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Phylogenetic Relationships of Xenodontine Snakes Inferred from 12S and 16S Ribosomal RNA Sequences

Nicolas Vidal,*,†,‡ Shannon G. Kindl,§ Alan Wong,§ and S. Blair Hedges§

*Service de Systématique Moléculaire, Institut de Systématique (CNRS FR 1541), Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris Cedex 05, France; †Laboratoire d'Anatomie Comparée (CNRS URA 1137), Muséum National d'Histoire Naturelle, 55 rue Buffon, 75231 Paris Cedex 05, France; ‡Programme Faune Sauvage, EDF-CNEH, Savoie Technolac, 73373 Le Bourget du Lac Cedex, France; and §Department of Biology and Institute of Molecular Evolutionary Genetics, 208 Mueller Lab, Pennsylvania State University, University Park, Pennsylvania 16802

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The phylogenetic relationships of xenodontine snakes are inferred from sequence analyses of portions of two mitochondrial genes (12S and 16S ribosomal RNA) in 85 species. Although support values for most of the basal nodes are low, the general pattern of cladogenesis observed is congruent with many independent molecular, morphological, and geographical data. The monophyly of xenodontines and the basal position of North American xenodontines in comparison with Neotropical xenodontines are favored, suggesting an Asian–North American origin of xenodontines. West Indian xenodontines (including endemic genera and members of the genus *Alsophis*) appear to form a monophyletic group belonging to the South American clade. Their mid-Cenozoic origin by dispersal using ocean currents is supported. Within South American mainland xenodontines, the tribes Hydropsini, Pseudoboini, and Xenodontini are monophyletic. Finally, our results suggest that some morphological and ecological traits concerning maxillary dentition, macrohabitat use, and foraging strategy have appeared multiple times during the evolution of xenodontine snakes.

Key Words: **phylogeny; evolution; 12S rRNA; 16S rRNA; Colubridae; Xenodontinae; Neotropics; West Indies; biogeography; venomous apparatus; plasticity.**

INTRODUCTION

Colubroids or advanced snakes form a monophyletic group (Dessauer *et al.,* 1987; Cadle, 1988; Heise *et al.,* 1995) comprising four families: Atractaspididae (14 genera, 65 species), Colubridae (290 genera, 1700 species), Elapidae (63 genera, 272 species), and Viperidae (30 genera, 230 species) (Greene, 1997). The majority of colubroid snakes belong to the family Colubridae, which has been shown to be paraphyletic (Heise *et al.,* 1995; Kraus and Brown, 1998). The American "colubrid" snake fauna comprises three major subfamilies: the Natricinae, the Colubrinae, and the Xenodontinae. The latter is one of the largest subfamilies of snakes with about 90 genera and more than 500 species, all restricted to the New World (Cadle and Greene, 1993). Xenodontines are primarily tropical species, with most occurring in Central America, South America, and the West Indies. They vary greatly in body length (10–250 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. Unfortunately, the phylogenetic relationships of this large group of tropical vertebrates are not well known, which limits understanding of their historical biogeography and general evolutionary history.

The defining character of subfamily Xenodontinae has been the forked sulcus spermaticus of the hemipenis (Cope, 1893; Dunn, 1928), but the usefulness of that character has been questioned in recent years (Cadle, 1984c). The most comprehensive molecular studies of xenodontine snakes have been those involving albumin immunological data (Cadle, 1984a,b,c, 1985). In those studies, the monophyly of the subfamily was not supported, but two major lineages were defined: the South American and the Central American xenodontines (based on respective centers of diversity). Relationships of the six primarily North American xenodontine genera (*Carphophis, Conophis, Contia, Diadophis, Farancia,* and *Heterodon*) are unresolved, and these genera do not show affinities with either the South American or the Central American clades (Cadle, 1984c).

In an allozyme study (four proteins) of 215 species of snakes representing nine families (Dowling *et al.,* 1996), nearly all of the Central and South American xenodontines formed a monophyletic group. Until now, DNA sequence studies (Heise *et al.,* 1995; Kraus and Brown, 1998) have included only a few species of xenodontines and therefore have not been conclusive regarding phylogeny of the group.

Several tribes of xenodontine snakes have been defined (Dowling, 1975, 1978; Jenner, 1981) but only two

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tribes, both within South American xenodontines, are currently recognized to be monophyletic on morphological and biochemical grounds: the Pseudoboini, comprising nine genera (*Boiruna, Clelia, Drepanoides, Oxyrhopus, Phimophis, Pseudoboa, Rhachidelus, Siphlophis,* and *Tripanurgos*) (Bailey, 1967; Cadle, 1984a; Zaher, 1994, 1996, 1999), and the Xenodontini, comprising six genera (*Erythrolamprus, Liophis, Lystrophis, Umbrivaga, Xenodon,* and *Waglerophis*) (Jenner, 1981; Cadle, 1984a; Myers, 1986).

The origin of the West Indian xenodontines, which include six endemic genera (*Antillophis, Arrhyton, Darlingtonia, Hypsirhynchus, Ialtris,* and *Uromacer*), is controversial. Some authors favor vicariance (Crother and Guyer, 1996), whereas others have supported an origin by dispersal (Maglio, 1970; Jenner, 1981; Pregill, 1981; Cadle, 1985; Hedges *et al.,* 1992; Hedges, 1996a,b,c). Moreover, Dunn (1932), Maglio (1970), and Crother and Hillis (1995) found West Indian xenodontines to be paraphyletic, while Cadle (1985) and Hedges (1996a,c) found them to be monophyletic.

Finally, the biogeographic origin of xenodontine snakes is a major unanswered question. They are thought to be the most basal "colubrids" in the New World and among the most basal "colubrids" (Dunn, 1931; Clark, 1944; Tihen, 1964; Savage, 1966, 1982; Rabb and Marx, 1973; Dowling *et al.,* 1983; Cadle, 1984c, 1985). According to Cadle (1985), "the ultimate origin of the (Xenodontinae) Neotropical clades could conceivably be associated with either an Asian–North American early Tertiary fauna or with a Gondwanan-derived fauna. Under either hypothesis, they have most likely been components of the Neotropical fauna for most of the Tertiary." In this study, we used 12S and 16S rRNA gene sequences to answer several evolutionary questions. Is the subfamily Xenodontinae monophyletic? What are the relationships among the North, Central, and South American xenodontines? Have xenodontines originated from a Gondwanan or an Asian–North American fauna? What is the origin of West Indian xenodontines?

MATERIALS AND METHODS

This work represents a collaboration between two laboratories, and therefore the materials and methods are described separately. Work involving the mainland species (and *Alsophis cantherigerus*) was conducted by Nicolas Vidal (France), whereas work involving the West Indian species was conducted by Shannon G. Kindl, Alan Wong, and S. Blair Hedges (U.S.A.).

Mainland Species

Tissue samples (tissue homogenate, liver, blood, tail tip, or shed skin) were obtained from the tissue collection of Nicolas Vidal (see Appendix 1). DNA extraction and amplification followed protocols previously described (Vidal *et al.,* 1997). The following sets of primers were used: L2510, 5′-CGC-CTG-TTT-ATC-AAA-AAC-AT-3′ (Palumbi *et al.,* 1991); and L16, 5′-ACG-GCC-GCG-GTA-YCC-TAA-CCG-TG-3′ and H3056, 5′-CTC-CGG-TCT-GAA-CTC-AGA-TCA-CGT-AGG-3′ (Hedges, 1994) for the 16S rRNA gene and L12, 5′-CGC-CAA-AYA-ACT-ACG-AG-3′; and 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 and Mindell, 1994) for the 12S rRNA gene. Direct sequencing was performed manually using the Thermo Sequenase cycle sequencing kit from Amersham.

West Indian Species

Tissue samples of West Indian xenodontines were obtained from the frozen tissue collection of S. Blair Hedges (see Appendix 1). The DNA of the West Indian species was extracted using a phenol–chloroform method (Hedges *et al.,* 1991). Polymerase chain reaction was used to amplify the extracted DNA using equal concentrations of the following light and heavy strand primers for the 12S rRNA gene: 12L17, 5′-CAA-ACT-AGG-ATT-AGA-TAC-CCT-ACT-ATG-3′; 12H10, 5′-AAF-TCG-TAA-CAR-GGT-AAY-RGR-ACR-GGA-AYG-TG-3′; 12H11, 5′-CGT-AAC-ATG-GTA-AGC-GTA-CTG-GAA-AGT-G-3′ and 12L15, 5′-CAA-ACT-GGG-ATT-AGA-TAC-CCC-ACT-AT-3′; 12H4 5′-CGY-ACA-CAC-CGC-CCG-TCA-CCC-T-3′; 12H1, 5′-ACA-CAC-CGC-CCG-TCA-CCC-TCT-GCA-GTC-A-3′; and H1557 (see above). The following primer combinations were used for the 16S rRNA gene: 16L1, 5′-CTG-ACC-GTG-CAA-AGG-TAG-CGT-AAT-CAC-T-3′; 16H1, 5′-CCT-ACG-TGA-TCT-GAG-TTC-AGA-CCG-GAG-3′ and 16L8, 5′-TGA-CCG-TGC-GAA-GGT-AGC-ATA-ATC-A-3′; and 16H13, 5′-TAC-GTG-ATC-TGA-GTT-CAG-ACC-GG-3′. The DNA was purified and cut on a low-melting-temperature agarose gel. After reamplification, the purified DNA was filtered with sterile water in a Millipore column (filter). Cycle sequencing reactions were performed using 3′ dye-labeled dideoxynucleotide triphosphates (fluorescent dye terminators) and run on a Perkin–Elmer ABI PRISM 377 DNA Sequencer. The two separate sequences obtained for each sequence (a forward and a reverse strand) were aligned using the ESEE program (Cabot and Beckenbach, 1989).

