M.C., & Bibron, G. (1853) Prodrome de la classification des reptiles ophidiens. *Mémoires de l'Académie des Sciences de l'Institut de France*, 23, 478.
Dunn, E.R. (1932) The colubrid snakes of the Greater Antilles. *Copeia*, 1932, 89–92.
Fitzinger, L. (1843) *Systema reptilium*. Braumüller et Seidel Bibliopolas, Wien, 106 pp.
Forstner, M.R.J., Davis, S.K. & Arévalo, E. (1995) Support for the hypothesis of anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 4, 93–102.
Gosse, P.H. (1851) *A Naturalist's Sojurn in Jamaica*. Longman, Brown, Green and Longmans, London. 508 pp.
Grant, C. (1940) The herpetology of the Cayman Islands. *Bulletin of the Institute of Jamaica*, 2, 1–65.
Grant, C., Smith, H. M., & Alayo, P. (1959) The status of the snakes of the genus *Arrhyton* in Cuba. *Herpetologica*, 15, 129–133.
Günther, A. (1858) *Catalogue of colubrine snakes of the British Museum.* British Museum, London, 281 pp.
Hall, T.A. (1999) Bioedit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
Hass, C.A., Maxson, L.R. & Hedges, S.B. (2001) Relationships and divergence times of West Indian amphibians and reptiles: insights from albumin immunology. *In*: Woods, C.A. & Sergile, F.E. (Eds.), *Biogeography of the West Indies: patterns and perspectives*. CRC Press, Boca Raton, Florida, pp. 157–174.
Hedges, S.B. (1994) Molecular evidence for the origin of birds. *Proceedings of the National Academy of Sciences USA*, 91, 2621–2624.
Hedges, S.B. (1996a) Historical biogeography of West Indian vertebrates. *Annual Review of Ecology and Systematics*, 27, 163–196.
Hedges, S.B. (1996b) The origin of West Indian amphibians and reptiles. *In*: Powell, R. & Henderson, R.W. (Eds.), *Contributions to West Indian herpetology: a tribute to Albert Schwartz.* Society for the Study of Amphibians and Reptiles. Ithaca, New York, pp. 95–128.
Hedges, S.B. (2001) Caribbean biogeography: an outline. *In*: Woods, C.A., & Sergile, F.E. (Eds.), *Biogeography of the West Indies: Patterns and Perspectives*. CRC Press, Boca Raton, Florida, pp. 15–33.
Hedges, S.B. (2002) Morphological variation and the definition of species in the snake genus *Tropidophis* (Tropidophiidae). *Bulletin of Natural History Museum (London), Zoology Series*, 68, 83–90.
Hedges, S.B. (2006) Paleogeography of the Antilles and origin of West Indian terrestrial vertebrates. *Annals of the Missouri Botanical Garden*, 93, 231–244.
Hedges, S.B. & Garrido, O.H. (1992) Cuban snakes of the genus *Arrhyton*: two new species and a reconsideration of *A. redimitum* Cope. *Herpetologica*, 48, 168–177.
Hedges, S.B., Hass, C.A. & Maxson, L.R. (1992) Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proceedings of the National Academy of Sciences USA*, 89, 1909–1913.
Heinicke, M.P., Duellman, W.E. & Hedges, S.B. (2007) Major Caribbean and Central American frog faunas originated by oceanic dispersal. *Proceedings of the National Academy of Sciences USA*, 104, 10092–10097.
Henderson, R.W. (1984) The diets of Hispaniolan colubrid snakes. 1. Introduction and prey genera. *Oecologia*, 62, 234–239.
Henderson, R.W. (1990) A new subspecies of *Alsophis antiguae* (Parker) from Great Bird Island (Antigua), Lesser Antilles. *Caribbean Journal of Science*, 25, 119–122.
Henderson, R.W. (1992) Consequences of predator introductions and habitat destruction on amphibians and reptiles in the post-Columbus West Indies. *Caribbean Journal of Science*. 28, 1–10.
Henderson, R.W. & Powell, R. (1996) *Alsophis ater. Catalogue of American Amphibians and Reptiles*, 633, 1–2.
