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Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal

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Abstract

We present a phylogenetic analysis of the New World dipsadids based on an expanded data matrix that includes 246 terminal taxa including 196 dipsadids. The species are sampled for eight genes (12S, 16S, cytb, nd2, nd4, bdnf, c-mos, rag2). The data are explored using two distinct optimality procedures—maximum parsimony and maximum likelihood—and two alignment strategies—dynamic homology and static homology. Two previously unsampled dipsadid genera, *Sordellina* and *Rhachidelus*, are now included in the analysis. The definitions of the genera, *Erythrolamprus*, *Clelia*, *Hypsirhynchus*, *Philodryas* and *Phimophis*, and the tribes Alsophiini, Echinantherini and Conophiini, are revised. In order to maintain monophyly, the genus *Umbrivaga* is synonymized with *Erythrolamprus*, and two new genera are erected to accommodate *Phimophis iglesiasi* and *Clelia rustica*, as well as their closely related species. The West Indian genera *Schwartzophis*, *Darlingtonia*, *Antillophis* and *Ocyophis* are resurrected.

Our understanding of the phylogenetic relationships of snakes has improved significantly in recent years coincident with the development of molecular genetics. DNA sequence data provide a great number of phylogenetically informative characters, and often in sufficient quantity and quality for phylogenetic inference. Although recent phylogenetic contributions have yielded significantly different hypotheses of relationships, some noteworthy consensus has emerged, including a basal position of the highly specialized family Viperidae and the paraphyletic nature of the traditional family Colubridae. Various phylogenetic studies of non-venomous "colubroid" snakes have produced a series of differing classifications, all of which were intended to include only monophyletic units (Kelly et al., 2003; Lawson et al., 2005; Vidal et al., 2007). Zaher et al. (2009) provided a detailed explanation of the taxonomic issues related to some of the names used in recent years. They also offered a new phylogenetic classification for the colubroid radiation of caenophidian snakes, herein termed the Colubroides [or colubroideans; but see Oguiura et al. (2010) and Pyron et al. (2011) for a different opinion].

The Colubroides contains approximately 440 genera and 2150 species (Uetz et al., 2011) arranged into 13 families (Zaher et al., 2009): Atractaspididae Günther 1858; Calamariidae Bonaparte 1838; Colubridae Oppel 1811; Dipsadidae Bonaparte 1838; Elapidae Boie 1827; Homalopsidae Bonaparte, 1845; Lamprophiidae Fitzinger 1843 (including the subfamilies Lamprophiinae

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and Pseudoxyrhophiinae Dowling, 1975); Natricidae Bonaparte 1838; Pareatidae Romer 1956; Psammophiidae Bonaparte, 1845; Viperidae Oppel 1811; Pseudoxenodontidae McDowell 1987; and Xenodermatidae Gray 1849.

The New World Dipsadidae are one of the largest radiations of colubroidean snakes, with approximately 700 species distributed throughout the Americas and the West Indies (Hedges et al., 2009; Zaher et al., 2009). Recent studies (Vidal et al., 2000, 2010; Pinou et al., 2004; He et al., 2009; Zaher et al., 2009) confirm three historically distinct lineages (Cadle, 1984a,b, 1985, 1988). These lineages are usually considered distinct subfamilies, although there is no consensus concerning the monophyly of the lineage composed of the five, mainly North American, genera *Carphophis*, *Contia*, *Diadophis*, *Farancia* and *Heterodon* (Zaher et al., 2009; Vidal et al., 2010).

Zaher et al. (2009) provided a comprehensive phylogenetic analysis of the Dipsadidae that combines one nuclear (c-mos) and two mitochondrial (12S and 16S) genes from 93 species representing 54 genera (56.8% of dipsadid genera). The authors recognized three subfamilies and 14 tribes that are characterized both morphologically and molecularly, and that display either a high bootstrap value ($> 70\%$) or high Bremer support (> 5 steps; Bremer, 1994).

In a paper published shortly thereafter, Hedges et al. (2009) used DNA sequence data from six genes (12S, 16S, cytb, nd2, nd4, rag2) to evaluate the phylogenetic affinities of 35 West Indian taxa belonging to the Alsophiini radiation of dipsadids. They revised Zaher et al.'s (2009) classification for the group. The branching order within the two studies is similar; however, both taxon coverage and nomenclature differ substantially. Hedges et al. (2009) included a larger number of species and subspecies from the West Indian radiation of the Alsophiini, whereas Zaher et al. (2009) presented a much broader coverage of the South American radiation of the Xenodontinae, to which Alsophiini belongs.

Vidal et al. (2010) used most of the DNA sequences available in GenBank for the genes 12S and 16S rRNAs to provide a phylogenetic analysis of Dipsadidae, but they excluded most West Indian genera (*Uromacer*, *Hypsirhynchus*, *Schwartzophis*, *Antillophis*, *Caraiba*, *Darlingtonia*, *Magliophis* and *Haitiophis*). They added data for seven genera not previously sequenced—*Crisantophis*, *Echinanthera*, *Manolepis*, *Nothopsis*, *Trimetopon*, *Umbrivaga* and *Xenopholis*. Vidal et al.'s (2010) results are largely congruent with those of Zaher et al. (2009) in recovering all tribes, save for their Conophiini, which is polyphyletic. Similarly, the intratribal relationships resolved by Vidal et al. (2010) are highly concordant with those of Zaher et al. (2009), differing substantially only within Dipsadinae, which is poorly sampled in both studies. Vidal et al. (2010) also recovered a paraphyletic lineage of North American dipsadids (their Heterodontinae; a name discussed in Appendix 1) with a monophyletic Carphophiinae (*sensu* Zaher et al., 2009). The analysis of Vidal et al. (2010) obtained low support for all deeper branches in the dipsadid tree [bootstrap $< 50\%$; Bayesian posterior probability (BPP) $< 90\%$], rendering questionable any taxonomic conclusion regarding these deeper clades; Zaher et al. (2009) also acknowledged this trend. While obtaining a concordant phylogeny, Vidal et al. (2010) disagreed with several taxonomic changes made by Zaher et al. (2009).

The most recent major contribution to colubroidean phylogeny is that of Pyron et al. (2011), who analysed the relationships of 761 species. Pyron et al. (2011) provided data for several additional genera (e.g. *Geophis*, *Hydromorphus* and *Adelphicos*). Their tree for Dipsadidae is highly consistent with those of Vidal et al. (2007, 2010) and Zaher et al. (2009).

To evaluate the conflicting classifications of Hedges et al. (2009), Zaher et al. (2009) and Vidal et al. (2010), we present a phylogenetic analysis of the New World dipsadids based on an expanded data matrix that combines all sequences from GenBank with 273 new sequences from 62 species. The matrix contains eight genes from 246 terminal taxa, of which 196 are dipsadids. Our dataset has species from 115 genera of colubroideans and 70 genera of dipsadids, including two previously unsampled genera (*Rhachidelus* and *Sordellina*). We add 95 dipsadid species to the data matrix published by Zaher et al. (2009), 75 to that of Vidal et al. (2010), and 126 to that of Pyron et al. (2011). All West Indian species in the Alsophiini used by Hedges et al. (2009) are included herein to test specifically the monophyly of the Alsophiini and its constituent parts. We include all new sequences generated by Vidal et al. (2010) to reanalyse phylogenetic relationships within a broader context. In contrast to Vidal et al. (2010), our primary goal remains defining a stable classification that does not conflict with a recovered hypothesis of phylogenetic interrelationships (Zaher et al., 2009).

Material and methods

Taxon and gene sampling

Our data matrix comprises 246 terminal taxa, and sequences for five mitochondrial (12S, 16S, cytb, nd2, nd4) and three nuclear genes (bdnf, c-mos, rag2; Appendix S1). We sequenced 273 DNA fragments for 62 species, including 63 sequences for 12S, 61 for 16S, 48 for cytb, two for nd4, 60 for bdnf and 39 for c-mos. We added 13 genera absent from Zaher et al. (2009): *Rhachidelus*, *Xenopholis*, *Echinanthera*, *Sordellina*, *Geophis*, *Hypsiglena*, *Tretanorhinus*, *Thermophis*,

Nothopsis, *Trimetopon*, *Crisantophis*, *Manolepis* and *Umbrivaga*. Our sampling also was broadened by adding species in the following genera: *Apostolepis*, *Atractus*, *Oxyrhopus*, *Phalotris*, *Philodryas*, *Xenodon* and *Erythrolamprus*.

We incorporated 761 additional sequences from GenBank including 178 for 12S, 172 for 16S, 96 for cytb, 56 for nd2, 75 for nd4, 13 for bdnf, 112 for c-mos and 59 for rag2. If multiple sequences were available in GenBank for a given taxon, we selected only one sequence and chose the most complete sequence for inclusion. The caenophidian tree was rooted using the boine *Boa constrictor* as the primary outgroup.

Our analysis included representatives of the following families of caenophidians (number of representative species in parentheses, taxonomy following Zaher et al., 2009): Acrochordidae (1), Atractaspididae (3); Calamariidae (3); Colubridae (5); Dipsadidae (188, including 146 Xenodontinae, 29 Dipsadinae, 3 Carphophinae and 10 Dipsadidae *incertae sedis*); Elapidae (5); Elapoidea *incertae sedis* (1, *Oxyrhabdium leporinum*); Homalopsidae (2); Lamprophiidae (5, including 2 Pseudoxyrhophiinae and 3 Lamprophiinae); Natricidae (8); Pareatidae (2); Psammophiidae (2); Pseudoxenodontidae (4); Viperidae (5); Xenodermatidae (3). Inclusion of the non-dipsadid colubroideans facilitated an evaluation of the monophyly of the Dipsadidae. Our choice of sequences aimed to sample the phylogenetic diversity in each family of Caenophidia.