Sequence data for the following species were obtained from GenBank: *Boiga cynodon* (Boie, 1827) (Accession Nos. Z46525, Z46468), *Bungarus fasciatus* (Schneider, 1801) (Z46501, Z46466), *Chironius carinatus* (Linnaeus, 1758) (Z46500, Z46463), *Coluber constrictor* Linnaeus, 1758 (L01765, L01770), *Dipsas catesbyi* (Sentzen, 1796) (Z46496, Z46459), *Dinodon semicarinatum* (Cope, 1860) (AB008539), *Elaphe obsoleta* (Say, 1823) (Z46493, Z46469), *Farancia abacura* (Holbrook, 1836) (Z46491, Z46467), *Gonyosoma oxycephala* (Boie, 1827) (Z46490, Z46465), *Lamprophis fuliginosum* (Boie, 1827) (Z46489, Z46457), *Lycodon laoensis* Günther,

1864 (Z46485, Z46455), *Micrurus diastema* (Duméril, Bibron, and Duméril, 1854) (Z46484, Z46454), *Nerodia rhombifera* (Hallowell, 1852) (Z46481, Z46452), *Psammophis condanarus* (Merrem, 1820) (Z46479, Z46450), *Rhamphiophis oxyrhynchus* (Reinhardt, 1843) (Z46738, Z46443), and *Xenodon severus* (Linnaeus, 1758) (Z46474, Z46449).

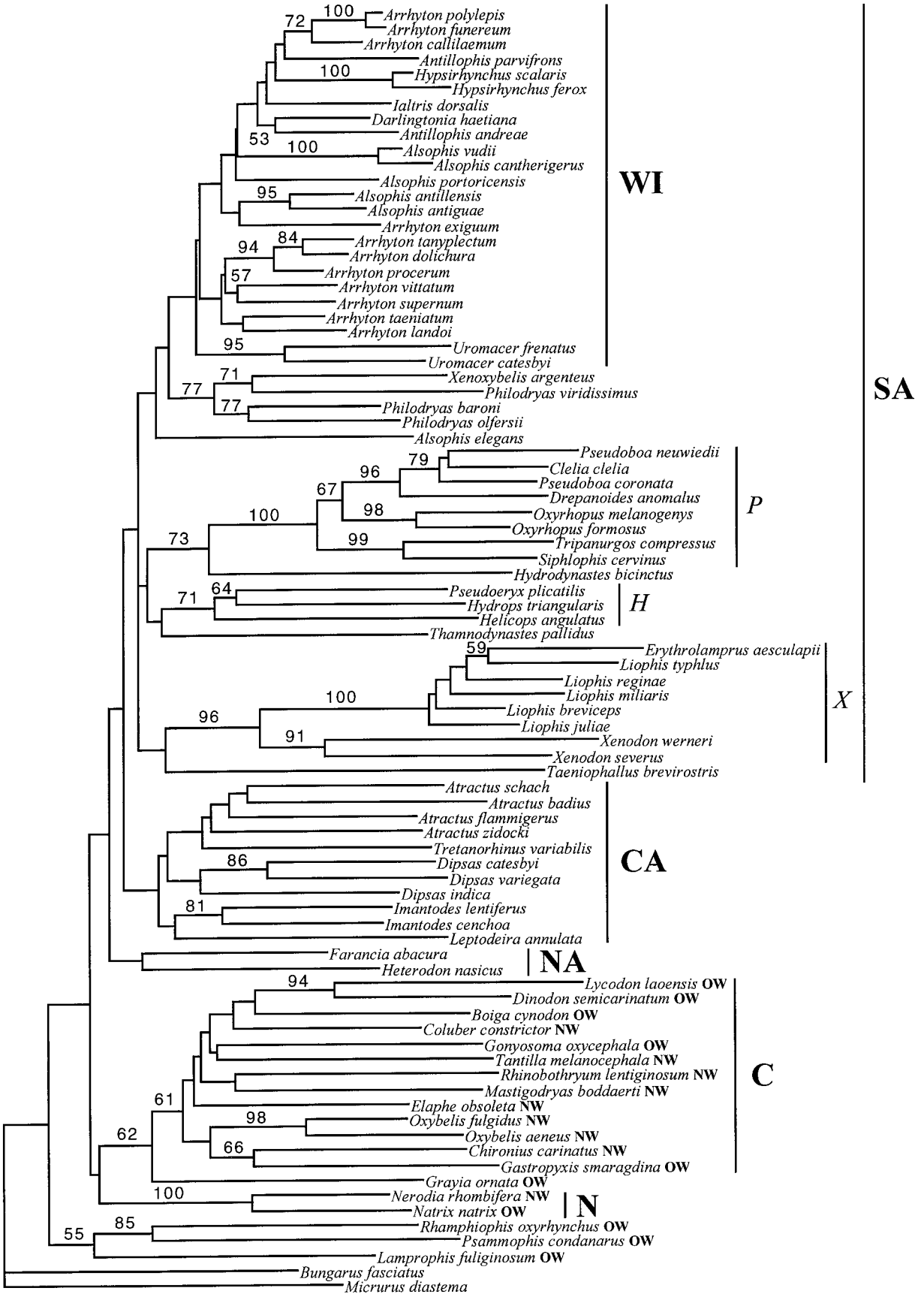
Sequence Analysis

Sequence entry and alignment were performed with the MUST software (Philippe, 1993). For the 16S rRNA sequences, alignment was unambiguous, except in two highly variable areas corresponding to loops that we deleted from the analyses (corresponding to sites 2145–2170 and 2183–2189 in *Dinodon semicarinatum*). To align the 12S rRNA sequences, we first used the secondary structure model described by Hickson *et al.* (1996). Then, for each gap zone, we retained the alignment giving the shortest most-parsimonious (MP) tree using PAUP 3.1.1. (Swofford, 1993) (with gaps treated as an additional character state). The complete alignments were deposited in the EMBL alignment database (Accession Nos. DS38918 and DS39019). Complete sequences (including deleted zones) were deposited in GenBank under Accession Nos. AF158401 to AF158538. For the two genes, mutational saturation was studied by plotting the pairwise observed number of sequence differences (in percentage) against the pairwise number of substitutions met in the pathway joining the two species in the MP tree as inferred by PAUP 3.1.1. Heuristic maximum parsimony searches were performed using PAUP 3.1.1. For parsimony analyses, gaps were coded after Barriel (1994) using a test version of the BARCOD software provided by Véronique Barriel. This coding of gaps "is defined in view to express the potential phylogenetic information contained in complex zones with interested insertion/deletion and substitutions. According to the hierarchy of internested states of characters (sites), this strategy introduces in the data matrix question marks, "?", which are optimized *in fine* in the cladogram based on all data" (Barriel, 1994). Neighbor-joining (NJ) (Saitou and Nei, 1987) searches using Kimura's (1980) two-parameter model were performed with the MUST software. For distance analyses, when sequences are compared two by two, if a site has a gap in one of the two sequences, it is automatically ignored. Support for monophyletic groups was evaluated by calculating decay index values (Bremer, 1988, 1994) using AutoDecay 2.9.10 (Eriksson, 1997). Bootstrap values (Felsenstein, 1985) were calculated using 2000 replicates for NJ searches and 100 replicates for parsimony searches. The elapids *Micrurus diastema* and *Bungarus fasciatus* were used as outgroups in our analyses after having checked that they were in a basal position, along with the "colubrids" *Lamprophis fuliginosum, Psammophis condanarus,* and *Rhamphiophis oxyrhynchus* in our taxonomic sampling. This was done by using two viperids (*Crotalus horridus* and *Vipera ammodytes*) as more distant outgroups.

RESULTS

Sequence data were obtained for 85 species of snakes. For the 12S rRNA fragment, there were 309 aligned sites, 185 of which were variable (147 informative under the conditions of parsimony). For the 16S rRNA fragment, there were 343 aligned sites, 137 of which were variable (101 informative under the conditions of parsimony). Saturation analyses showed no severe saturation (data not shown), and consequently all substitutions were equally weighted. For the phylogenetic analyses, the 12S and 16S rRNA portions were combined, resulting in 652 aligned sites, 322 of which were variable (248 informative under the conditions of parsimony). Tree reconstruction by the neighbor-joining method is shown in Fig. 1. Parsimony analysis produced 14 most-parsimonious trees 2092 steps long, the strict consensus of which is shown in Fig. 2. Bootstrap and decay index values are written on the figures and will not be reported below.

The two analyses result in very similar trees. The subfamily Colubrinae is monophyletic. The genus *Grayia* appears to be the sister group to the Colubrinae. The subfamily Natricinae (represented by two species, *Nerodia rhombifera* and *Natrix natrix*) is monophyletic. The subfamily Xenodontinae forms a monophyletic group. Within Xenodontinae, the two North American genera used in our study (*Farancia abacura* and *Heterodon nasicus*) are the sister group to the remaining xenodontines (Neotropical species). Within the latter clade, the Central and South American xenodontines each appear to be monophyletic. Within Central American xenodontines, the genera *Atractus, Dipsas,* and *Imantodes* are each monophyletic. Within South American xenodontines, the Pseudoboini and the Xenodontini clades are clearly defined. The genus *Hydrodynastes* appears to be the sister group to the Pseudoboini. Within Pseudoboini, the basal genera *Siphlophis* and *Tripanurgos* cluster together and form the sister group to the remaining Pseudoboini. A clade is formed by the genera *Drepanoides, Clelia,* and *Pseudoboa.* Together, the genera *Clelia* and *Pseudoboa* form a monophyletic group. Within Xenodontini, the monophyletic genus *Xenodon* clusters with a group formed by the genera *Liophis* and *Erythrolamprus,* the latter being rooted within the genus *Liophis.* Among the remaining South American xenodontines, a clade is formed by the genera *Helicops, Hydrops,* and *Pseudoeryx,* with *Helicops* the sister group to the genera *Hydrops* and *Pseudoeryx.* Another South American clade is formed by the genera *Philodryas* and *Xenoxybelis. Philodryas baroni* and *Philodryas olfersii* form a monophyletic group. West Indian xenodontines form a monophyletic group. Within