Henderson, R.W. & Powell, R. (1996) *Alsophis sanctaecrucis*. *Catalogue of American Amphibians and Reptiles*, 634, 1–2.
Henderson, R.W., Powell, R., Daltry, J.C. & Day, M.L. (1996) *Alsophis antiguae*. *Catalogue of American Amphibians and Reptiles*, 632, 1–3.
Henderson, R.W. & Sajdak, R.A. (1996) Diets of West Indian racers (Colubridae: *Alsophis*): Composition and biogeographic implications. *In*: Powell, R. & Henderson, R.W. (Eds.), *Contributions to West Indian herpetology: a tribute to Albert Schwartz.* Society for the Study of Amphibians and Reptiles. Ithaca, New York, pp. 327–338.
Henderson, R.W., Schwartz, A. & Noeskehallin, T.A. (1987) Food habits of three colubrid tree snakes (Genus *Uromacer*)

on Hispaniola. *Herpetologica*, 43, 241–248.
Horn, H.S. (1969) Polymorphism and evolution of the Hispaniola snake genus *Uromacer* (Colubridae). *Breviora, Museum of Comparative Zoology*, 324, 1–23.
Hower, L.M. & Hedges, S.B. (2003) Molecular phylogeny and biogeography of West Indian teiid lizards of the genus *Ameiva*. *Caribbean Journal of Science*, 39, 298–306.
Iturralde-Vinent, M.A. & MacPhee, R.D.E. (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, 238, 1–95.
IUCN (2008) IUCN Redlist of Threatened Species. Available from http://www.iucnredlist.org/ (accessed 21 December 2008).
Knight, A. & Mindell, D.P. (1994) On the phylogenetic relationships of Colubrinae, Elapidae and Viperidae and the evolution of front fanged venom systems in snakes. *Copeia*, 1994, 1–9.
Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Villablanca, F.X. & Wilson, A.C. (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences USA*, 86, 6196–6200.
Kumazawa, Y., Ota, H., Nishida, M. & Ozawa, T. (1996) Gene rearrangements in snake mitochondrial genomes: highly concerted evolution of control-region-like sequences duplicated and inserted into a tRNA gene cluster. *Molecular Biology and Evolution*, 13, 1242–1254.
Lazell, J.D., Jr. (1967) Wiederentdeckung von zwei angeblich ausgestorbenen Schlangenarten der westindischen Inseln. *Salamandra*, 3, 91–97.
Lynn, W. G., & Grant, C. (1940) The Herpetology of Jamaica. *Bulletin of the Institute of Jamaica, Science Series*, 1, 1–148.
Maglio, V.J. (1970) West Indian xenodontine colubrid snakes: their probable origin, phylogeny, and zoogeography. *Bulletin of the Museum of Comparative Zoology*, 141, 1–54.
Mitchell, S.F. (2004) Lithostratigraphy and palaeogeography of the White Limestone Group. *Cainozoic Research*, 3, 5–30.
Myers, C.W. (1973) A new genus for Andean snakes related to *Lygophis boursieri* and a new species (Colubridae). *American Museum Novitates*, 2522, 1–37.
Palumbi, S.R., Martin, A., Romano, S., Mcmillan, W.O., Stice, L. & Grabowski, G. (1991) *The simple fool's guide to P.C.R.*, Univ. of Hawaii Press, Honolulu, 43 pp.
Parker, H.W. (1933) Some amphibians and reptiles from the Lesser Antilles. *Annals of the Magazine of Natural History*, 11, 151–158.
Peters, W.C.H. (1863) Uber einige neue oder weniger bekannte Schlangenarten des zoologischen Museums zu Berlin. *Monatsbericht Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1863, 272–289.
Philippe, H. (1993) MUST2000: a computer package of management utilities for sequences and trees. *Nucleic Acids Research*, 21, 5264–5272.
Pinou, T., Vicario, S., Marschner, M. & Caccone, A. (2004) Relict snakes of North America and their relationships within caenophidia, using likelihood-based Bayesian methods on mitochondrial sequences. *Molecular Phylogenetics and Evolution*, 32, 563–574.
Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
Powell, R. & Henderson, R.W. (1994) *Ialtris. Catalogue of American Amphibians and Reptiles*, 590, 1–2.
Powell, R. & Henderson, R.W. (1998) *Alsophis anomalus. Catalogue of American Amphibians and Reptiles*, 659, 1–2.
Powell, R. & Henderson, R.W. (1998) *Alsophis melanichnus*. *Catalogue of American Amphibians and Reptiles*, 660, 1–2.
Powell, R., Henderson, R.W., Adler, K. & Dundee, H.A. (1996) An annotated checklist of West Indian amphibians and reptiles. *In*: Powell, R. & Henderson, R.W. (Eds.), *Contributions to West Indian Herpetology: a tribute to Albert Schwartz*. Society for the Study of Amphibians and Reptiles, S.S.A.R., Ithaca, New York, pp. 51–93.
Reinhardt, J. & Lütken, C.F. (1862) Bidrag tii det vestindiske Öriges og navnligen tii de dansk-vestindiske Oers Herpetologie. *Vidensk. Meddel. Naturhist. For. Kjöbenhavn*, 153–291.
Ronquist, F. & Huelsenbeck, J.P. (2003) Mr Bayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
Rosen, D.E. (1975) A vicariance model of Caribbean biogeography. *Systematic Zoology*, 24, 431–464.
Ruibal, R. (2003) Introduction. *In*: Barbour, T. & C. T. Ramsden, *The herpetology of Cuba*. Facsimile Reprints in Herpetology, Society for the Study of Amphibians and Reptiles, Ithaca, New York, pp. iii–vii.
Schlegel, H. (1837) *Essai sur la physionomie des serpens*. Kips et van Stockum, La Haye, The Netherlands, 606 pp.
Schmidt, K.P. (1926) The amphibians and reptiles of Mona Island, West Indies. *Field Museum Natural History Series*, 12, 149–163.
Schwartz, A. (1966) Snakes of the genus *Alsophis* in Puerto Rico and the Virgin Islands. *Studies on the Fauna of Curacao and Other Caribbean Islands*, 90, 177–227.
Schwartz, A. (1967) A review of the genus *Dromicus* in Puerto Rico and the Virgin Islands. *Stahlia*, 9, 1–14.

Schwartz, A. (1970) A systematic review of *Uromacer catesbyi* Schlegel (Serpentes, Colubridae). *Tulane Studies in Zoology and Botany*, 16, 131–149.
Schwartz, A. (1971) A systematic review of the Hispaniolan snake genus *Hypsirhynchus*. *Studies on the Fauna of Curacao and Other Caribbean Islands*, 128, 63–94.
Schwartz, A. (1976) Variation in the Hispaniola colubrid snake *Uromacer frenatus* Günther (Reptilia, Serpentes, Colubridae). *Journal of Herpetology*, 10, 319–327.
Schwartz, A. & Garrido, O.H. (1981) A review of the Cuban members of the genus *Arrhyton* (Reptilia, Serpentes, Colubridae). *Annals of the Carnegie Museum of Natural History*, 50, 207–230.
Schwartz, A. & Henderson, R.W. (1991) *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*. University of Florida Press, Gainesville, 720 pp.
Schwartz, A., & Rossman, D.A. (1976) A review of the Hispaniolan colubrid snake genus *Ialtris*. *Studies on the Fauna of Curacao and Other Caribbean Islands*, 50, 76–102.
Schwartz, A. & Thomas, R. (1965) The Genus *Darlingtonia* (Serpentes) in Hispaniola including a new subspecies from the Dominican Republic. *Breviora*, 229, 1–10.
Stamatakis, A. (2006) RAxML-VI-HPC: Maximum Likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML Web-Servers. *Systematic Biology*, 57, 758–771.
Thomas, R., Henderson, R.W., Powell, R. & Rodríguez, P.G. (2007) *Alsophis anomalus* (Hispaniolan Brown Racer). *Herpetological Review*, 38, 338–339.