DNA sequencing

DNA was extracted from scales, blood, liver, or shed skins, following specific protocols for each tissue (Bricker et al., 1996; Hillis et al., 1996). Sequences were amplified via polymerase chain reaction (PCR) using the primers for 12S, 16S, and c-mos described by Zaher et al. (2009). The following additional primers were used: cytb, 703Botp.mod (5′-TCA AAY ATC TCA ACC TGA TGA AAY TTY GG-3′) and MVZ16p.mod (5′-GGC AAA TAG GAA GTA TCA YTC TGG YTT-3′) based on Pook et al. (2000); nd4, NAD4 (5′-CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC-3′) and Leu (5′-CAT TAC TTT TAC TTG GAR RRG CAC CA-3′), both based on Arévalo et al. (1994); and bdnf, BDNFF (5′-GAC CAT CCT TTT CCT KAC TAT GGT TAT TTC ATA CTT-3′) and BDNFR (5′-CTA TCT TCC CCT TTT AAT GGT CAG TGT ACA AAC-3′), as described by Noonan and Chippindale (2006). PCRs were performed using standard protocols, with some adjustments to increase the efficiency of amplification as follows: the addition of either 0.4% of Triton 100 for 12S, 16S, bdnf and c-mos, or BSA for cytb; an annealing temperature of 54 °C for 12S and 16S, 56 °C for bdnf, c-mos and nd4, and 60 °C for cytb.

PCRs were purified with shrimp alkaline phosphatase and exonuclease I (GE Healthcare, Piscataway, NJ) and the sequences for 12S, 16S, nd4 and c-mos were processed using the DYEnamic ET Dye Terminator Cycle Sequencing Kit in a MegaBACE 1000 automated sequencer (GE Healthcare) following the manufacturer's protocols. The cytb and bdnf sequences were processed using BigDye Terminator cycle sequencing kit in an ABI 3700 sequencer (Applied Biosystems, Foster City, CA). Both strands were checked and, when necessary, edited manually using FinchTV (Geopiza, Seattle, WA). The consensus of the two strands was constructed manually with Bioedit 7.0.9 (Hall, 1999).

Homology and search strategy

We used two distinct procedures for analysing the unaligned sequences: (i) dynamic homology (DH) using POY version 4.1.2 (Varón et al., 2008); and (ii) static homology via multiple alignment using Clustal X (Thompson et al., 1997) and MAFFT (Katoh et al., 2002). The terms ''implied alignment'' (IA) and ''multiple alignment'' (MA) were used only to distinguish the two methodologically distinct static alignments that resulted from the dynamic homology and static homology procedures, respectively (Wheeler, 2003). DH was performed using maximum parsimony (MP) as the optimality criterion, whereas MA was analysed by MP and maximum likelihood (ML; see sections on dynamic and static homologies below). Thus three sets of consensus trees were produced as follows: (i) a consensus tree derived from a maximum parsimony analysis using dynamic homology (MP/DH); (ii) a consensus tree derived from a maximum parsimony analysis using multiple alignment (MP/MA); (iii) a consensus tree derived from a maximum likelihood analysis using multiple alignment (ML/MA). The discussion and comparisons emphasize the results of the MP/DH and ML/MA analyses, but when relevant we also comment on results derived from the MP/MA analysis.

We used two optimality criteria (MP and ML) and two distinct methods of analysing the unaligned sequences (DH and MA) to allow comparisons with the results of Hedges et al. (2009), Zaher et al. (2009) and Vidal et al. (2010), to avoid controversy regarding a specific approach and to assess to what extent the different approaches affected the results.

Dynamic homology

This methodology followed that of Zaher et al. (2009), in which only non-coding rRNAs (12S and 16S) were submitted to the direct optimization procedure of POY. First, non-coding sequences (rRNAs) were pre-aligned using the E-INS-I algorithm implemented in MAFFT (Katoh et al., 2002). Noncoding 12S

and 16S rRNAs sequences were split into six fragments (Zaher et al., 2009), each comprising approximately 100 bp, flanked by conserved regions with unambiguous homologies (likely stem regions). The fragments were used as regions of homology constraint during searching. The remaining coding genes (cytb, nd4, nd2, rag2, bdnf and c-mos) were translated to amino-acid sequences, aligned with Clustal X using the Gonnet series matrix, and subsequently retro-translated to nucleotides for analysis in POY. This approach was justified by codon frame evolution and the influence of acting hidden stop codons in coding genes (Seligmann and Pollock, 2004; Di Giulio, 2005; Baranov et al., 2009; Singh and Pardasani, 2009). It also increased the speed of the DH analysis (Faivovich et al., 2005) for gene fragments without indels (e.g. cytb, nd4 and rag2).

The nucleotide alignment and phylogenetic tree were simultaneously estimated based on the algorithm described by Sankoff (1975) as implemented in POY through the method of direct optimization (Wheeler, 1996) with a transformation cost matrix of 1 : 1 (weights for substitution and gap insertion set to 1).

Search strategies for the DH analysis were performed using the command "Search" constrained by time, which implements tree buildings by random addition sequences (RAS), swapping by TBR, perturbations using ratchet, and tree fusing. This command repeated the same strategy as many times as possible within the specified time. We conducted six rounds of 24-h runs using the Cluster of the Museu de Zoologia da Universidade de São Paulo with 12 processors built in parallel.

To assess support values (*sensu* Grant and Kluge, 2003) for clades in the strict consensus of our best trees, we calculated the Bremer support indices using POY. We generated a pool of suboptimal trees by keeping all visited trees generated by 100 RAS followed by TBR. After that we used the command "report", with the option "graphsupports : bremer" to calculate the Bremer based on the saved suboptimal trees.

To assess corroboration values (*sensu* Grant and Kluge, 2003), we followed the recommendation provided in the POY manual for resampling individual nucleotides in our matrix, instead of sequence segments. Although this approach is not equivalent to a DH strategy, it was used as a strategy to increase the number of characters for bootstrapping because our matrix retained only 15 sequence segments. Absolute frequencies for bootstrap were calculated using the TNT software (Goloboff et al., 2008) by conducting 1000 pseudoreplications using the New Technology algorithm with the exported implied alignment matrix from POY.

Static homology

The result of DH analysis was compared with MA as implemented above. The multiple sequence alignment process (Feng and Doolittle, 1987) of MAFFT was applied using the iterative refinement method implemented in the E-INS-I algorithm for the rRNAs sequences (Katoh et al., 2005). We concatenated the rRNAs with the retro-aligned coding genes. The concatenated MA was analysed in TNT using the command "xmult", which implements rounds of SPR, TBR, tree drifting, ratchet and tree fusing. Tree searches were stopped after the consensus stabilized for five rounds and a final step of TBR was conducted ("xmult = consense 5" and "bb" commands).

We also carried out ML analysis using RAxML 7.2.8 (Stamatakis, 2006). We divided our matrix in 20 partitions, in which the coding genes were partitioned by codon positions while each rRNA gene was analysed as a separate partition (Lawson et al., 2005; Hedges et al., 2009; Vidal et al., 2010; Pyron et al., 2011). GTR was the only substitution model implemented in RAxML (Stamatakis, 2006). As recommended in the program documentation, the GTR GAMMA model was used for all partitions instead of GTR + GAMMA + I. One hundred RAS were built and the rapid hill-climbing algorithm, known as LSR (lazy subtree rearrengment), was used to swap the trees. We opted for RAxML as it provided a fast ML algorithm that proved to be effective with large datasets (Stamatakis, 2006). One thousand pseudoreplications of non-parametric bootstrap were performed using the Cluster hosted at the Laboratório de Alto Desempenho–Pontifícia Universidade Católica do Rio Grande do Sul (LAD-PUCRS). This probabilistic approach enabled a comparison with results from two other studies that concentrated on dipsadid relationships (Hedges et al., 2009; Vidal et al., 2010) and with Pyron et al.'s (2011) broader analysis of colubroidean relationships.

Comparison of topologies using subtree pruning and regrafting

Subtree pruning and regrafting (SPR), as implemented by TNT, was used to compare tree length differences in the topologies derived from our three approaches. We used the amount of SPR steps to transform one topology into another and access the amount of topological differences among the results from different approaches.

Results

Sequence characterization

The implied alignment derived from DH on POY produced a concatenated matrix comprised of 6030 characters. In comparison, MA produced a matrix of 5574 characters (complete alignments available in

Supplementary Information, Appendices S4 and S5). The difference in length between IA and MA (456 characters) was the result of homology determinations and the proportion of gaps inferred by the two methods, which tended to be inflated in the former given the nature of IAs that rather represent synapomorphy schemes. The IA increased the sequence length of the unaligned files of 12S and 16S by approximately 61 and 70%, respectively. In contrast, the multiple alignment approach increased the sequence lengths by 16% for 12S and 6% for 16S (Table 1).