Arrhyton polylepis
Arrhyton funereum
Arrhyton callilaemum
Antillophis parvifrons
Hypsirhynchus scalaris
Hypsirhynchus ferox
Ialtris dorsalis
Darlingtonia haetiana
Antillophis andreae
Alsophis vudii
Alsophis cantherigerus
Alsophis portoricensis
Alsophis antillensis
Alsophis antiguae
Arrhyton exiguum
Arrhyton tanyplectum
Arrhyton dolichura
Arrhyton procerum
Arrhyton vittatum
Arrhyton supernum
Arrhyton taeniatum
Arrhyton landoi
Uromacer frenatus
Uromacer catesbyi
Xenoxybelis argenteus
Philodryas viridissimus
Philodryas baroni
Philodryas olfersii
Alsophis elegans
Pseudoboa neuwiedii
Clelia clelia
Pseudoboa coronata
Drepanoides anomalus
Oxyrhopus melanogenys
Oxyrhopus formosus
Tripanurgos compressus
Siphlophis cervinus
Hydrodynastes bicinctus
Pseudoeryx plicatilis
Hydrops triangularis
Helicops angulatus
Thamnodynastes pallidus
Erythrolamprus aesculapii
Liophis typhlus
Liophis reginae
Liophis miliaris
Liophis breviceps
Liophis juliae
Xenodon werneri
Xenodon severus
Taeniophallus brevirostris
Atractus schach
Atractus badius
Atractus flammigerus
Atractus zidocki
Tretanorhinus variabilis
Dipsas catesbyi
Dipsas variegata
Dipsas indica
Imantodes lentiferus
Imantodes cenchoa
Leptodeira annulata
Farancia abacura
Heterodon nasicus
Lycodon laoensis OW
Dinodon semicarinatum OW
Boiga cynodon OW
Coluber constrictor NW
Gonyosoma oxycephala OW
Tantilla melanocephala NW
Rhinobothryum lentiginosum NW
Mastigodryas boddaerti NW
Elaphe obsoleta NW
Oxybelis fulgidus NW
Oxybelis aeneus NW
Chironius carinatus NW
Gastropyxis smaragdina OW
Grayia ornata OW
Nerodia rhombifera NW
Natrix natrix OW
Rhamphiophis oxyrhynchus OW
Psammophis condanarus OW
Lamprophis fuliginosum OW
Bungarus fasciatus
Micrurus diastema
WI
P
H
X
SA
CA
NA
C
N

West Indian xenodontines, the genera *Uromacer* and *Hypsirhynchus* are each monophyletic. Cuban and Jamaican members of the genus *Arrhyton* are each monophyletic. The two Lesser Antillean members of the genus *Alsophis* (*Alsophis antiguae* and *Alsophis antillensis*) form a monophyletic group. *Alsophis cantherigerus* (Cuba) and *Alsophis vudii* (Bahamas) are monophyletic.

Nearly all the basal nodes of our trees are weakly supported and it is clear that more sequence data are needed. However, internal robustness is not the only method used for assessing phylogenetic accuracy, and we regard congruence (the corroboration of results between independent sets of characters) as strong evidence of relationship (Miyamoto and Cracraft, 1991; Lanyon, 1993; Grande, 1994; Keogh, 1998).

DISCUSSION

Monophyly of Colubrinae

The subfamily Colubrinae is monophyletic (Figs. 1 and 2), which is in accordance with molecular results obtained by previous authors (Schwaner and Dessauer, 1982; Dowling *et al.,* 1983, 1996; Cadle, 1984c, 1988; Dessauer *et al.,* 1987; Heise *et al.,* 1995; Kraus and Brown, 1998). Morphologically, members of the subfamily Colubrinae are generally characterized by the possession of a single sulcus spermaticus on the hemipenis and the reduction to keels of posterior hypapophyses (Dunn, 1928; McDowell, 1987). Interestingly, the enigmatic genus *Grayia,* which has been associated immunologically by Cadle (1994) with the "colubrine–natricine" lineage and which is the sister group to colubrines in our study, has a forked sulcus spermaticus (McDowell, 1987). Within Colubrinae, phylogenetic relationships are poorly resolved; nevertheless, it appears that several exchanges have taken place between the Old and the New World (Figs. 1 and 2), as shown by others (Dowling *et al.,* 1983, 1996; Cadle, 1984c, 1987; Lopez and Maxson, 1995).

Monophyly of Xenodontinae

The subfamily Xenodontinae appears to be monophyletic, although with low support values (Figs. 1 and 2). This finding agrees with the conclusions of Dunn (1928) and the results of a previous molecular study using ND4 sequences (Kraus and Brown, 1998). From a morphological point of view, there are no known uniquely derived characters that unite xenodontine snakes (Cadle, 1984c; Whistler and Wright, 1989). Nevertheless, xenodontines can be recognized as being American "colubrids" that have a hemipenis with a forked sulcus or, if the sulcus is simple, that have a unicapitate hemipenis (Jenner, 1981). Within the subfamily, North American xenodontines (*Heterodon nasicus* and *Farancia abacura* in our study) are in the most basal position and are the sister group to Central and South American xenodontines (Figs. 1 and 2). Although weakly supported, this pattern of cladogenesis is biogeographically coherent and is in accordance with molecular results obtained by Cadle (1984a,b,c) (monophyly of Central American xenodontines and of South American xenodontines) and Dowling *et al.* (1996) (monophyly of the group formed by Central and South American xenodontines). The subfamily Xenodontinae would therefore have an Asian–North American origin, as do all of the other American colubroid snakes (Cadle, 1987).

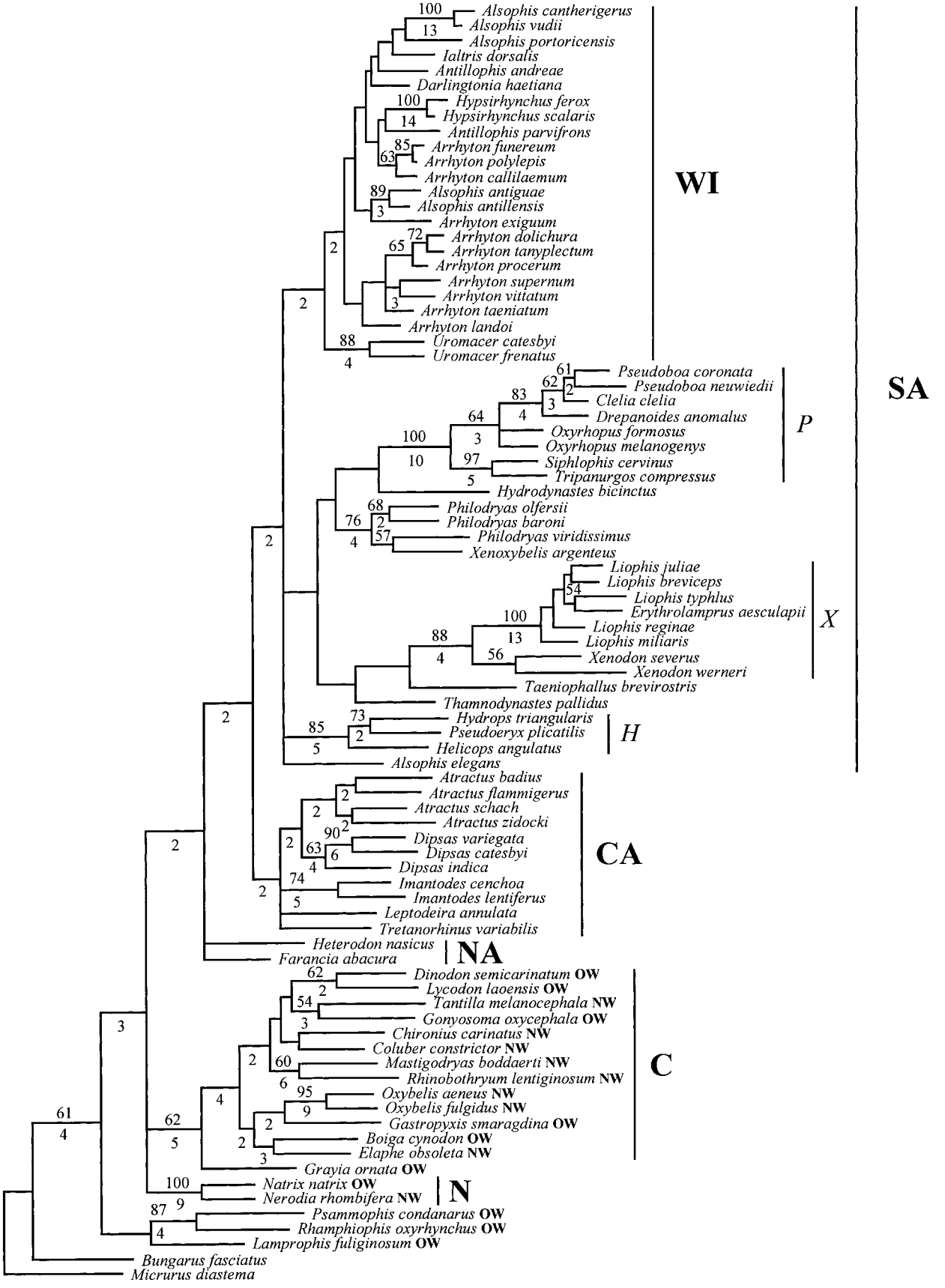
Central and South American Xenodontinae

Central American xenodontines appear to form a monophyletic group (although with low support values) (Figs. 1 and 2), which confirms molecular results obtained by Cadle (1984b). Morphologically, Central American xenodontines generally can be characterized by the "derived hemipenial features of (1) reduction or loss of bilobation, (2) (uni) capitation, and (3) distal division of the sulcus spermaticus" (Myers and Cadle, 1994).

South American xenodontines form a monophyletic group (although with low support values) (Figs. 1 and 2), in agreement with Cadle's result (1984a). Morphologically, South American xenodontines usually have a bilobed, noncapitate or semicapitate hemipenis, with the sulcus bifurcating often near the base of the hemipenis and usually on the basal half of the organ (Cadle, 1984c; Myers and Cadle, 1994).

Xenodontini. The monophyly of the group formed by representatives of the tribe Xenodontini (genera *Erythrolamprus, Liophis,* and *Xenodon* in our study) (Figs. 1 and 2) is congruent with molecular (Cadle, 1984a) and morphological (Dowling, 1975; Dixon, 1980; Jenner, 1981; Myers, 1986) results. The members of the tribe Xenodontini (genera *Erythrolamprus, Liophis, Lystrophis, Umbrivaga, Xenodon,* and *Waglerophis*) have bilobed hemipenes with nude apical disks (Myers, 1986) and share a particular defensive behavior (neck flattening or hood display) (Myers, 1986). The genus *Erythrolamprus* appears to be rooted within the genus *Liophis* (Figs. 1 and 2). Morphologically, the two genera have similar hemipenes (Dixon, 1980) and the main character used to distinguish them is the coral snake

FIG. 1. Neighbor-joining tree (Kimura's two-parameter model) using MUST. Numbers above branches are bootstrap proportions above 50% obtained from 2000 replicates using MUST. OW, Old World; NW, New World; N, Natricinae; C, Colubrinae; X, Xenodontini; H, Hydropsini; P, Pseudoboini; NA, North American xenodontines; CA, Central American xenodontines; SA, South American xenodontines; WI, West Indian xenodontines.