Thomas, R.A. (1997) Galapagos terrestrial snakes: biogeography and systematics. *Herpetological Natural History* 5, 19–40.
Thorne, J.L. & Kishino, H. (2002) Divergence time and evolutionary rate estimation with multilocus data. *Systematic Biology*, 51, 689–702.
Uetz, P., Goll, J. & Hallerman, J. (2008) *The TIGR Reptile Database*. Available: http://www.reptile-database.org/ (Accessed: August 4, 2008).
Vidal, N. (2002) Colubroid systematics: evidence for an early appearance of the venom apparatus followed by extensive evolutionary tinkering. *Journal of Toxicology – Toxin Reviews*, 21, 21–41.
Vidal, N. & Hedges, S.B. (2002a) Higher-level relationships of snakes inferred from four nuclear and mitochondrial genes. *Comptes Rendus Biologies*, 325, 977–985.
Vidal, N. & Hedges, S.B. (2002b) Higher-level relationships of caenophidian snakes inferred from four nuclear and mitochondrial genes. *Comptes Rendus Biologies*, 325, 987–995.
Vidal, N. & Hedges, S.B. (2005) The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes Rendus Biologies*, 328, 1000–1008.
Vidal, N., Kindl, S.G., Wong, A. & Hedges, S.B. (2000) Phylogenetic relationships of xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences, *Molecular Phylogenetics and Evolution*, 14, 389–402.
Vidal, N., Delmas, A.-S., David, P., Cruaud, C., Couloux, A. & Hedges, S.B. (2007) The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. *Comptes Rendus Biologies*, 330, 182–187.
Vidal, N., Rage, J.-C., Couloux, A. & Hedges, S.B. (2009) Snakes (Serpentes). *In*: Hedges, S.B. & Kumar, S. (Eds.), *The Timetree of Life*. Oxford University Press, New York, pp. 390–397.
Wiens, J.J., Brandley, M.C. & Reeder, T.W. (2006) Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. *Evolution*, 60, 123–141.
Winnepenninckx, B., Backeljau, T. & Dewachter, R. (1993) Extraction of high molecular weight DNA from molluscs. *Trends in Genetics*, 9, 407.
Yang, Z. & Yoder, A.D. (2003) Comparison of likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. *Systematic Biology*, 52, 705–716.
Yang, Z. (1997) PAML: a program package for phylogenetic analysis by maximum likelihood. *CABIOS*, 13, 555–556.
Zaher, H. (1999) Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 240, 1–168.
Zaher, H., Grazziotin, F.G., Cadle, J.E., Murphy, R.W., Moura-Leite, J.C. & Bonatto, S.L. (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South America xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia*, 49,115–153.

Appendix

List of taxa used for this study, specimen numbers, geographic origin, and DNA sequence accession numbers. In each case, the first number listed (before the locality) is the museum catalog number (if known) followed by the tissue collection catalog number. Abbreviations are: AM (Anita Malhotra, Bangor University, U.K.), SBH (S. Blair Hedges, Pennsylvania State University, U.S.A.), NV (Nicolas Vidal, Muséum National d'Histoire Naturelle, Paris, France), and USNM (National Museum of Natural History, Washington, D.C., U.S.A.). The 168 sequences generated for this work have been deposited in GenBank under accession numbers FJ416691–FJ416856 and FJ666091–FJ666092. They are listed after the locality, in the following gene order: 12S, 16S, cytochrome b, ND4, ND2, and RAG2.