As reported previously by Zaher et al. (2009), the c-mos sequences had a frame-shift mutation that involved all sequenced *Xenodon*. A deletion occurred at site 299, and *X. histricus*, *X. pulcher* and *X. matogrossensis* had an insertion of five nucleotides at positions 373–377. These three species formed a monophyletic group that also included *X. guentheri* and *X. semicinctus*. Although we were not able to sequence the final portion of c-mos for *X. guentheri*, and Vidal et al. (2010) did not sequence *X. semicinctus* for that gene, the phylogenetic positions of the species suggested that both also shared the frame shift. Given the stop codon in amino acid position 101, this mutation remained unexplained. However, as argued by Zaher et al. (2009), no evidence suggested the presence of a pseudogene in the sequences. Nevertheless, we removed these suspicious sequences from our matrix.

Comparison among methodologies

Four most parsimonious trees with 28911 steps were found in our MP/DH analysis using POY. These most parsimonious trees resulted in an almost fully resolved strict consensus tree (Fig. 1). The MP analysis based on the MA found 8568 best trees with 28 188 steps. The strict consensus tree (Appendix S2) had a greater number of polytomies than MP/DH. The MP/MA analysis obtained 87% (214) of the possible (244) clades. In contrast, the MP/DH analysis resolved 97% of all possible dichotomies (237/244; but see comments above on sequence characterization). Apart from the larger number of polytomies, most of the main clades and higher taxa were recovered in the MP/MA analysis, with a significant number of differences occurring only among tribes and genera within the Dipsadidae (see below). All of these differences had low Bremer and bootstrap support values in MP/MA (Appendix S2). Additionally, MP/MA tended to produce lower support values (Bremer mean = 8.15; bootstrap mean = 64.02) than did MP/DH (Bremer mean = 11.14; bootstrap mean = 73.29).

Table 1
Sequence size for the gene fragments used in this study. Fragment length in base pairs

Gene	Sequences	Original length	Multiple alignment	Implied alignment
12S	241	338	395	544
16S	233	434	463	770
cytb	144	1100	1100	1100
nd2	56	1039	1039	1039
nd4	76	694	694	694
bdnf	73	673	673	673
c-mos	151	496	496	496
rag2	59	714	714	714
Total	246		5574	6030

Our search procedure in RAxML included 100 RAS and produced a topology with a score of $-\ln L = -177190.1343$. As for the MP/MA analysis, ML/MA recovered most of the main clades and higher taxa present in the MP/DH tree and as defined by Zaher et al. (2009), with high bootstrap values.

SPR manipulations indicated that the two topologies based on MP optimizations were the most similar, regardless of the homology criterion used (MP/DH versus MP/MA = 25 steps). Topologies using the same homology criterion but distinct optimization criteria were more dissimilar (MP/MA vs ML/MA = 31 SPR steps), while topologies that differ in both method of tree construction and homology criteria were the most dissimilar of all three combinations (MP/DH and ML/MA = 59 steps).

Although tree topologies varied with methodology, the differences occurred only on poorly supported nodes. The basal relationships within Caenophidia were always recovered (Fig. 1), as were the relationships among genera within almost all tribes in the Xenodontinae. In contrast, relationships among xenodontine tribes and the position of some taxa (e.g. *Sordellina punctata*, *Crisantophis nevermanni*, *Caaeteboia amarali*, *Manolepis putnami* and *Pseudalsophis*) were unstable. Branch lengths in the ML tree (Appendix S3) indicated that most of the conflicts occurred on very short branches. These short branches are connected to long terminal branches, and this association might reflect long-branch attraction (Felsenstein, 1978), although this hypothesis is difficult to test (Bergsten, 2005).

Phylogenetic relationships and branch support among different tree topologies

Our analyses recovered the same broad pattern of relationships as Zaher et al. (2009) for caenophidian snakes (Fig. 1). The following higher-level clades were obtained by all methodologies with strong support (bootstrap for POY analysis, Bremer for POY analysis, and bootstrap for ML analysis, respectively): Colubroides (93/19/100), Colubriformes (99/25/100), Endoglyptodonta (88/12/< 70) and Colubroidea (90/9/99). Compared with the tree of Zaher et al. (2009), our

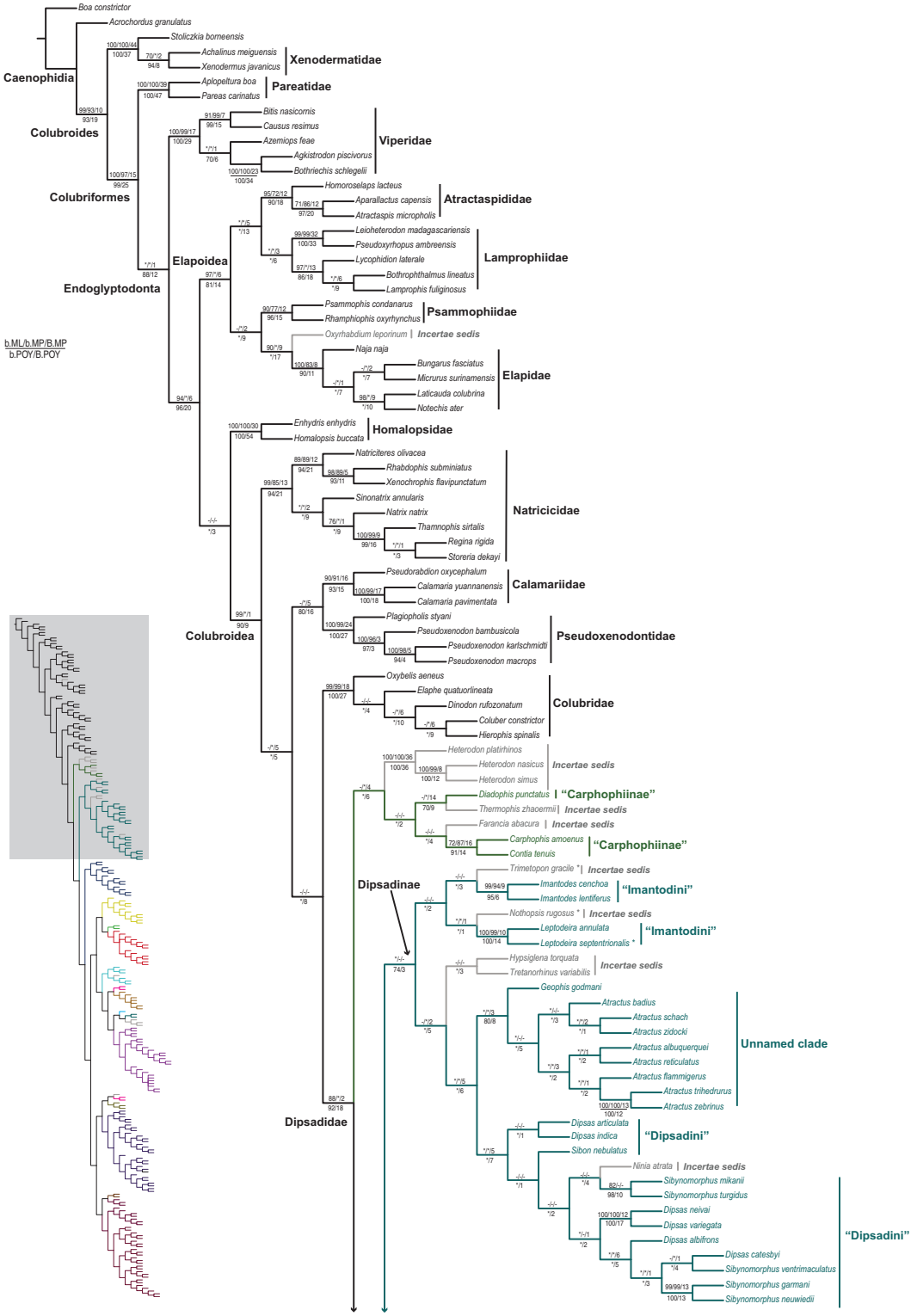

Fig. 1. Strict consensus of four most parsimonious trees found in POY. Numbers above and below branches show support values for Bremer and bootstrap. Abbreviations: b.POY, bootstrap support values from POY; B.POY, Bremer support values from POY; b.ML, bootstrap values from the ML analysis in RAxML; b.MP, bootstrap support values from MP analysis in TNT; B.MP, Bremer support values from MP analysis in TNT. Asterisks indicate bootstrap values lower than 70%. Dashes indicate clades not recovered by specific analysis. Names of the higher taxa are shown near their respective clades. Quoted higher taxa names represent non-monophyletic taxa in this analysis. Asterisk following a terminal name indicates taxa from Vidal et al. (2010).