Alsophis cantherigerus
Alsophis vudii
Alsophis portoricensis
Ialtris dorsalis
Antillophis andreae
Darlingtonia haetiana
Hypsirhynchus ferox
Hypsirhynchus scalaris
Antillophis parvifrons
Arrhyton funereum
Arrhyton polylepis
Arrhyton callilaemum
Alsophis antiguae
Alsophis antillensis
Arrhyton exiguum
Arrhyton dolichura
Arrhyton tanyplectum
Arrhyton procerum
Arrhyton supernum
Arrhyton vittatum
Arrhyton taeniatum
Arrhyton landoi
Uromacer catesbyi
Uromacer frenatus
WI
Pseudoboa coronata
Pseudoboa neuwiedii
Clelia clelia
Drepanoides anomalus
Oxyrhopus formosus
Oxyrhopus melanogenys
Siphlophis cervinus
Tripanurgos compressus
Hydrodynastes bicinctus
P
SA
Philodryas olfersii
Philodryas baroni
Philodryas viridissimus
Xenoxybelis argenteus
Liophis juliae
Liophis breviceps
Liophis typhlus
Erythrolamprus aesculapii
Liophis reginae
Liophis miliaris
Xenodon severus
Xenodon werneri
Taeniophallus brevirostris
X
Thamnodynastes pallidus
Hydrops triangularis
Pseudoeryx plicatilis
Helicops angulatus
H
Alsophis elegans
Atractus badius
Atractus flammigerus
Atractus schach
Atractus zidocki
Dipsas variegata
Dipsas catesbyi
Dipsas indica
Imantodes cenchoa
Imantodes lentiferus
Leptodeira annulata
Tretanorhinus variabilis
CA
Heterodon nasicus
Farancia abacura
NA
Dinodon semicarinatum OW
Lycodon laoensis OW
Tantilla melanocephala NW
Gonyosoma oxycephala OW
Chironius carinatus NW
Coluber constrictor NW
Mastigodryas boddaerti NW
Rhinobothryum lentiginosum NW
Oxybelis aeneus NW
Oxybelis fulgidus NW
Gastropyxis smaragdina OW
Boiga cynodon OW
Elaphe obsoleta NW
Grayia ornata OW
C
Natrix natrix OW
Nerodia rhombifera NW
N
Psammophis condanarus OW
Rhamphiophis oxyrhynchus OW
Lamprophis fuliginosum OW
Bungarus fasciatus
Micrurus diastema

color pattern displayed by the genus *Erythrolamprus* (Cadle, 1984a), a common mimicry color pattern among Neotropical "colubrids" (Greene and McDiarmid, 1981; Campbell and Lamar, 1989).

Hydropsini. The aquatic genera *Helicops, Hydrops,* and *Pseudoeryx* form a monophyletic group (Figs. 1 and 2), which is in accordance with morphological results obtained by Zaher (1994, 1999). According to this author, members of the tribe Hydropsini (genera *Helicops, Hydrops,* and *Pseudoeryx*) are characterized by an important development of the adductor mandibulae externus superficialis at its origin site. Moreover, the sister taxon relationship between the genera *Hydrops* and *Pseudoeryx* was also found by Zaher (1994, 1999) on the basis of common features of the adductor mandibulae externus medialis.

Pseudoboini. The monophyly of the group formed by representatives of the tribe Pseudoboini (genera *Clelia, Drepanoides, Oxyrhopus, Pseudoboa, Siphlophis,* and *Tripanurgos* in our study) (Figs. 1 and 2) is congruent with morphological (Bailey, 1967; Jenner and Dowling, 1985; Zaher, 1994, 1996, 1999) and molecular (Cadle, 1984a) results. Zaher (1994) lists the eight following morphological synapomorphies: (1) a pair of pigmented spots on the palate; (2) pouches between the hemipenian lobes, on the distal area of the asulcated side of the hemipenes; (3) highly developed crest on the internal side of the hemipenian lobes; (4) enlarged lateral spines on the crest of the hemipenial lobes; (5) antero-dorsal process on the lateral wing of the prefrontal; (6) posterior area of the palatine (posterior to the vomerian process) much shorter than the dental process; (7) dorsal area of the palatine process of the vomer forming an apophyse for the retractor vomeris (resulting in the loss of the vomerian foramen); and (8) distinct maxillary articular process of the prefrontal. Finally, the position of the genus *Hydrodynastes* as sister group to the Pseudoboini (Figs. 1 and 2) is supported by Zaher (1994, 1996), who found them to share the two following derived characters: (1) corporal calyces forming two distinct rows from the base to the distal extremity of the lobes and (2) presence of a crest on the internal side of the lobes.

Philodryas and *Xenoxybelis.* The removal of *Xenoxybelis argenteus* (characterized by a typical South American xenodontine hemipenis) from the colubrine genus *Oxybelis* (Machado, 1993) is supported. From this point of view, the morphological, ecological, and behavioral convergences of the genera *Oxybelis* and *Xenoxybelis* are particularly striking (Henderson and Binder, 1980). Although our data cannot assess the validity of the genus *Xenoxybelis,* the association of *Xenoxybelis argenteus* with some members of the genus *Philodryas* (belonging to a group called "olfersii," the genus *Philodryas* being thought to be paraphyletic by Zaher (1994, 1999)) is supported by the two following synapomorphies: (1) development of corporal calyces on the entire asulcated side of the hemipenis, from the distal extremity of the lobes to the base of the hemipenis, and (2) "heart shaped" hemipenis with capitula confined on the sulcated side of the hemipenis (Zaher, 1994, 1999).

Alsophiini. West Indian xenodontines (including endemic genera and members of the genus *Alsophis*) appear to form a monophyletic group (although with low support values) (Figs. 1 and 2), which is in accordance with results obtained by Cadle (1985) and Hedges (1996a,c). Within West Indian xenodontines (34 species belonging to seven genera), the situation is very complex from a phylogenetic point of view; nevertheless, several patterns can be recognized. Cuban members of the genus *Arrhyton* (*Arrhyton dolichura, Arrhyton landoi, Arrhyton procerum, Arrhyton supernum, Arrhyton taeniatum, Arrhyton tanyplectum,* and *Arrhyton vittatum* in our study) form a monophyletic group, which is in agreement with immunological results (Hedges *et al.,* 1992; Hedges, Hass, and Maxson, unpubl.). Based on the examination of three species (*Arrhyton landoi, Arrhyton taeniatum,* and *Arrhyton vittatum*), Zaher (1999) proposed the following synapomorphy uniting Cuban members of the genus *Arrhyton:* "presence of a medial papillate crest extending from the lobular crotch to the edge of the capitulum on each lobe and forming a "Y-shaped" structure on the distal region of the body." Jamaican members of the genus *Arrhyton* (*Arrhyton callilaemum, Arrhyton funereum,* and *Arrhyton polylepis*) also form a monophyletic group, as found by Crother and Hillis (1995). According to Zaher (1999), the three Jamaican species of the genus *Arrhyton* share two synapomorphies: "complete loss of the capitular calyces and presence of an apical awn." The two Lesser Antillean members of the genus used in our study (*Alsophis antiguae* and *Alsophis antillensis*) form a monophyletic group. Our results also support the very close relationship found by Maglio (1970), Cadle (1984a), Crother and Hillis (1995), and Zaher (1999) between *Alsophis cantherigerus* (Cuba) and *Alsophis vudii* (Bahamas).

Origin and Biogeography of Xenodontine Snakes

In our phylogenetic trees, xenodontines appear to be in a nested position. They would then be among the most derived snakes. This result is weakly supported;

FIG. 2. Strict consensus MP tree using PAUP 3.1.1. Gaps are coded after Barriel (1994); 14 equally parsimonious trees are recovered (2092 steps, C.I. 0.255, R.I. 0.511). Branch lengths are shown under ACCTRAN optimization. Numbers above branches are bootstrap proportions above 50% obtained from 100 replicates using PAUP 3.1.1. Numbers below branches are decay index values obtained using AutoDecay 2.9.10. Same abbreviations as in Fig. 1.

nevertheless, if we examine the traditional arguments in favor of an ancient origin of xenodontines, they do not appear to be robust. So, if immunological results show high IDs within xenodontines compared to those obtained within natricines and colubrines (Dowling *et al.,* 1983; Cadle, 1984c, 1985), it does not follow, unless we assume a "molecular clock," that xenodontines diverged before natricines and colubrines (Kraus and Brown, 1998). Another argument in favor of an old age of xenodontines, proposed by Dunn (1931) and Tihen (1964), is that they are, unlike colubrines and natricines, restricted to the New World, with no known relatives in the Old World. We think that this last argument can be reversed with no difficulty.

Xenodontines are by far the dominant lineage of colubrid snakes in the Neotropics, but even if they appeared in the New World sooner than colubrines and natricines (Tihen, 1964; Cadle, 1984c, 1985), it does not imply that they are older. In the absence of a well-documented fossil record (Estes and Báez, 1985; Rage, 1987; Cadle, 1988; Whistler and Wright, 1989), we consider the question of the relative age of the subfamily Xenodontinae to be unresolved, although some major biogeographical patterns can be distinguished.