Alsophis antillensis (SBH 266740, Guadeloupe, Basse Terre, Capesterre belle-eau, FJ416691, FJ416702, FJ416726, FJ416800, FJ416764, FJ416837); *Alsophis manselli* (SBH 192791, Montserrat, St. Peter, Woodlands Spring, AF158459, AF158528, FJ416727, FJ416801, FJ416765, FJ416838); *Alsophis rijgersmaei* (SBH 266429, Anguilla; FJ416697, FJ416708, FJ416729, FJ416803, FJ416767, FJ416840); *Alsophis rufiventris* (AM, Saba, FJ416698, FJ416709, FJ416730, FJ416804, FJ416768, FJ416841); *Alsophis sajdaki* (SBH 194104, Antigua, Great Bird Island, AF158455, AF158524, FJ416731, FJ416805, FJ416769, FJ416842); *Alsophis sibonius* (SBH 268000, Dominica, Cabrits, FJ416692, FJ416703, FJ416728, FJ416802, FJ416766, FJ416839); *Arrhyton dolichura* (USNM 306534, SBH 172601, Cuba, Ciudad de la Habana Prov., Jardin Botánico Nacional [14 k S, 5.3 km E of Old Havana Center (airline)], AF158438, AF158507, FJ416721, FJ416795, FJ416759, FJ416832); *Arrhyton procerum* (SBH 191526, Cuba, Matanzas Prov., 11.4 km ESE Playa Girón, AF158452, AF158521, FJ416723, FJ416797, FJ416761, FJ416834); *Arrhyton redimitum* (USNM 335891, SBH 161985, Cuba, Guantanamo Bay USNS, Blue Beach, AF158439, AF158508, FJ416720, FJ416794, FJ416758, FJ416831); *Arrhyton supernum* (SBH 190230, Cuba, Guantánamo Prov., SW slope El Yunque de Baracoa, AF158436, AF158505, FJ416718, FJ416792, FJ416756, FJ416829); *Arrhyton taeniatum* (SBH 191163, Cuba, Guantánamo Prov., 2 km N La Munición, AF158453, AF158522, FJ416717, FJ416791, FJ416755, FJ416828); *Arrhyton tanyplectum* (USNM 306538, SBH 191492, Cuba, Pinar de Río Prov., 4.0 km NW San Vicente, AF158446, AF158516, FJ416722, FJ416796, FJ416760, FJ416833); *Arrhyton vittatum* (SBH 191528, Cuba, Pinar del Río Prov., Soroa, AF158437, AF158506, FJ416719, FJ416793, FJ416757, FJ416830); *Borikenophis portoricensis prymnus* (USNM 327162, SBH 160062, United States, Puerto Rico, 1.5 km W [airline] Playa de Tamarindo, AF158448, AF158517, FJ416733, FJ416807, FJ416771, FJ416844); *Borikenophis portoricensis portoricensis* (SBH 101830, Puerto Rico, Rio Piedras, FJ416696, FJ416707, FJ416732, FJ416806, FJ416770, FJ416843); *Borikenophis portoricensis anegadae* (SBH 267836, British Virgin Islands, Guana Island), all sequences are identical to those from *Borikenophis portoricensis portoricensis* (SBH 101830); *Borikenophis variegatus* (SBH266424, Puerto Rico, Mona Island, southwest corner, FJ416700, FJ416711, FJ416734, FJ416808, FJ416772, FJ416845); *Caraiba andreae* (USNM 335887, SBH 172603, Cuba, Pinar de Río Prov., Soroa, AF158442, AF158511, FJ416743, FJ416817, FJ416781, FJ416854); *Cubophis cantherigerus* (NV, Cuba, AF158405, AF158475, AF544669, FJ416818, FJ416782, EF144109); *Cubophis caymanus* (SBH 267081, Cayman Islands, Grand Cayman, near Botanic Park, FJ416693, FJ416704, FJ416745, FJ416820, FJ416784, FJ416856); *Cubophis fuscicauda* (SBH 266565, Cayman Islands, Cayman Brac, West End, FJ416695, FJ416706, FJ416747, FJ416822, FJ416786); *Cubophis ruttyi* (SBH 266495, Cayman Islands, Little Cayman, South Town, FJ416699, FJ416710, FJ416746, FJ416821, FJ416785); *Cubophis vudii* (SBH 192985, Bahamas, New Providence, Nassau, west