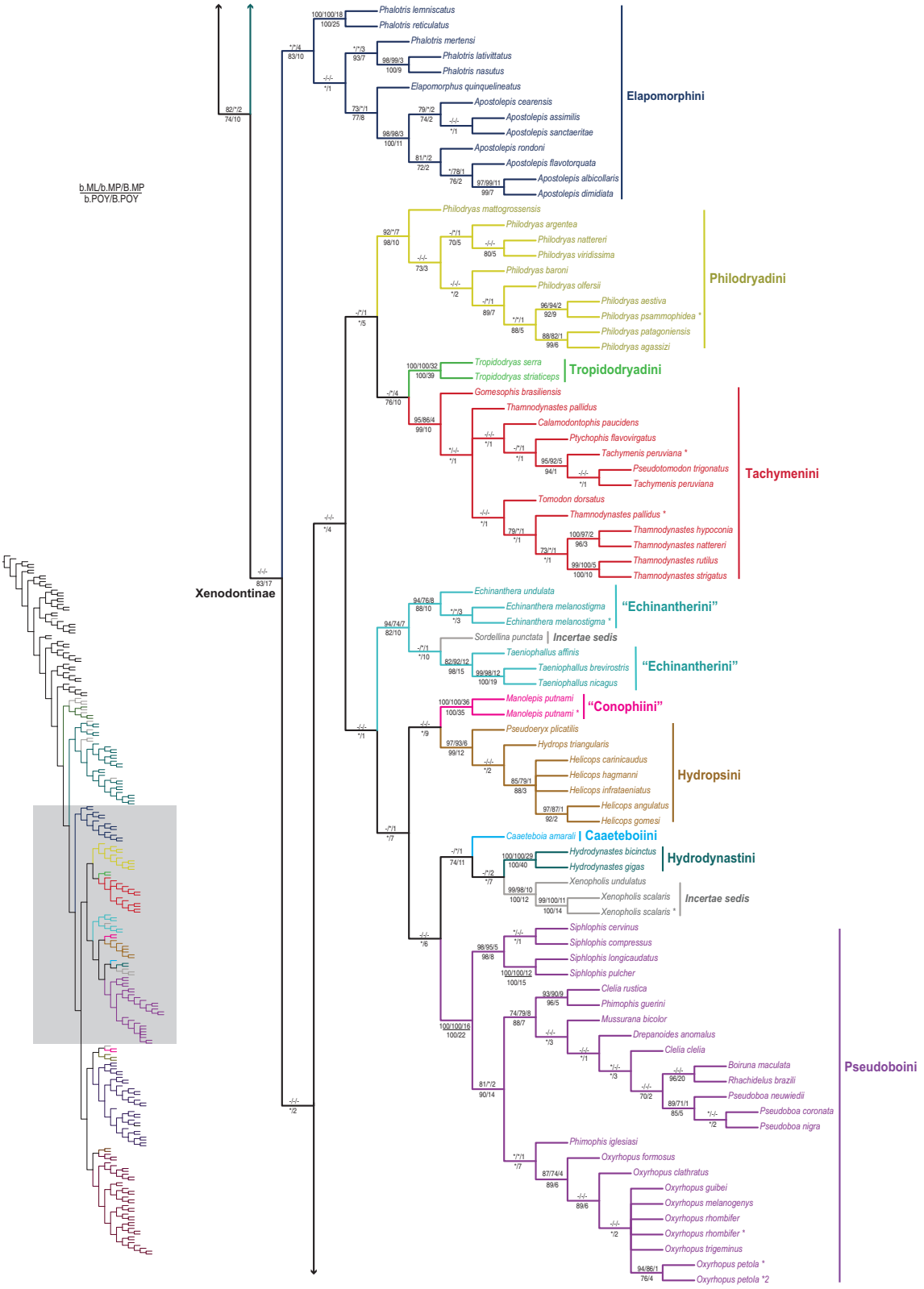

Fig. 1.
(*Continued*).

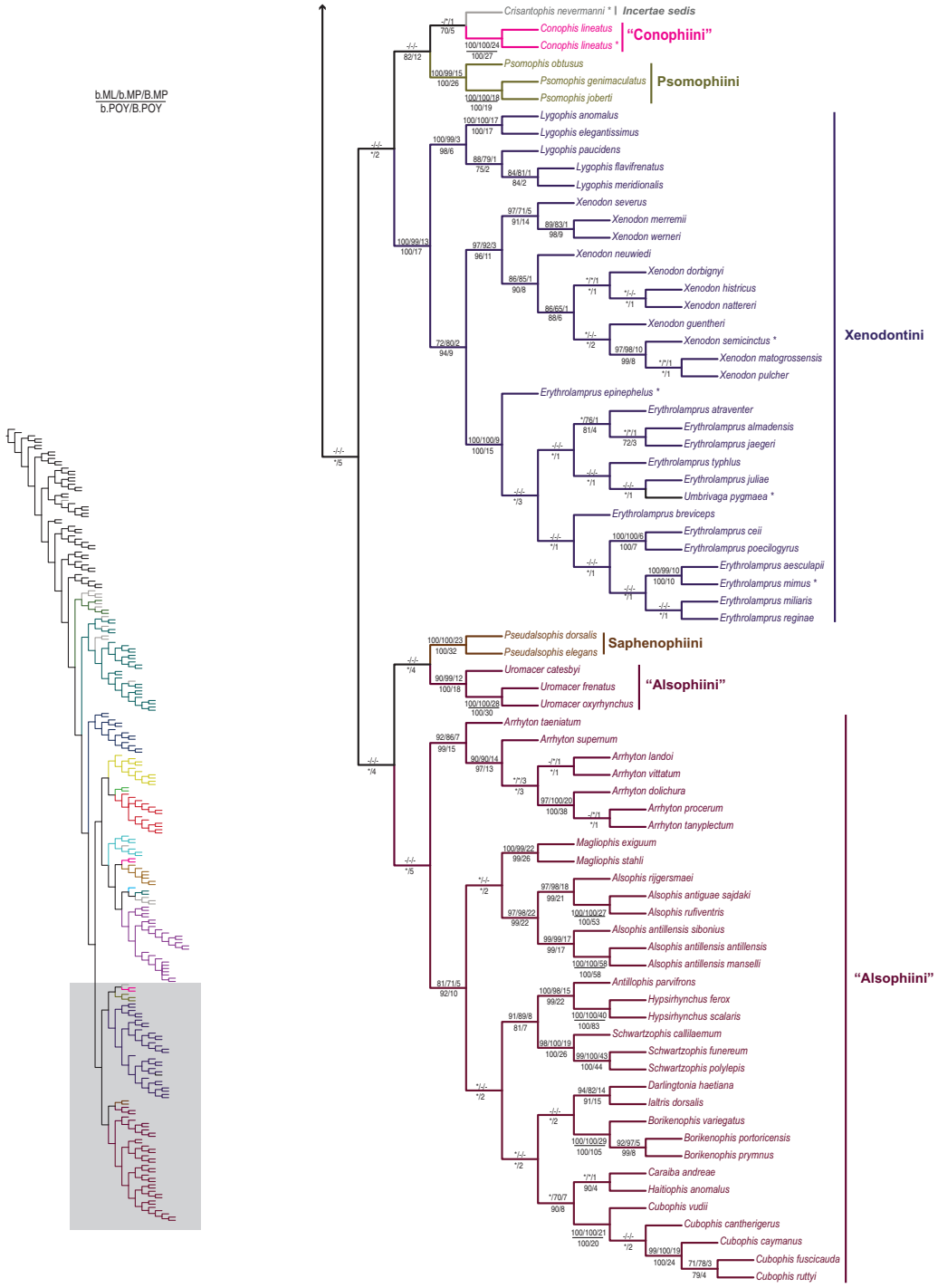

Fig. 1.
(*Continued*).

expanded sampling weakened bootstrap support for the Elapoidea (81%), yet increased Bremer support (14), and produced a bootstrap value of 97% for ML. The changes were probably related to the inclusion of *Oxyrhabdium leporinum*, the sister group to the Elapidae in our analysis (but see Pyron et al., 2011). The elapoid families Elapidae (90/11/100), Atractaspididae (90/18/95) and Psammophiidae (96/15/90) were all robustly supported. Within Elapoidea, the bootstrap and Bremer values for Lamprophiidae were low

(< 70/6/< 70). Homalopsidae was retrieved in the MP/DH analysis as the sister group of Colubroidea, although with very low support values (< 70/3), while falling as the sister group of the clade formed by Elapoidea and Colubroidea in the ML/MA analysis with high bootstrap value (84).

Within Colubroidea, Natricidae (94/21/99) and Colubridae (100/27/99) retained very high support, which corroborated the long-standing view of their monophyly. Calamariidae (93/15/90) and Pseudoxenodontidae (100/27/100), represented in Zaher et al.'s (2009) analysis by only one terminal each, were well supported herein after the inclusion of *Pseudorabdion* and *Plagiopholis*, respectively, and after adding one additional species of *Calamaria* and two *Pseudoxenodon*. The clade formed by Calamariidae and Pseudoxenodontidae was robustly supported (80/16) in the MP/DH and this represented a novel hypothesis, although it was not recovered in the ML approach. Using ML, Calamariidae appeared as the sister group of Colubridae with a moderate bootstrap value (77), and Pseudoxenodontidae rooted more basally on the tree as the sister group of the remaining Colubroidea, but with a low bootstrap (< 70). In Zaher et al. (2009), Calamariidae was resolved as the sister group of Colubridae while Pseudoxenodontidae formed the sister group of a clade comprised of Natricidae and Dipsadidae. Also differing from Zaher et al. (2009), Colubridae was the sister group of Dipsadidae in the MP/DH, while the ML/MA recovered Natricidae as the sister group of Dipsadidae (Appendix S3). However, the MP/DH's sister-group relationship was poorly supported (< 70/8), revealing a highly unstable topology in both herein and in Zaher et al. (2009). Pyron et al. (2011), using a much larger sampling of non-dipsadid colubroideans, also obtained weak support for a sister-group relationship between Disadidae and Pseudoxenodontidae.

Dipsadidae obtained greater overall support (92/18/88) than in Zaher et al. (2009) and in Pyron et al. (2011), suggesting that more extensive sampling within the family helped to define the monophyly of the family more consistently. We also recovered most of the tribes defined by Zaher et al. (2009), all with strong support values, albeit with very low support for the deeper nodes within Dipsadidae.