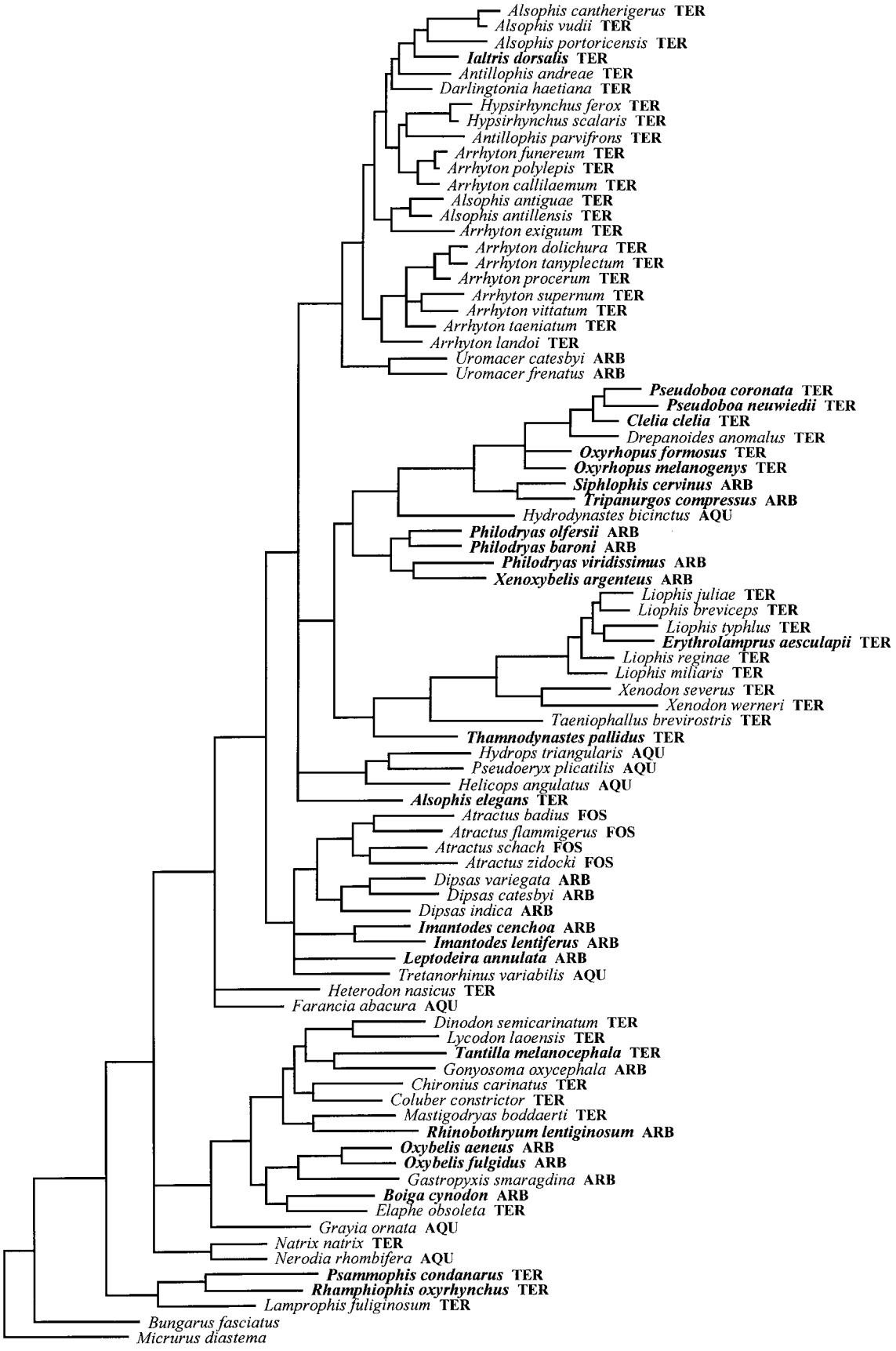
Xenodontines have an Asian–North American origin. According to Cadle (1985), they have been present in the New World for most of the Tertiary, with an early separation of the Central and the South American xenodontines, followed by several dispersal events between these two clades through much of the Tertiary. These exchanges have been asymmetrical, with Central American xenodontines playing a significant role in shaping xenodontine assemblages in South America but not the reverse (Cadle, 1985). Our results are congruent with these inferences. In particular, all the Central American xenodontines used in this study (except *Tretanorhinus variabilis* from Cuba) have been collected in French Guiana (South America). Moreover, Central American genera such as *Atractus* and *Sibynomorphus* are widespread within and endemic to South America (Cadle, 1985). According to most interpretations of geological data (reviewed by Zamudio and Greene, 1997), Central and South America have been separated since the late Cretaceous or early Tertiary until the Pliocene formation of the Isthmian Link (about 3.5 Mya). On the other hand, we have some evidence for several exchanges between Central and South America through much of the Tertiary for xenodontines, pitvipers (reviewed by Vidal *et al.,* 1999), and salamanders (Hanken and Wake, 1982). As stated by Zamudio and Greene (1997), this "underscores a continuing enigma in Middle American biogeography, the interchange of terrestrial organisms across what is usually portrayed as a marine barrier."

The West Indian clade clearly belongs to the South American clade, which agrees with the results of Cadle (1985) and Hedges (1996a,b,c). Accordingly, the origin of this lineage was probably from a single mid-Cenozoic dispersal event, as proposed by those authors. Based on immunological data (Cadle, 1984a), Hedges *et al.* (1992) inferred a 26-mya split between *Alsophis cantherigerus* and *Philodryas viridissimus.* In addition to this single major clade, the occurrence in the West Indies of other xenodontine genera (*Clelia, Coniophanes, Diadophis, Liophis, Pseudoboa,* and *Tretanorhinus*) suggests that there were at least five Late Cenozoic dispersal events, the genus *Diadophis* having been accidentally introduced (Schwartz and Henderson, 1991; Hedges, 1996c). Interestingly, among the 45 xenodontine species present in the West Indies, only 2 (*Coniophanes andresensis* and *Tretanorhinus variabilis*) have dispersed from Central America. Our data thus support the hypothesis that the nearly unidirectional (southeast to northwest) ocean currents have carried organisms on flotsam from the mouths of major rivers in South America to islands of the West Indies throughout the Cenozoic (Hedges, 1996a,b,c).

Evolutionary Trends of the Venomous Apparatus

Recent phylogenetic studies have shown that the front-fanged venom system evolved several times independently (Cadle, 1987; Knight and Mindell, 1994; Heise *et al.,* 1995; Kraus and Brown, 1998) and that viperids appeared early within colubroids (Cadle, 1987; Knight and Mindell, 1994; Heise *et al.,* 1995). The back-fanged venom system has been less studied than the front-fanged system, although it is clear that opisthoglyph "colubrids" (with enlarged grooved rear maxillary teeth) constitute a polyphyletic group (Cope, 1893; Dunn, 1928; Smith, 1952; Anthony, 1955; Johnson, 1955; Haas, 1962; Hoffstetter, 1962; Bailey, 1966, 1967; Taub, 1967a). Our results show (Fig. 3) the great diversity of maxillary dentition displayed by xenodontines, which can be opisthoglyph or aglyph (with ungrooved rear maxillary teeth enlarged or not). Even within a genus, such as *Erythrolamprus,* both aglyph and opistoglyph dentition types can be found (McKinstry, 1983; Chippaux, 1986). Moreover, the aglyph

FIG. 3. Maxillary dentition (boldface type: opisthoglyph species; plain type: aglyph species) and habit (AQU, aquatic species; ARB, arboreal species; FOS, fossorial species; TER, terrestrial species) data mapped on the strict consensus MP tree shown in Fig. 2. Habit data are generalizations: i.e., a species is considered to be aquatic if its members spend most of their activity time in water. Data were obtained from Bailey (1966, 1967), Maglio (1970), Dixon and Soini (1977), Duellman (1978, 1990), Jenner (1981), McKinstry (1983), Chippaux (1986), Obst *et al.* (1988), Henderson and Crother (1989), Schwartz and Henderson (1991), Cadle and Greene (1993), Zaher (1994), Lee (1996), and Vidal (unpubl.).


Alsophis cantherigerus TER
Alsophis vudii TER
Alsophis portoricensis TER
Ialtris dorsalis TER
Antillophis andreae TER
Darlingtonia haetiana TER
Hypsirhynchus ferox TER
Hypsirhynchus scalaris TER
Antillophis parvifrons TER
Arrhyton funereum TER
Arrhyton polylepis TER
Arrhyton callilaemum TER
Alsophis antiguae TER
Alsophis antillensis TER
Arrhyton exiguum TER
Arrhyton dolichura TER
Arrhyton tanyplectum TER
Arrhyton procerum TER
Arrhyton supernum TER
Arrhyton vittatum TER
Arrhyton taeniatum TER
Arrhyton landoi TER
Uromacer catesbyi ARB
Uromacer frenatus ARB
Pseudoboa coronata TER
Pseudoboa neuwiedii TER
Clelia clelia TER
Drepanoides anomalus TER
Oxyrhopus formosus TER
Oxyrhopus melanogenys TER
Siphlophis cervinus ARB
Tripanurgos compressus ARB
Hydrodynastes bicinctus AQU
Philodryas olfersii ARB
Philodryas baroni ARB
Philodryas viridissimus ARB
Xenoxybelis argenteus ARB
Liophis juliae TER
Liophis breviceps TER
Liophis typhlus TER
Erythrolamprus aesculapii TER
Liophis reginae TER
Liophis miliaris TER
Xenodon severus TER
Xenodon werneri TER
Taeniophallus brevirostris TER
Thamnodynastes pallidus TER
Hydrops triangularis AQU
Pseudoeryx plicatilis AQU
Helicops angulatus AQU
Alsophis elegans TER
Atractus badius FOS
Atractus flammigerus FOS
Atractus schach FOS
Atractus zidocki FOS
Dipsas variegata ARB
Dipsas catesbyi ARB
Dipsas indica ARB
Imantodes cenchoa ARB
Imantodes lentiferus ARB
Leptodeira annulata ARB
Tretanorhinus variabilis AQU
Heterodon nasicus TER
Farancia abacura AQU
Dinodon semicarinatum TER
Lycodon laoensis TER
Tantilla melanocephala TER
Gonyosoma oxycephala ARB
Chironius carinatus TER
Coluber constrictor TER
Mastigodryas boddaerti TER
Rhinobothryum lentiginosum ARB
Oxybelis aeneus ARB
Oxybelis fulgidus ARB
Gastropyxis smaragdina ARB
Boiga cynodon ARB
Elaphe obsoleta TER
Grayia ornata AQU
Natrix natrix TER
Nerodia rhombifera AQU
Psammophis condanarus TER
Rhamphiophis oxyrhynchus TER
Lamprophis fuliginosum TER
Bungarus fasciatus
Micrurus diastema

and opisthoglyph grades comprise a great variety of structures. So, Marx and Rabb (1972) have shown that "colubrids" may have no enlarged maxillary teeth, enlarged anterior maxillary teeth, enlarged posterior maxillary teeth, enlarged anterior and posterior maxillary teeth, enlarged medial and posterior maxillary teeth, or enlarged medial maxillary teeth.