end, Sandy Port Development, AF158443, AF158512, FJ416744, FJ416819, FJ416783, FJ416855); *Haitiophis anomalus* (SBH 268413, Dominican Republic; Independencia; near Batey Nuevo, FJ666091, FJ666092); *Hypsirhynchus callilaemus* (USNM 328394, SBH 172463, Jamaica, St. Mary Prov., 2.9 km N Port Maria, AF158440, AF158509, FJ416737, FJ416811, FJ416775, FJ416848); *Hypsirhynchus ferox* (USNM 329438, SBH 101393, Dominican Republic, Barahona Prov., vicinity Barahona, AF158447, AF158515, FJ416742, FJ416816, FJ416780, FJ416853); *Hypsirhynchus funereus* (USNM 328400, SBH 172462, Jamaica, St. Mary Prov., 2.9 km N Port Maria, AF158451, AF158520, FJ416739, FJ416813, FJ416777, FJ416850); *Hypsirhynchus parvifrons* (USNM 329378, SBH 103086, Dominican Republic, Barahona Prov., 19.5 km SW Barahona, AF158441, AF158510, FJ416740, FJ416814, FJ416778, FJ416851); *Hypsirhynchus polylepis* (USNM 328392, SBH 101581, Jamaica, Portland Prov., 3 km S Alligator Church, AF158450, AF158519, FJ416738, FJ416812, FJ416776, FJ416849); *Hypsirhynchus scalaris* (SBH 191992, Haiti, Dept. de la Grand' Anse, 0.8 km E Dame-Marie, AF158449, AF158518, FJ416741, FJ416815, FJ416779, FJ416852); *Ialtris dorsalis* (USNM 329439, SBH 103702, Haiti, Grand' Anse, ca. 3 km N Bois Sec, AF158456, AF158525, FJ416735, FJ416809, FJ416773, FJ416846); *Ialtris haetianus* (USNM 329419, SBH 103806, Haiti, Grande'Anse, ca. 2-3 km S Castillion, AF158458, AF158527, FJ416736, FJ416810, FJ416774, FJ416847); *Magliophis exiguus* (SBH 266833, U.S. Virgin Islands, St. Thomas, Santa Maria, FJ416694, FJ416705, FJ416724, FJ416798, FJ416762, FJ416835); *Magliophis stahli* (USNM 327164, SBH 160050, United States, Puerto Rico, 1.9 km NE Vista Alegre, AF158457, AF158526, FJ416725, FJ416799, FJ416763, FJ416836); *Uromacer catesbyi* (SBH 192456, Dominican Republic, La Altagracia

Prov., 4.4 km W Cañada Honda, AF158454, AF158523, FJ416714, FJ416788, FJ416752, FJ416825); *Uromacer frenatus* (USNM 329444, SBH 104668, Haiti, Dept. de la Grand' Anse, ca. 6 km E Jérémie, AF158444, AF158513, FJ416715, FJ416789, FJ416753, FJ416826); *Uromacer oxyrhynchus* (SBH 192457, Dominican Republic, La Altagracia Prov., 4.4 km W Cañada Honda, FJ416701, FJ416712, FJ416716, FJ416790, FJ416754, FJ416827).

Non-alsophiine samples: *Helicops angulatus* (NV, RN1 road between Kourou and Petit Saut, 22 km from Kourou, French Guiana, 12S: AF158408, 16S: AF158478, cytochrome b: AF471037, ND2: FJ416751, RAG2: FJ416824); *Helicops infrataeniatus* (ND4: U49310); *Heterodon nasicus* (NV, captive born, 12S: AF158428, 16S: AF158494); *Heterodon nasicus* (ND4: Forstner *et al.* (1995)); *Heterodon simus* (cytochrome b: AF217840); *Heterodon platyrhinos* (SBH 268311, United States, unknown locality, ND2: FJ416750, RAG2: FJ416823); *Leptodeira annulata* (NV, Kaw, French Guiana, AF158404, AF158473, FJ416713, FJ416787, FJ416749, EF144108); *Xenochrophis flavipunctatus* (NV, CUB MZ R 1998.12.11.16, Ban Had Sai, Ban Lat District, Phetchaburi Province, Thailand, 12S: AF544780, 16S: AF544809, ND2: FJ416748, RAG2: EF144112); *Xenochrophis punctulatus* (cytochrome b: AF544714); *Xenochrophis trianguligerus* (ND4: U49321).