As for Zaher et al. (2009), we frequently recovered the following three main clades within Dipsadidae: the subfamilies Dipsadinae (77/3/< 70) and Xenodontinae (74/10/82), and a clade composed by the subfamily Carphophiinae, and the *incertae sedis* genera *Heterodon*, *Farancia* and *Thermophis*. *Thermophis* nested within Carphophiinae as the sister group of *Diadophis* in the MP trees, receiving moderate bootstrap (70) but high Bremer (9) support values in the MP/DH analysis. It clustered as the sister group of Dipsadidae in the ML/MA with high bootstrap (0.98) support. *Farancia* also nested inside Carphophiinae in MP/DH tree, as the sister group of a clade composed by *Carphophis* and *Contia*. However, such hypotheses received low support values (< 70/4). In contrast, the clade formed by *Carphophis* and *Contia* was recovered in both analyses, with high bootstrap and Bremer support values (91/14/72).

Within Dipsadinae, the following two clades were retrieved in all analyses with moderate to high support values: (i) a highly supported clade formed by the genera *Geophis* and *Atractus* (80/8/< 70); and (ii) a clade composed of the genera *Dipsas*, *Ninia*, *Sibon* and *Sibynomorphus* (69/7/< 70). The tribe Imantodini (*sensu* Myers, 2011), represented by *Imantodes* and *Leptodeira* (Mulcahy et al., 2011), was not monophyletic in both analyses, with *Nothopsis* falling as the sister group of *Leptodeira* in both MP and ML analyses, and *Trimetopon* as the sister group of *Imantodes* in the ML analysis. However, these clades were all very poorly supported (< 70/< 3). Our analyses also corroborated the paraphyly of the genera *Dipsas* and *Sibynomorphus* and suggested that *Ninia* belonged to the tribe Dipsadini of snail-eating snakes. The genera *Tretanorhinus* and *Hypsiglena* always nested inside Dipsadinae and as sister groups in the MP analyses, albeit with low support values (< 70/3). In the ML analysis, the former "leptodeirine" *Hypsiglena* appeared as the sister group of *Trimetopon*, with a low bootstrap (< 70), while *Tetranorhinus* positioned at the base of a weakly supported clade (–/6/0.85) containing *Trimetopon*, *Hypsiglena*, *Geophis*, *Atractus* and Dipsadini (including *Ninia*). In turn, *Trimetopon* showed a highly unstable position. It nested within Dipsadinae in both MP/DH (as sister group of *Imantodes*) and ML/MA (as sister group of *Hypsiglena*) trees, but appeared within Xenodontinae as the sister group of Psomophiini in the MP/MA tree.

Within Xenodontinae, the following clades were retrieved with high support values in all analyses: Xenodontini (100/17/100), Psomophiini (100/26/100), Saphenophiini (100/32/100), Tropidrodryadini (100/39/100), Tachymenini (99/10/95), Pseudoboini (100/22/100), Hydropsini (98/12/97), Hydrodynastini (100/40/100) and Philodryadini (98/10/97). Elapomorphini was retrieved with moderate support (83/10/< 70). A clade formed by the genera *Echinanthera* and *Taeniophallus*, which corresponded to the tribe Echinantherini of Zaher et al. (2009), was retrieved with low support (< 70) in the ML analysis. In both MP analyses, *Sordellina* nested inside Echinantherini, as the sister group of *Taeniophallus*, rendering the tribe paraphyletic. However, support values were also very low for this hypothesis; bootstrap and Bremer values dropped from < 70/10 in the MP/DH to < 70/1 in MP/MA. The strongly supported monophyletic genus

Arrhyton (99/15/92) clustered within Alsophiini as the sister group to the remaining members of the tribe in the MP/DH tree, but it fell outside the alsophiines in the ML/MA tree. However, both hypotheses received very low support values.

The following xenodontine genera represented by more than one species were strongly supported: *Pseudalsophis* (100/32/100), *Psomophis* (100/26/100), *Apostolepis* (100/10/1.0), *Arrhyton* (99/15/92), *Alsophis* (99/22/97), *Schwartzophis* (100/26/98), *Hypsirhynchus* (100/83/100), *Magliophis* (100/26/100), *Borikenophis* (100/105/100), *Cubophis* (100/20/100), *Uromacer* (100/18/90), *Lygophis* (98/6/100), *Xenodon* (96/11/100), *Taeniophallus* (98/15/82), *Echinanthera* (88/10/94), *Tropidodryas* (100/39/100), *Siphlophis* (98/8/98), *Oxyrhopus* (89/6/87), *Pseudoboa* (85/5/89), *Hydrodynastes* (100/40/100), *Xenopholis* (100/12/99) and *Philodryas* (98/10/92). The following genera were not monophyletic for all analyses: *Tachymenis*, *Thamnodynastes* and *Erythrolamprus*. The genus *Phalotris* was recovered as monophyletic only in analyses based on MA. Highly unstable xenodontine genera included *Pseudalsophis*, *Crisantophis*, *Hydrodynastes*, *Caaeteboia* and *Sordellina*; they showed differing phylogenetic affinities in all three analyses.

Discussion

Higher-level phylogeny of Colubroides and the sister group of Dipsadidae

Lawson et al. (2005), Vidal et al. (2007) and Pyron et al. (2011) investigated the higher-level phylogeny of Colubroides based on the analysis of two, seven and five genes, respectively. The three analyses used different sets of taxa. Lawson et al. (2005) sampled extensively in Colubridae but poorly in Dipsadidae (11), Natricidae (9), Calamariidae (1) and Pseudoxenodontidae (1). Alternatively, Vidal et al.'s (2007) sample was sparse for Dipsadidae (3), Colubridae (4), Natricidae (1) and Pseudoxenodontidae (1). Pyron et al. (2011) analysed an impressive suite of 761 colubroideans, including 99 dipsadids.

Zaher et al.'s (2009) clades Colubroides, Colubriformes, Endoglyptodonta, Elapoidea and Colubroidea were recovered with high support values by Vidal et al. (2007), Pyron et al. (2011), and herein. Lawson et al. (2005) recovered only Elapoidea and Colubroidea consistently. However, the latter study did not effectively sample the xenodermatids, because *Oxyrhabdium* seems to belong to the elapoid radiation rather than to Xenodermatidae. Further, they included only one terminal for the pareatids.

Homalopsidae has an unstable position among these studies, clustering as the sister group of the clade formed by the Elapoidea and Colubroidea (Lawson et al., 2005; Vidal et al., 2007; Zaher et al., 2009) or as the sister group of the Elapoidea (Pyron et al., 2011, their Lamprophiidae). In the ML/MA our analysis recovers a sister-group relationship of the homalopsids with the clade formed by elapoids and colubroids with high support values (84); however, in the MP/DH the homalopsids are the sister group of Colubroidea, with low support values (< 70/3).

Within Elapoidea, the MP and ML analyses recover a poorly supported clade (< 70/13/< 70) composed of Atractaspididae, Pseudoxyrhophiinae and Lamprophiinae. As previously reported by Zaher et al. (2009), Psammophiidae forms the sister group of the remaining elapoids in the ML/MA tree, but with a low bootstrap support (< 70); however, Psammophiidae is the sister group of a clade formed by *Oxyrhabdium* and Elapidae in the MP/DH tree, although with low support (< 70/9). Pyron et al. (2011) recovered the clade Psammophiidae (their Psammophiinae) nested within Lamprophiidae, whereas Elapidae appears as the sister group of all other elapoids. However, none of these clades is strongly supported and, as Pyron et al. (2011) noted, relationships within the Elapoidea remain elusive.

The molecular phylogeny of the superfamily Colubroidea (*sensu* Zaher et al., 2009) has been discussed for more than 25 years, since the seminal biochemical studies of Dowling et al. (1983) and Cadle (1984a,b, 1985, 1988). Although the content of the group has been modified, the relationships among the families Colubridae, Natricidae, Dipsadidae, Calamariidae and Pseudoxenodontidae have remained largely unknown. Thus the sister group of the family Dipsadidae and the evolutionary history that shaped its current distribution also has eluded resolution.

Lawson et al. (2005) and Vidal et al. (2007) suggested a sister-group relationship between Dipsadidae and Pseudoxenodontidae, whereas Zaher et al. (2009) reported that Natricidae nests within Colubroidea as the sister group of Dipsadidae. However, none of these hypotheses is strongly supported. Although Pyron et al.'s (2011) analysis has a robust taxon sampling, their results also obtained weak support for a sister-group relationship between Dipsadidae and Pseudoxenodontidae. These conflicting hypotheses indicate that higher-level relationships among colubroid families remain largely unresolved.

Despite our comprehensive sampling of Dipsadidae, the MP and ML analyses recover three disparate and poorly supported hypotheses of sister-group relationship among the families of Colubroidea (Fig. 1; Appendix S3). ML/MA recovers Zaher et al.'s (2009) result, with Natricidae being the sister group of Dipsadidae (< 70), whereas MP/DH analysis recovers Colubridae as the sister group of Dipsadidae (< 70/8). MP/MA retrieves a clade formed by Pseudoxenodontidae and Calamariidae as the sister group of Dipsadidae

(< 70/4). Thus the relationships of the family Dipsadidae within the colubroid radiation remain uncertain.