The ridges and the grooves on the maxillary teeth can be present on all sides (anterior, posterior, lingual, or labial) (Jackson and Fritts, 1995, 1996), but two or more enlarged maxillary teeth can form (between them) a functional equivalent to a groove in a single tooth (Taub, 1967b). Moreover, teeth with furrows can be found on the dentary, pterygoid, and palatine (Young and Kardong, 1996). To complicate matters, the structure of the Duvernoy's glands of "colubrids" shows a great range of variations (Taub, 1967b), and "establishing a functional relationship between posterior maxillary teeth and Duvernoy's gland cannot be easily accomplished by simple matching of their respective anatomies alone" (Kardong, 1980). To recognize the apparent aptitude of advanced snakes (including most of the "colubrids") for evolving toxic saliva associated with diverse delivery systems (McKinstry, 1983), we think the phylogenetically and descriptively useless terms aglyph and opisthoglyph should be abandoned. So, morphological studies, as those by Jackson and Fritts (1995) and Young and Kardong (1996), associated with toxicological studies (Weinstein and Kardong, 1994; Kardong, 1996), in "taking into consideration the extensive experimentation that must have occurred in the evolution of a highly variable adaptation" (Taub, 1967b), are badly needed before elaborating evolutionary scenarios of the venom systems of colubroids.

Plasticity of the Xenodontinae

The subfamily Xenodontinae is characterized by a great morphological and ecological diversity (Cadle and Greene, 1993). Even within our restricted taxonomic sample, it appears that each xenodontine lineage (North, Central, and South American xenodontines) is able to invade many ecological niches (Fig. 3). This trend is also apparent at the tribe level. So, the sister group to Pseudoboini (the genus *Hydrodynastes*) is aquatic while members of the Pseudoboini tribe are mainly terrestrial and arboreal. Given the morphological constraints linked to the ophidian bauplan, which offers a restricted set of major morphological adaptations (Dowling *et al.,* 1996), retrieving the history of Xenodontinae using morphological and ecological clues is a very difficult task. Xenodontines display such a high degree of plasticity that their history is almost "erased," whatever the trait considered (i.e., hemipenis, maxillary dentition, habit). As a crude analogy, such a degree of plasticity is displayed by Cichlidae of the African Lakes and finches of the Galapagos islands (West-Eberhard, 1989). So, Cadle and Greene (1993) find that, concerning size distribution and macrohabitat use, even if important differences are noticeable between Central and South American xenodontines, there is considerable overlap. Moreover, "within each of these clades, all nonterrestrial macrohabitat associations (and their morphological correlates) have evolved repeatedly" (Cadle and Greene, 1993). To explore the role played by historical constraints in the evolution of Xenodontinae, the most suitable clade may be the West Indian xenodontines.

Henderson and Crother (1989) found that, unlike continental xenodontines, most West Indian taxa "share a number of morphological, ecological, and behavioral characteristics in common: 1) small to moderate size with a relatively slender habitus, 2) diurnal, 3) prey is subdued by a method other than constriction, 4) employ an active foraging mode, 5) are ground-dwelling" and 6) eat lizards. At first sight, this distinctive pattern would seem to argue in favor of strong historical constraints. Nevertheless, some of these presumed constraints appear to have been released on one of the most physiographically and ecologically diverse islands (Hispaniola), where both sit-and-wait foragers and arboreal species occur (Henderson and Crother, 1989). Moreover, the endemic genera concerned (*Hypsirhynchus:* terrestrial with a sit-and-wait strategy; and *Uromacer:* arboreal with a sit-and-wait strategy) are not closely related according to this study (contrary to the view expressed by Maglio, 1970, followed by Henderson *et al.,* 1988 and Brooks and McLennan, 1991). The sit-and-wait strategy then appears to have evolved twice independently within Hispaniolan xenodontines. The relative uniformity of West Indian xenodontines can therefore be partly explained by the restricted choice of habitats offered by most of the West Indian islands coupled to the availability of a very abundant and ubiquitous kind of prey (lizards of the genus *Anolis*). So, both continental and West Indian xenodontines can be characterized by their plasticity. Nevertheless, the mechanisms underlying this pattern remain to be explained, as our results fail to show any accelerated rate of evolution of xenodontines in comparison to other "colubrids."

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APPENDIX 1

Tissue Sample Collections

Tissue samples (tissue homogenate, liver, blood, tail tip, or shed skin) were obtained from the tissue collection of Nicolas Vidal for the following species: *Alsophis cantherigerus* (Bibron, 1843) (Cuba); *Alsophis elegans* (Tschudi, 1845) (Chaca Valley, Northern Chili); *Atractus badius* (Boie, 1827) (BPS road, pK 12, Petit Saut, French Guiana); *Atractus flammigerus* (Boie, 1827) (Musée National d'Histoire Naturelle [MNHN] 1997.2145, BPS road, pK 24, Petit Saut, French Guiana); *Atractus schach* (Boie, 1827) ([MNHN] 1997.2371, Saint Eugène, Petit Saut, French Guiana); *Atractus zidocki* Gasc and Rodrigues, 1979 ([MNHN] 1997.2046, BPS road, pK 24, Petit Saut, French Guiana); *Clelia clelia* (Daudin, 1803) ([MNHN] 1997.2094, Petit Saut, French Guiana); *Dipsas indica* Laurenti, 1768 (French Guiana); *Dipsas variegata* (Duméril, Bibron, and Duméril, 1854) (BPS road, pK 25, Petit Saut, French Guiana); *Drepanoides anomalus* (Jan, 1863) ([MNHN] 1996.4239, BPS road, pK 13.5, Petit Saut, French Guiana); *Erythrolamprus aesculapii* (Linnaeus, 1766) ([MNHN] 1996.7896, BPS road, Petit Saut, French Guiana); *Gastropyxis smaragdina* (Schlegel, 1837) ([MNHN] 1997.6516, Ivindo river, Ogooué, Gabon); *Grayia ornata* (Bocage, 1866) ([MNHN] 1997.6517, Ivindo river, Ogooué, Gabon); *Helicops angulatus* (Linnaeus, 1758) (RN1 road between Kourou and Petit Saut, 22 km from Kourou, French Guiana); *Heterodon nasicus* Baird and Girard, 1852 (captive born); *Hydrodynastes bicinctus* (Herrmann, 1804) ([MNHN] 1997.2347, RN1 road between Cayenne and Kourou, French Guiana); *Hydrops triangularis* (Wagler, 1824) (Cayenne, French Guiana); *Imantodes cenchoa* (Linnaeus, 1758) (Saint Eugène, Petit Saut, French Guiana); *Imantodes lentiferus* (Cope, 1894) ([MNHN] 1996.7882, RN1 road between Kourou and Petit Saut, French Guiana); *Leptodeira annulata* (Linnaeus, 1758) (Kaw, French Guiana); *Liophis breviceps* Cope, 1861 ([MNHN] 1996.7879, BPS road, pK 17, Petit Saut, French Guiana); *Liophis miliaris* (Linnaeus, 1758) (BPS road, pK 20, Petit Saut, French Guiana); *Liophis reginae* (Linnaeus, 1758) ([MNHN] 1996.7846, Petit Saut Hydroelectric Plant, French Guiana); *Liophis typhlus* (Linnaeus, 1758) (BPS road, pK 27, Petit Saut, French Guiana); *Mastigodryas boddaerti* (Sentzen, 1796) (French Guiana); *Natrix natrix* (Linnaeus, 1758) (Forêt de Carnelle, Viarmes, Val d'Oise, France); *Oxybelis aeneus* (Wagler, 1824) ([MNHN] 1996.7855, Petit Saut, French Guiana); *Oxybelis fulgidus* (Daudin, 1803) (Saint Eugène, Petit Saut, French Guiana); *Oxyrhopus formosus* (Wied, 1820) ([MNHN] 1997.2048, RN1 road between Kourou and Petit Saut, French Guiana); *Oxyrhopus melanogenys* (Tschudi, 1845) (BPS road, pK 2, Petit Saut, French Guiana); *Philodryas baroni* Berg, 1895 (Argentina); *Philodryas olfersii* (Lichtenstein, 1823) (state of Sao Paulo, Brazil); *Philodryas viridissimus* (Linnaeus, 1758) ([MNHN] 1996.7889, Sinnamary river, 14.5 km upstream from Petit Saut, French Guiana); *Pseudoboa coronata* Schneider, 1801 (RN1 road between Kourou and Petit Saut, French Guiana); *Pseudoboa neuwiedii* (Duméril, Bibron, and Duméril, 1854) (CSG road, 10 km from Kourou, French Guiana); *Pseudoeryx plicatilis* (Linnaeus, 1758) ([MNHN] 1996.7886, RN1 road between Kourou and Petit Saut, French Guiana); *Rhinobothryum lentiginosum* (Scopoli, 1785) (Petit Saut Hydroelectric Plant, French Guiana); *Siphlophis cervinus* (Laurenti, 1768) ([MNHN] 1996.7858, RN1 road between Kourou and Petit Saut, 28 km from Kourou, French Guiana); *Taeniophallus brevirostris* (Peters, 1863) ([MNHN] 1996.4240, BPS road, Petit Saut, French Guiana); *Tantilla melanocephala* (Linnaeus, 1758) ([MNHN] 1996.7876, Kourou, French Guiana); *Thamnodynastes pallidus* (Linnaeus, 1758) (Mont Matoury, French Guiana); *Tripanurgos compressus* (Daudin, 1803) (French Guiana); *Xenodon werneri* Eiselt, 1963 (Petit Saut, French Guiana); *Xenoxybelis argenteus* (Daudin, 1803) (Saint Eugène, Petit Saut, French Guiana).