Basal relationships in Dipsadidae

Zaher et al. (2009) defined Carphophiinae as containing only *Carphophis*, *Contia* and *Diadophis*, with the positioning of *Heterodon* and *Farancia* as needing further investigation. In contrast, Vidal et al. (2007) defined the subfamily Heterodontinae (Appendix 1) to include all of the North American relictual dipsadids (*Carphophis*, *Contia*, *Diadophis*, *Farancia* and *Heterodon*). The inclusion of *Thermophis zhaoermii* renders both arrangements non-monophyletic in the MP/DH tree by clustering it as the sister group of *Diadophis* (70/9) within a poorly supported clade (< 70/2) that also includes *Farancia* but not *Heterodon*. Conversely, in the MP/MA analysis, *Thermophis* and *Diadophis* cluster together, whereas *Farancia* forms a clade with *Heterodon* (< 70/4). Thus the positioning of *T. zhaoermii* in the North American Dipsadidae probably is not driven by the DH approach, but by the MP criterion. The ML/MA analysis resolves *T. zhaoermii* as the sister group of all other dipsadids and recovers Carphophiinae as a monophyletic group, although with low support (< 70). *Heterodon* and *Farancia* form a clade that appears in the ML/MA as the sister group to all other dipsadines, with low bootstrap support (< 70). Pyron et al. (2011) reported an alternative set of relationships, with both *Heterodon* and *Farancia* nested inside Carphophiinae, and *Thermophis* resolved as the sister group of Pseudoxenodontidae instead of related to Dipsadidae. None of the above hypotheses can be excluded because of poorly supported relationships.

As noted above, the phylogenetic placements of *Diadophis*, *Farancia*, *Heterodon* and *Thermophis* are unstable and controversial (Fig. 1; Appendices S2 and S3). More specifically, both *D. punctatus* and *T. zhaoermii* have exceedingly long branches, which suggests that either long-branch attraction or repulsion may be biasing the MP analyses. Probabilistic models of molecular evolution might handle such cases better (Swofford et al., 1996; Phillippe et al., 2005), but this conclusion is highly controversial (Bergsten, 2005). The only consensus—if there is one—is that clades with long branches linked by small branches represent a problem for phylogenetic inference (Felsenstein, 2004; Kolaczkowski and Thornton, 2004) and no methodology can unequivocally detect it *a priori* (Huelsenbeck et al., 1996; Siddall and Whiting, 1999; Clements et al., 2003; Bergsten, 2005).

Zaher et al. (2009) assigned *Thermophis* to Dipsadidae, based on the results presented by Guo et al. (2009) and He et al. (2009), who showed that the hemipenes of *Thermophis* and some dipsadines are similar. Indeed, the hemipenis of *Thermophis* has a bifurcated sulcus in a single calyculate lobe, a condition present in Dipsadinae and Carphophiinae. Although these characteristics could serve as evidence for a sister-group relationship between *Thermophis* and *Diadophis*, they also could be plesiomorphic conditions for Dipsadidae. Nevertheless, the species distributions agree with the results of the ML analysis, in which all extant New World dipsadids form the sister group of the Old World genus *Thermophis*. In contrast, allocation of *Thermophis* inside Carphophiinae requires a less parsimonious biogeographical explanation of two dispersal events for dipsadids from Asia to the Americas or a reinvasion of Asia from the Americas. Certainly, more work is needed to define the relationship between these basal dipsadids. Until then, we maintain *Thermophis*, *Farancia* and *Heterodon* as Dipsadidae *incertae sedis*.

The subfamily Dipsadinae

Our inclusion of more terminals than Zaher et al. (2009) still leaves dipsadine relationships broadly unresolved. Few clades enjoy high support, and each approach obtains a unique topology (Fig. 1; Appendices S2 and S3). Similarly, independent studies often obtain different phylogenetic arrangements for dipsadine species (Mulcahy, 2007, 2008; Daza et al., 2009; Mulcahy and Macey, 2009; Zaher et al., 2009; Mulcahy et al., 2011; Pyron et al., 2011). Nevertheless, two clades are recovered in each of our three analyses with low to moderate support: (i) a clade comprised of *Atractus* and *Geophis* (80/8/< 70); and (ii) a clade formed by *Dipsas*, *Sibynomorphus*, *Sibon* and *Ninia* (< 70/7/< 70).

Atractus (< 70/5/< 70) is monophyletic in both MP/DH and ML/MA, but paraphyletic with respect to *Geophis* in the MP/MA tree. *Trimetopon*, *Tretanorhinus* and *Hypsiglena* are inconsistently allocated. Their phylogenetic positions are weakly supported in all three analyses.

Despite its unstable position, *Hypsiglena* never clusters with the other two sampled representatives of Cadle's (1984b) leptodeirine assemblage of Central American snakes *Imantodes* and *Leptodeira*, thereby supporting Mulcahy's (2007) hypothesis that this assemblage is a paraphyletic or even polyphyletic group. Recently, Myers (2011) erected the tribe Imantodini to include only *Leptodeira* and *Imantodes*, a decision previously suggested by Mulcahy (2007) and endorsed by Mulcahy et al. (2011). Here, Imantodini forms a weakly supported paraphyletic assemblage (< 70/2/< 70) that also includes *Nothopsis* in all three analyses (MP/DH, MP/MA, ML/MA) and *Trimetopon* in the MP/DH analysis. Our analyses corroborate Vidal et al.'s (2010) results in which *Nothopsis* appears for the first time as the sister group of *Leptodeira*. Vidal et al. (2010) decided to add *Nothopsis* to Imantodini (their Leptodeirini), despite poor support values pro-

vided by their phylogenetic analyses. Although the clade composed by *Nothopsis* and *Leptodeira* is retrieved consistently in our analyses, support values for the hypothesis are always low (< 70/1/< 70), suggesting that Vidal et al.'s (2010) nomenclatural decision might have been premature. The lack of other "nothopsines" (e.g. *Synophis*, *Diaphorolepis* and *Emmochliophis*) in the analysis, and the low support values for the clade formed by *Nothopsis*, *Leptodeira*, *Trimetopon* and *Imantodes*, preclude an unequivocal allocation for *Nothopsis*. Therefore we prefer to follow Zaher (1999) and Mulcahy et al. (2011), and consider this genus as a Dipsadinae *incertae sedis*.

The highly unstable placement of *Trimetopon*, which nests within Imantodini in the MP/DH analysis, is the sister group of *Hypsiglena* in the ML/MA analysis and falls in Xenodontinae as the sister group of Psomophiini in the MP/MA analysis, does not support Zaher et al.'s (2009) allocation of the genus in the Dipsadinae *incertae sedis*. Instead, we prefer to consider *Trimetopon* as a Dipsadidae *incertae sedis* until additional evidence becomes available.

Surprisingly, the tribe Dipsadini, as defined by Zaher (1999) and Harvey et al. (2008) (i.e. including the genera *Dipsas*, *Sibynomorphus*, *Sibon*, *Tropidodipsas* and *Plesiodipsas*), is paraphyletic in respect to *Ninia* in the MP trees. However, the tribe is retrieved as monophyletic in the ML tree, although with low support (< 70). In the MP trees, *Ninia* consistently nests inside a larger clade formed by *Sibon*, *Sibynomorphus* and *Dipsas* in one of two positions—either as the sister group of (i) *Sibynomorphus turgidus* and *S. mikanii* in MP/DH; or (ii) as the sister group of *S. mikanii* in MP/MA. Similarly, *Sibon* also shows three distinct sister-group relationships, as follows: (i) sister to all the other Dipsadini in ML/MA; (ii) sister to a clade formed by the other Dipsadini and *Ninia*, with the exclusion of *Dipsas articulata* and *D. indica*, in MP/DH; and (iii) sister to *Sibynomorphus turgidus* in MP/MA. Each association is weakly supported. Further, all three analyses point to paraphyly in the genera *Sibynomorphus* and *Dipsas* with respect to each other. Several species of both genera are more closely related to each other than to their congeners, a result that finds support in morphology (Fernandes, 1995). To render both genera monophyletic, *Sibynomorphus* Fitzinger, 1843 would have to be synonymized with *Dipsas* Laurenti, 1768. However, the poor taxonomic sampling for Dipsadini (only three of the five genera and 16% of their species) and the unstable positions of *Sibon* and *Ninia* suggest that such a decision would be premature. No taxonomic consensus can emerge without a broader sampling of the remaining snail-eating snakes and further clarification of the phylogenetic affinities of the genus *Ninia*, represented here by only one species.

Xenopholis and polyphyly of the "Nothopsini"

Upon adding the second known species of *Xenopholis*, *X. undulatus*, the genus appears to be monophyletic (Fig. 1; Appendix S3) and with high support values (100/12/99). Our analyses support the allocation of *Xenopholis* to Dipsadidae (Zaher, 1999), although as a member of Xenodontinae rather than a Dipsadinae *incertae sedis*. Further, the relationships of *Xenopholis* suggest that the unilobed hemipenis of *X. scalaris* represents a secondary loss of one of the lobes as opposed to the retention of the dipsadine condition.

Xenopholis never clusters inside any suprageneric taxon within Xenodontinae, confirming its uniqueness. Further, the placements of *Nothopsis* and *Xenopholis* in Dipsadinae and Xenodontinae (Vidal et al., 2010), respectively, preclude recognition of the tribe Nothopsini as defined by either Savitzky (1974) or Dowling (1975). This result also rejects allocation of these genera to Xenodermatidae, as suggested by Dowling and Pinou (2003). Therefore we consider *Xenopholis* as Xenodontinae *incertae sedis*, pending a better sampling in Dipsadinae and inclusion of other "nothopsines".

The subfamily Xenodontinae

Our results support the main taxonomic changes proposed by Zaher et al. (2009). Among the 14 tribes discussed by these authors, only Alsophiini is not recovered in our three analyses. Additionally, the monophyly of Conophiini and Echinantherini is not supported in the MP analyses; however, in the ML analysis, these taxa appear as poorly supported monophyletic clades. Ten tribes are well supported clades in all phylogenetic approaches: Xenodontini, Elapomorphini, Psomophiini, Saphenophiini, Tropidrodryadini, Tachymenini, Pseudoboini, Hydropsini, Hydrodynastini and Philodryadini. Shifting its phylogenetic position and receiving low levels of support, monotypic Caaeteboini (*Caaeteboia amarali*) appears as an unstable taxon. However, it never clusters inside any other tribe. These results confirm the validity of *Caaeteboia* as an independent lineage within Xenodontinae.

Our analyses support the generic arrangement of Zaher et al. (2009) in Philodryadini. The new arrangements for *Philodryas argentea* and *Ph. agassizii* (formerly *Xenoxybelis argenteus* and *Pseudablabes agassizii*, respectively) are maintained after a broader sampling of *Philodryas*. *Philodryas agassizii* clusters with *Ph. patagoniensis* with high support values (99/6/88), and *Ph. argentea* clusters either with a clade formed by *Ph. viridissima* and *Ph. nattereri* (70/5) in MP/DH, or with *Ph. viridissima* (< 70) in ML/MA. Similarly, Pyron et al. (2011) placed *X. boulengeri* in *Philodryas* as the sister taxon of *Ph. baroni*. Therefore we maintain Zaher et al.'s (2009) synonymy of *Xenoxybelis* with

Philodryas. The genus *Philodryas* now contains 20, instead of 18, species (Zaher et al., 2008; Appendix 1).

The tribe Saphenophiini

Our study unequivocally supports Zaher's (1999) hypothesis based on morphology that continental *Pseudalsophis elegans* is closely related to the Galapagos Island species of Xenodontinae (herein represented by *Pseudalsophis dorsalis*), rather than to West Indian *Alsophis* and *Antillophis*, and mainland *Philodryas* (Thomas, 1997). Following Zaher (1999), Zaher et al. (2009) assigned all Galapagos species to a new genus, *Pseudalsophis* (along with *Alsophis elegans*), and created the tribe Saphenophiini for the genera *Pseudalsophis* and *Saphenophis*. Sampling only *P. elegans* as a representative of Saphenophiini, Vidal et al. (2010) stated that their resolution of *Manolepis putnami* (a dipsadid *incertae sedis*) as the sister group of *P. elegans* rendered the Saphenophiini paraphyletic. However, paraphyly in the Saphenophiini requires *Manolepis* to cluster inside the Saphenophiini, a test not performed by Vidal et al. (2010) because they only sampled one species of Saphenophiini. Although our sampling of Saphenophiini does not include *Saphenophis*, the phylogenetic analyses never recover *M. putnami* as the sister group of *P. elegans* (Fig. 1; Appendices S2 and S3). A monophyletic *Pseudalsophis* is always recovered with high support values (100/32/100). Therefore we resurrect the tribe Saphenophiini, as originally stated by Zaher et al. (2009), and pending further testing with the inclusion of *Saphenophis*.

The tribe Conophiini and the genera Manolepis and Crisantophis

Zaher et al. (2009) erected the tribe Conophiini on the basis of the peculiar hemipenial morphology shared by *Conophis* and *Manolepis* (Zaher, 1999) and the phylogenetic position of the former within xenodontines. Although our results for MP agree with Vidal et al.'s (2010) conclusion that this tribe is not monophyletic, our ML/MA analysis retrieves a monophyletic Conophiini with a low bootstrap support (< 70). However, the position of *Manolepis* is highly unstable within Xenodontinae, and three distinct hypotheses of sister-group relationship are obtained from our analyses, all with low support values: (i) as the sister group of Hydropsini in the MP/DH (< 70/9); (ii) as the sister group of *Conophis* in the ML/MA (< 70); and (iii) as the sister group of Pseudoboini in the MP/MA (< 70/1). Therefore we consider *Manolepis* as Xenodontinae *incertae sedis* and redefine the tribe Conophiini to contain *Conophis* only, pending future analysis.

Crisantophis nevermanni originally was allocated to *Conophis* by Dunn (1937) because of the similarities in scutellation and dentition that it shares with *Co. lineatus* (Villa, 1971). It is only later that Villa (1971) created the genus *Crisantophis* for *Co. nevermanni*, based mainly on the striking uniqueness of its hemipenial morphology. Not surprisingly, Vidal et al. (2010) recovered a sister-group relationship between *Conophis* and *Crisantophis*, although with poorly supported values. Two out of three solutions in our analyses recover the same relationship found by Vidal et al. (2010). Whereas both MP analyses recover *Crisantophis* as the sister group of *Conophis* with moderate support values (70/5), ML/MA places *Crisantophis* as the sister group of the subfamily Dipsadinae, with low bootstrap support values (< 70). Despite the contradictory affinities shown by our MP and ML analyses, MP results corroborate the morphological affinities shared by *Conophis* and *Crisantophis* (Dunn, 1937; Villa, 1971). However, we refrain from formally allocating *Crisantophis* to the tribe Conophiini (along with *Conophis*) until further evidence clarifies the apparent conflict shown between our MP and ML results.

The tribe Xenodontini

Zaher et al. (2009) resurrected *Lygophis* for a clade comprising *Liophis meridionalis* and *Li. elegantissimus*, which do not cluster with the former *Liophis* and *Erythrolamprus*. *Lygophis* contains two species complexes—the *Ly. lineatus* Group (*Ly. lineatus*, *Ly. paucidens*, *Ly. meridionalis*, *Ly. flavifrenatus* and *Ly. dilepis*) and the *Ly. anomalus* Group (*Ly. anomalus*, *Ly. elegantissimus* and *Ly. vanzolinii*), as designated by Michaud and Dixon (1987) and Dixon (1985), respectively. Herein, the inclusion of three more species confirms the taxonomy of Zaher et al. (2009) and supports recognition of the two species complexes. *Lygophis elegantissimus* clusters with *Ly. anomalus* with high support values (100/17/100), and *Ly. paucidens*, *Ly. meridionalis* and *Ly. flavifrenatus* cluster together with moderate support values in the MP analyses (75/2) and a high bootstrap (88) in the ML/MA.

Our results support the synonymization of *Waglerophis* and *Lystrophis* with *Xenodon* (Zaher et al., 2009). The inclusion of seven additional species (total of 11 species) obtains a congruent topology (Fig 1; Appendix S3), with former genera *Lystrophis* and *Waglerophis* nested within the traditional *Xenodon* in a sequence of well supported clades. This taxonomic change is also supported by morphological evidence (Zaher, 1999; Moura-Leite, 2001; Masiero, 2006). As previously suggested by Zaher (1999), *X. werneri* clusters inside *Xenodon* as the sister group of *X. merremi*. Hence the absence of the apical disk in their hemipenis is a reversal within the Xenodontini (*contra* Yuki, 1993). The loss of the disk and the elongated hemipenial lobes are two morphological synapomorphies that support the clade formed by *X. merremi* and *X. werneri* (Zaher, 1999).

Our phylogenetic results and those of Vidal et al. (2010) support the taxonomic changes in the tribe Xenodontini made by Zaher et al. (2009). However, controversy remains with respect to the recognition of *Liophis* and *Erythrolamprus*. Our results recover a monophyletic *Erythrolamprus* (priority of the name *Erythrolamprus* over *Liophis* in Appendix 1) with high support values in all approaches (100/15/100), except for the inclusion of *Umbrivaga pygmaea*, as first reported by Vidal et al. (2010). Both MP and ML approaches place *E. aesculapii*, *E. mimus* and *U. pygmaea* in this clade with strong support (Fig. 1; Appendix S3). This is not surprising because a close phylogenetic affinity between species traditionally included in *Liophis* and *Erythrolamprus* is recovered persistently in recent literature; Vidal et al. (2000) were first to report a paraphyletic *Liophis* in relation to *Erythrolamprus*, and Zaher et al. (2009) and Vidal et al. (2010) do the same.

Paraphyly of *Liophis* with respect to *Erythrolamprus* and *Umbrivaga* is supported here by a significant sampling that includes up to 30% of all known species. Therefore we synonymize *Umbrivaga* Roze, 1964 into *Erythrolamprus* Boie, 1826, which now contains 50 species (Appendix 1). This arrangement of 50 species for the genus *Erythrolamprus* probably will be challenged after a more densely sampled analysis. We cannot predict whether or not the genus will be split in the future, and agree with Frost et al. (2008) that instead of creating taxonomic instability, a taxonomy based on monophyletic groups provides an evolutionary framework for this kind of progress (*contra* Curcio et al., 2009; Vidal et al., 2010).