Tissue samples of West Indian xenodontines were obtained from the frozen tissue collection of S. Blair Hedges for the following species: *Alsophis antiguae* Parker, 1933 (SBH 194104, Antigua, Great Bird Island); *Alsophis antillensis* (Schlegel, 1837) (SBH 192791, Montserrat, St. Peter, Woodlands Spring); *Alsophis portoricensis* Reinhardt and Lütken, 1862 (SBH 160062, United States, Puerto Rico, 1.5 km W [airline] Playa de Tamarindo); *Alsophis vudii* Cope, 1862 (SBH 192985, Bahamas, New Providence, Nassau, west end, Sandy Port Development); *Antillophis andreae* (Reinhardt and Lütken, 1862) (SBH 172603, Cuba, Pinar de Río Prov., Soroa); *Antillophis parvifrons* (Cope, 1862) (SBH 103086, Dominican Republic, Barahona Prov., 19.5 km SW Barahona); *Arrhyton callilaemum* (Gosse, 1851) (SBH 172463, Jamaica, St. Mary Prov., 2.9 km N Port Maria); *Arrhyton dolichura* Werner, 1909 (SBH 172601, Cuba, Ciudad de la Habana Prov., Jardin Botánico Nacional [14 k S, 5.3 km E of Old Havana Center [airline]]); *Arrhyton exiguum* (Cope, 1862) (SBH 160050, United States, Puerto Rico, 1.9 km NE Vista Alegre); *Arrhyton funereum* (Cope, 1862) (SBH 172462, Jamaica, St. Mary Prov., 2.9 km N Port Maria); *Arrhyton landoi* Schwartz, 1965 (SBH 161985, Cuba, Guantanamo Bay USNS, Blue Beach); *Arrhyton procerum* Hedges and Garrido, 1992 (SBH 191526, Cuba, Matanzas Prov., 11.4 km ESE Playa Girón); *Arrhyton polyle-*

pis (Buden, 1966) (SBH 101581, Jamaica, Portland Prov., 3 km S Alligator Church); *Arrhyton supernum* Hedges and Garrido, 1992 (SBH 190230, Cuba, Guantánamo Prov., SW slope El Yunque de Baracoa); *Arrhyton taeniatum* Günther, 1858 (SBH 191163, Cuba, Guantá namo Prov., 2 km N La Munición); *Arrhyton tanyplectum* Schwartz and Garrido, 1981 (SBH 191492, Cuba, Pinar de Río Prov., 4.0 km NW San Vicente); *Arrhyton vittatum* (Gundlach *in* Peters, 1861) (SBH 191528, Cuba, Pinar del Río Prov., Soroa); *Darlingtonia haetiana* Cochran, 1935 (SBH 103806, Haiti, Grande'Anse, ca. 2–3 km S Castillion); *Hypsirhynchus ferox* Günther, 1858 (SBH 101393, Dominican Republic, Barahona Prov., vicinity Barahona); *Hypsirhynchus scalaris* Cope, 1863 (SBH 191992, Haiti, Dept. de la Grand' Anse, 0.8 km E Dame-Marie); *Ialtris dorsalis* (Günther, 1858) (SBH 103702, Haiti, Grand'Anse, ca. 3 km N Bois Sec); *Liophis juliae* (Cope, 1879) (SBH 194227, Dominica, 12.0 km E Roseau); *Tretanorhinus variabilis* Duméril, Bibron, and Duméril, 1854 (SBH 172473, Cuba, Pinar de Río, Soroa); *Uromacer catesbyi* (Schlegel, 1837) (SBH 192456, Dominican Republic, La Altagracia Prov., 4.4 km W Cañada Honda); *Uromacer frenatus* (Günther, 1865) (SBH 104668, Haiti, Dept. de la Grand'Anse, ca. 6 km E Jérémie).

REFERENCES

Anthony, J. (1955). Essai sur l'évolution anatomique de l'appareil venimeux des ophidiens. *Ann. Sc. Nat. Zool.* **11:** 7–53.

Bailey, J. R. (1966). Modes of evolution in New World opisthoglyph snakes. *Mem. Inst. Butantan* **33:** 67–72.

Bailey, J. R. (1967). The synthetic approach to colubrid classification. *Herpetologica* **23:** 155–161.

Barriel, V. (1994). Phylogénies moléculaires et insertions-délétions de nucléotides. *C. R. Acad. Sci. III.* **317:** 693–701.

Bremer, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42:** 795–803.

Bremer, K. (1994). Branch support and tree stability. *Cladistics* **10:** 295–304.

Brooks, D. R., and McLennan, D. A. (1991). "Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology," Univ. of Chicago Press, Chicago.

Cabot, E. L., and Beckenbach, A. T. (1989). Simultaneous editing of multiple nucleic acid and protein sequences with ESEE. *Comput. Appl. Biosci.* **5:** 233–234.

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

Cadle, J. E. (1984b). Molecular systematics of xenodontine colubrid snakes: II. Central American xenodontines. *Herpetologica* **40:** 21–30.

Cadle, J. E. (1984c). Molecular systematics of xenodontine colubrid snakes. III. Overview of xenodontine phylogeny and the history of New World snakes. *Copeia* **1984:** 641–652.

Cadle, J. E. (1985). The Neotropical colubrid snake fauna: Lineage components and biogeography. *Syst. Zool.* **34:** 1–20.

Cadle, J. E. (1987). Geographic distribution: Problems in phylogeny and zoogeography. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 77–105. Macmillan Co., New York.

Cadle, J. E. (1988). Phylogenetic relationships among advanced snakes: A molecular perspective. *Univ. California Publ. Zool.* **119:** 1–77.

Cadle, J. E., and Greene, H. W. (1993). Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. *In* "Species Diversity in Ecological Communities: Historical and Geographical Perspectives" (R. E. Ricklefs and D. Schluter, Eds.), pp. 281–293. Univ. of Chicago Press, Chicago.

Cadle, J. E. (1994). The colubrid radiation in Africa (Serpentes: Colubridae): Phylogenetic relationships and evolutionary patterns based on immunological data. *Zool. J. Linn. Soc.* **110:** 103–140.

Campbell, J. A., and Lamar, W. W. (1989). "The Venomous Reptiles of Latin America," Cornell Univ. Press, Ithaca, NY.

Chippaux, J. P. (1986). Les serpents de la Guyane française. *Faune Tropicale* **27:** 1–165.

Clark, H. (1944). The anatomy and embryology of the hemipenis of *Lampropeltis, Diadophis* and *Thamnophis* and their value as criteria of relationship in the family Colubridae. *Proc. Iowa Acad. Sci.* **51:** 411–445.

Cope, E. D. (1893). Prodromus of a new system of the non-venomous snakes. *Am. Nat.* **27:** 477–483.

Crother, B. I., and Hillis, D. M. (1995). Nuclear ribosomal DNA restriction sites, phylogenetic information, and the phylogeny of some xenodontine (Colubridae) snakes. *J. Herpetol.* **29:** 316–320.

Crother, B. I., and Guyer, C. (1996). Caribbean historical biogeography: Was the dispersal–vicariance debate eliminated by an extraterrestrial bolide? *Herpetologica* **52:** 440–465.

Dessauer, H. C., Cadle, J. E., and Lawson, R. (1987). Patterns of snake evolution suggested by their proteins. *Fieldiana: Zool. n. s.* **34:** 1–34.

Dixon, J. R., and Soini, P. (1977). The reptiles of the upper Amazon Basin, Iquitos region, Peru. II. Crocodilians, turtles, and snakes. *Milwaukee Publ. Mus. Contr. Biol. Geol.* **12:** 1–91.

Dixon, J. R. (1980). The Neotropical colubrid snake genus *Liophis:* The generic concept. *Milwaukee Publ. Mus. Contr. Biol. Geol.* **31:** 1–40.

Dowling, H. G. (1975). The neartic snake fauna. *In* "1974 Yearbook of Herpetology" (H. G. Dowling, Ed.), pp. 191–202. HISS Publ., New York.

Dowling, H. G. (1978). Xenodontinae. *In* "Systematic Herpetology: A Synopsis of Families and Higher Categories" (H. G. Dowling and W. E. Duellman, Eds.), pp. 112a.1–112a.4. HISS Publ., New York.

Dowling, H. G., Highton, R., Maha, G. C., and Maxson, L. R. (1983). Biochemical evaluation of colubrid snake phylogeny. *J. Zool.* **201:** 309–329.

Dowling, H. G., Hass, C. A., Hedges, S. B., and Highton, R. (1996). Snake relationships revealed by slow-evolving proteins: A preliminary survey. *J. Zool.* **240:** 1–28.

Duellman, W. E. (1978). The biology of an equatorial herpetofauna in Amazonian Ecuador. *Misc. Pub. Mus. Nat. Hist. Kansas* **65:** 1–352.

Duellman, W. E. (1990). Herpetofaunas in Neotropical rainforests: Comparative composition, history, and resource use. *In* "Four Neotropical Rainforests" (A. H. Gentry, Ed.), pp. 455–505. Yale Univ. Press, New Haven, CT.

Dunn, E. R. (1928). A tentative key and arrangement of the American genera of Colubridae. *Bull. Antivenin Inst. Am.* **2:** 18–24.

Dunn, E. R. (1931). The herpetological fauna of the Americas. *Copeia* **1931:** 106–119.

Dunn, E. R. (1932). The colubrid snakes of the Greater Antilles. *Copeia* **1932:** 89–92.

Eriksson, T. (1997). AutoDecay ver. 2.9.10. Stockholm Univ., Stockholm.

Estes, R., and Báez, A. (1985). Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: Evidence for

interchange? *In* "The Great American Interchange" (G. Stehli and D. S. Webb, Eds.), pp. 139–197. Plenum, New York.

Felsenstein, J. (1985). Confidence limits on phylogenies: An approach using bootstrap. *Evolution* **39:** 783–791.

Grande, L. (1994). Repeating patterns in nature, predictability, and "impact" in science. *In* "Interpretating the Hierarchy of Nature" (L. Grande and O. Rieppel, Eds.), pp. 61–84. Academic Press, New York.

Greene, H. W., and McDiarmid, R. W. (1981). Coral snake mimicry: Does it occur? *Science* **213:** 1207–1212.

Greene, H. W. (1997). "Snakes: The Evolution of Mystery in Nature," Univ. of California Press, Berkeley.

Haas, G. (1962). Remarques concernant les relations phylogénétiques des diverses familles d'ophidiens fondées sur la différenciation de la musculature mandibulaire. *Coll. Int. CNRS* **104:** 215–241.

Hanken, J., and Wake, D. B. (1982). Genetic differenciation among plethodontid salamanders (genus *Bolitoglossa*) in Central and South America: Implications for the South American invasion. *Herpetologica* **38:** 272–287.

Hedges, S. B., Bezy, R. L., and Maxson, L. R. (1991). Phylogenetic relationships and biogeography of xantusiid lizards, inferred from mitochondrial DNA sequences. *Mol. Biol. Evol.* **8:** 767–780.

Hedges, S. B., Hass, C. A., and Maxson, L. R. (1992). Caribbean biogeography: Molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proc. Natl. Acad. Sci. USA* **89:** 1909–1913.

Hedges, S. B. (1994). Molecular evidence for the origin of birds. *Proc. Natl. Acad. Sci. USA* **91:** 2621–2624.

Hedges, S. B. (1996a). Historical biogeography of West Indian vertebrates. *Annu. Rev. Ecol. Syst.* **27:** 163–196.

Hedges, S. B. (1996b). Vicariance and dispersal in Caribbean biogeography. *Herpetologica* **52:** 466–473.

Hedges, S. B. (1996c). The origin of West Indian amphibians and reptiles. *In* "Contributions to West Indian Herpetology: A Tribute to Albert Schwartz" (R. Powell and R. W. Henderson, Eds.), pp. 95–128. S.S.A.R. Ithaca, NY.

Heise, P. J., Maxson, L. R., Dowling, H. G., and Hedges, S. B. (1995). Higher-level snake phylogeny inferred from mitochondrial DNA sequences of 12S rRNA and 16S rRNA genes. *Mol. Biol. Evol.* **12:** 259–265.

Henderson, R. W., and Binder, M. H. (1980). The ecology and behavior of vine snakes (*Ahaetulla, Oxybelis, Thelotornis, Uromacer*): A review. *Milwaukee Publ. Mus. Contr. Biol. Geol.* **37:** 1–38.

Henderson, R. W., Noeske-Hallin, T. A., Crother, B. I., and Schwartz, A. (1988). The diets of Hispaniolan colubrid snakes II. Prey species, prey size, and phylogeny. *Herpetologica* **44:** 55–70.

Henderson, R. W., and Crother, B. I. (1989). Biogeographic patterns of predation in West Indian colubrid snakes. *In* "Biogeography of the West Indies: Past, Present, and Future" (C. A. Woods, Ed.), pp. 479–518. Sand Hill Crane Press, Gainesville.

Hickson, R. E., Simon, C., Cooper, A., Spicer, G. S., Sullivan, J., and Penny, D. (1996). Conserved sequence motifs, alignment, and secondary structure for the third domain of animal 12S rRNA. *Mol. Biol. Evol.* **13:** 150–169.

Hoffstetter, R. (1962). Revue des récentes acquisitions concernant l'histoire et la systématique des Squamates. *Coll. Int. CNRS* **104:** 243–279.

Jackson, K., and Fritts, T. H. (1995). Evidence from tooth surface morphology for a posterior maxillary origin of the proteroglyph fang. *Amphibia-Reptilia* **16:** 273–288.

Jackson, K., and Fritts, T. H. (1996). Observations of a grooved anterior fang in *Psammodynastes pulverulentus:* Does the mock viper resemble a protoelapid? *J. Herpetol.* **30:** 128–131.

Jenner, J. V. (1981). "A Zoogeographic Study and the Taxonomy of the Xenodontine Colubrid Snakes," Ph.D. dissertation, New York Univ.

Jenner, J. V., and Dowling, H. G. (1985). Taxonomy of American xenodontine snakes: The tribe Pseudoboini. *Herpetologica* **41:** 161–172.

Johnson, R. G. (1955). The origin and evolution of the venomous snakes. *Evolution* **10:** 56–65.

Kardong, K. V. (1980). Evolutionary patterns in advanced snakes. *Am. Zool.* **20:** 269–282.

Kardong, K. V. (1996). Snake toxins and venoms: An evolutionary perspective. *Herpetologica* **52:** 36–46.

Keogh, J. S. (1998). Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biol. J. Linn. Soc.* **63:** 177–203.

Kimura, M. (1980). A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *J. Mol. Evol.* **16:** 111–120.

Knight, A., and 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., and Wilson, A. C. (1989). Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. *Proc. Natl. Acad. Sci. USA* **86:** 6196–6200.

Kraus, F., and Brown, W. M. (1998). Phylogenetic relationships of colubroid snakes based on mitochondrial DNA sequences. *Zool. J. Linn. Soc.* **62:** 421–442.

Lanyon, S. M. (1993). Phylogenetic frameworks: Towards a firmer foundation for the comparative approach. *Biol. J. Linn. Soc.* **49:** 45–61.

Lee, J. C. (1996). "The Amphibians and Reptiles of the Yucatán Peninsula," Cornell Univ. Press, Ithaca, NY.

Lopez, T. J., and Maxson, L. R. (1995). Mitochondrial DNA sequence variation and genetic differentiation among colubrine snakes (Reptilia: Colubridae: Colubrinae). *Biochem. Syst. Ecol.* **23:** 487–505.

Machado, S. R. (1993). A new genus of Amazonian vine snake (Xenodontinae: Alsophiini). *Acta Biol. Leopoldensia* **15:** 99–108.

Maglio, V. J. (1970). West Indian xenodontine colubrid snakes: Their probable origin, phylogeny, and zoogeography. *Bull. Mus. Comp. Zool.* **141:** 1–54.

Marx, H., and Rabb, G. B. (1972). Phyletic analysis of fifty characters of advanced snakes. *Fieldiana: Zool.* **63:** 1–321.

McDowell, S. B. (1987). Snake systematics. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 3–50. Macmillan Co., New York.

McKinstry, D. M. (1983). Morphological evidence of toxic saliva in colubrid snakes: A checklist of world genera. *Herpetol. Rev.* **14:** 12–15.

Miyamoto, M. M., and Cracraft, J. (1991). Phylogenetic inference, DNA sequence analysis, and the future of molecular systematics. *In* "Phylogenetic Analysis of DNA Sequences" (M. M. Miyamoto and J. Cracraft, Eds.), pp. 3–17. Oxford Univ. Press, New York.

Myers, C. W. (1986). An enigmatic new snake from the Peruvian Andes, with notes on the Xenodontini (Colubridae: Xenodontinae). *Am. Mus. Nov.* **2853:** 1–12.

Myers, C. W., and Cadle, J. E. (1994). A new genus for South American snakes related to *Rhadinae obtusa* Cope (Colubridae) and resurrection of *Taeniophallus* Cope for the "*Rhadinae*" *brevirostris* group. *Am. Mus. Nov.* **3102:** 1–33.

Obst, F. J., Richter, K., and Jacob, U. (1988). "The Completely Illustrated Atlas of Reptiles and Amphibians for the Terrarium," T. F. H. Publ., Neptune.

Palumbi, S. R., Martin, A., Romano, S., Mcmillan, W. O., Stice, L., and

Grabowski, G. (1991). "The Simple Fool's Guide to P.C.R.," Univ. of Hawaii Press, Honolulu.

Philippe, H. (1993). MUST: A computer package of management utilities for sequences and trees. *Nucleic Acids Res.* **21:** 5264–5272.

Pregill, G. K. (1981). An appraisal of the vicariance hypothesis of Carribean biogeography and its application to West Indian terrestrial vertebrates. *Syst. Zool.* **30:** 147–155.

Rabb, G. B., and Marx, H. (1973). Major ecological and geographic patterns in the evolution of colubroid snakes. *Evolution* **27:** 69–83.

Rage, J. C. (1987). Fossil history. *In* "Snakes: Ecology and Evolutionary Biology" (R. A. Seigel, J. T. Collins, and S. S. Novak, Eds.), pp. 51–76. Macmillan Co., New York.

Saitou, N., and Nei, M. (1987). The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* **4:** 406–425.

Savage, J. M. (1966). The origins and history of the Central American herpetofauna. *Copeia* **1966:** 719–766.

Savage, J. M. (1982). The enigma of the Central American herpetofauna: Dispersals or vicariance? *Ann. Missouri Bot. Gard.* **69:** 464–547.

Schwaner, T. D., and Dessauer, H. C. (1982). Comparative immunodiffusion survey of snake transferrins focused on the relationships of the natricines. *Copeia* **1982:** 541–549.

Schwartz, A., and Henderson, R. W. (1991). "Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History," Univ. of Florida Press, Gainesville.

Smith, H. M. (1952). A revised arrangement of maxillary fangs of snakes. *Turtox News* **30:** 214–218.

Swofford, D. L. (1993). PAUP. Phylogenetic analysis using parsimony, version 3.1.1. Computer program distributed by the Illinois National History Survey. Champaign.

Taub, A. M. (1967a). Systematic implications from the labial glands of the Colubridae. *Herpetologica* **23:** 145–148.

Taub, A. M. (1967b). Comparative histological studies on Duvernoy's gland of colubrid snakes. *Bull. Am. Mus. Nat. Hist.* **138:** 1–50.

Tihen, J. (1964). Tertiary changes in the herpetofaunas of temperate North America. *Senck. Biol.* **45:** 265–279.

Vidal, N., Lecointre, G., Vié, J. C., and Gasc, J. P. (1997). Molecular systematics of pitvipers: Paraphyly of the *Bothrops* complex. *C. R. Acad. Sci. III.* **320:** 95–101.

Vidal, N., Lecointre, G., Vié, J. C., and Gasc, J. P. (1999). What can mitochondrial gene sequences tell us about intergeneric relationships of pitvipers? *Kaupia,* **8:** 107–112.

Weinstein, S. A., and Kardong, K. V. (1994). Properties of Duvernoy's secretions from opisthoglyphous and aglyphous colubrid snakes. *Toxicon* **32:** 1161–1185.

West-Eberhard, M. J. (1989). Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20:** 249–278.

Whistler, D. P., and Wright, J. W. (1989). A late Miocene rear-fanged colubrid snake from California with comments on the phylogeny of North American snakes. *Herpetologica* **45:** 350–367.

Young, B. A., and Kardong, K. V. (1996). Dentitional surface features in snakes (Reptilia: Serpentes). *Amphibia-Reptilia* **17:** 261–276.

Zaher, H. (1994). "Phylogénie des Pseudoboini et Évolution des Xenodontinae Sud-Américains (Serpentes, Colubridae)," Ph.D. dissertation, M. N. H. N. Paris.

Zaher, H. (1996). A new genus and species of pseudoboine snake, with a revision of the genus *Clelia* (Serpentes, Xenodontinae). *Boll. Mus. Reg. Sci. Nat. Torino* **14:** 289–337.

Zaher, H. (1999). Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bull. Am. Mus. Nat. Hist.* **240:** 1–168.

Zamudio, K. R., and Greene, H. W. (1997). Phylogeography of the bushmaster (*Lachesis muta:* Viperidae): Implications for neotropical biogeography, systematics, and conservation. *Biol. J. Linn. Soc.* **62:** 421–442.