The tribe Pseudoboini

The tribe Pseudoboini contains *Boiruna*, *Clelia*, *Drepanoides*, *Mussurana*, *Oxyrhopus*, *Phimophis*, *Pseudoboa*, *Rhachidelus* and *Siphlophis* (Zaher et al., 2009). Monophyly of the tribe is highly supported molecularly (100/22/100) and morphologically (Zaher, 1994, 1999; Zaher et al., 2009). Both *Siphlophis* and *Oxyrhopus* are retrieved with high support values (98/8/98 and 89/6/87, respectively). A third clade, comprising *Phimophis guerini*, *Clelia rustica*, *C. clelia*, *Boiruna maculata*, *Pseudoboa coronata*, *Ps. neuwiedii*, *Ps. nigra*, *Rhachidelus brazili*, *Mussurana bicolor* and *Drepanoides anomalus*, also receives high support values in all analyses (88/7/74). The genus *Rhachidelus* is sampled for the first time in a molecular analysis and, although it firmly nests in Pseudoboini, its phylogenetic position differs in the MP/DH and ML/MA analyses. It is the sister group of *Boiruna* in the MP/DH analysis, but clusters as the sister group of *Pseudoboa* in the ML/MA tree, showing strong support in MP/DH (96/20) but low support in ML/MA (< 70). The MP/MA tree recovers the same affinities as in ML/MA.

Although Zaher et al. (2009) corrected several problems with respect to the monophyly of Pseudoboini, further adjustments are needed. Our results render the genera *Clelia* Fitzinger, 1826 and *Phimophis* Cope, 1860 polyphyletic. Surprisingly, *Ph. iglesiasi* is positioned as the sister group of *Oxyrhopus*, with low support (< 70/7/< 70). Further, *Ph. guerini*, the other sampled species of *Phimophis*, clusters with *Clelia rustica* with strong support in all three analyses (96/5/93). Zaher (1994) provided morphological evidence for this affinity; *C. rustica* appears as the sister group of the genus *Phimophis* with which it shares the presence of an antero-dorsally enlarged and ossified premaxilla and "Y-shaped" divergent anterior extremities of the nasals. We create a new genus for *C. rustica* (Cope, 1878) to maintain a monophyletic *Clelia* (Appendix 1). Further, we create a new genus for *Ph. iglesiasi* to maintain the monophyly of *Phimophis* (Appendix 1). The small, psammophilous species *Ph. chui* and *Ph. scriptorcibatus*, from the sand dunes of the Rio São Franciso, Brazil, are allocated into this new genus due to their morphological similarities with *Ph. iglesiasi*. This new genus is characterized by the absence of loreal scales. The genus *Phimophis* Cope, 1860 now includes *Ph. guerini* (Duméril, Bibron, and Duméril, 1854), *Ph. guianensis* (Troschel, 1848) and *Ph. vittatus* (Boulenger, 1896), and is characterized by the presence of a slightly to strongly upcurved spatulate, rostral scale and an enlarged and distally rounded terminal caudal scale.

Phylogenetic affinities of Sordellina and the tribe Echinantherini

The poorly known genus *Sordellina* is sampled here for the first time, and it appears associated with the species of the tribe Echinantherini (*sensu* Zaher et al., 2009). This novel hypothesis receives high support values in all three analyses (82/10/94) and, although confirming the allocation of the genus in Dipsadidae, the result is unexpected owing to the morphological divergence with Echinantherini.

Zaher et al. (2009) defined the tribe Echinantherini and provided hemipenial synapomorphies for the group. Monophyly of Echinantherini is recovered with low support values only in ML/MA (< 70), in which *Sordellina* is retrieved as the sister group of the tribe. The tribe is paraphyletic in both MP/DH and MP/MA analyses, with *Sordellina* nesting inside as the sister group of *Taeniophallus* with low support values (< 70/10 and < 70/1, respectively).

Zaher et al. (2009) did not address the long-standing taxonomic issue of whether or not *Echinanthera* and *Taeniophallus* are monophyletic (Di-Bernardo, 1992, 1996; Myers and Cadle, 1994; Schargel et al., 2005). Following Schargel et al. (2005) and Santos-Jr et al. (2008), *Taeniophallus* contains nine species—*T. affinis*,

T. bilineatus, *T. brevirostris*, *T. nebularis*, *T. nicagus*, *T. occipitalis*, *T. persimilis*, *T. poecilopogon* and recently described *T. quadricellatus*. *Echinanthera* comprises six species—*E. amoena*, *E. cephalomaculata*, *E. cephalostriata*, *E. cyanopleura*, *E. melanostigma* and *E. undulata*. Our sampling of five of the 15 recognized species in Echinantherini shows that the current generic delimitation is natural and concordant with all phylogenetic analyses. Recently, Myers (2011) questioned the definition of Echinantherini given by Zaher et al. (2009), based on the distinct hemipenial morphology of *T. nebularis*. However, assignment of *T. nebularis* to the genus *Taeniophallus* is problematic, as noted by Schargel et al. (2005), and we consider it as tentative because there is no compelling evidence (morphological or molecular) supporting such allocation.

Although no morphological synapomorphy is known so far to support the clade formed by *Sordellina*, *Echinanthera* and *Taeniophallus*, our results strongly support the assignment of the former genus to the tribe. Therefore we allocate *Sordellina* to Echinantherini. Further analyses will be necessary to clarify its phylogenetic affinities with the other two genera of the tribe (Zaher et al., 2009).

Monophyly of Alsophiini

Vidal et al. (2010) argued that Hedges et al. (2009) extensively resolved the relationships, classification and biogeography of the West Indian Xenodontinae (WIX). However, our results reveal that some aspects of the phylogenetic relationships and the taxonomy of the WIX remain controversial. Hedges et al. (2009), like Zaher et al. (2009), considered the tribe Alsophiiini to be a monophyletic unit. However, our data matrix with a larger sampling of WIX and mainland xenodontines resulted in a polyphyletic Alsophiini in all three analyses (Fig. 1; Appendices S2 and S3). *Uromacer* always clusters outside of the other WIX, either as the sister group of Saphenophiini (MP/DH; < 70/4) or as the sister group of Xenodontini (MP/MA and ML/MA; < 70/1/< 70), although with low bootstrap and Bremer support values. *Arrython* (*sensu* Zaher et al., 2009) also clusters outside the WIX in the ML/MA analysis, forming the sister group to the clade composed by *Uromacer* and Xenodontini (< 70). However, the MP/DH analysis places *Arrhyton* in the West Indian radiation, clustering it as the sister group to the other alsophiines (excluding *Uromacer*) in a clade with low support values (< 70/5). In the MP/MA tree, *Arrhyton* falls in a polytomy with a clade formed by *Uromacer* and Xenodontini, and another clade containing the remaining Alsophiini. No morphological synapomorphies support the monophyly of any of the clades formed by *Uromacer*, *Arrhyton* and Xenodontini in the MP/DH and ML/MA analyses.

Although polyphyly of Alsophiini receives low support in all three analyses, the unambiguous exclusion of *Uromacer* forces a revision of the tribe's taxonomic content to render it monophyletic. We redefine the tribe Alsophiini to include only the clade obtained by the MP/DH analysis (Fig. 1; Appendix 1), and consider the genus *Uromacer* as a Xenodontinae *incertae sedis*. This arrangement requires future testing with more characters and representatives sampled for mainland xenodontines. Until such analysis is made, biogeographical conclusions for the WIX based on estimated divergence times (e.g. Hedges et al., 2009; Burbrink et al., 2011) should be interpreted as being premature. Our taxonomy better represents the current phylogenetic evidence with the uncertain allocation of *Uromacer*.

Monophyletic components within Alsophiini

According to Zaher et al. (2009), the tribe Alsophiini contains 11 genera—*Caraiba*, *Schwartzophis*, *Magliophis*, *Ialtris*, *Darlingtonia*, *Hypsirhynchus*, *Arrhyton*, *Antillophis*, *Alsophis*, *Uromacer* and *Ocyophis*; the first three genera represent new taxa and the last one is resurrected (Fig. 2). Hedges et al. (2009) rejected most of Zaher et al.'s (2009) taxonomic scheme (Fig. 2). They synonymized *Schwartzophis* and *Antillophis* with *Hypsirhynchus* and *Darlingtonia* with *Ialtris*; they also described the new genera *Borikenophis*, *Haitiophis* and *Cubophis* to accommodate the species previously arranged by Zaher et al. (2009) in *Ocyophis*. Further, Hedges et al. (2009) placed *Oc. ater* and *Oc. melanichnus*, two probably extinct species, in their expanded *Hypsirhynchus*.

Our three analyses unambiguously support the recognition of the genera *Antillophis*, *Hypsirhynchus*, *Darlingtonia* and *Schwartzophis*, as originally suggested by Zaher et al. (2009). They also corroborate Hedges et al.'s (2009) genera *Haitiophis*, *Cubophis* and *Borikenophis* by recovering a paraphyletic *Ocyophis* (*sensu* Zaher et al., 2009; Fig. 2). Additionally, we believe that *Ocyophis* should be retained for *O. ater* (Gosse, 1863) and *O. melanichnus* (Cope, 1863), for reasons detailed in Appendix 1. Given this new arrangement, the tribe Alsophiini contains 13 genera that are morphologically diagnosable (Hedges et al., 2009; Zaher et al., 2009; Fig. 3; Appendix 1).

Except for the position of *Arrhyton*, *Uromacer* (discussed above) and *Alsophis anomalus* (not included in their analysis), the topology of our ML/MA tree (Appendix S3) is identical to the Bayesian tree given by Hedges et al. (2009). However, our MP/DH tree differs slightly from the latter, with *Borikenophis* forming a clade with *Ialtris* and *Darlingtonia* (< 70/2) that is the sister group of the clade composed by *Cubophis*, *Haitiophis* and *Caraiba* (< 70/2). Both arrangements have low support values.

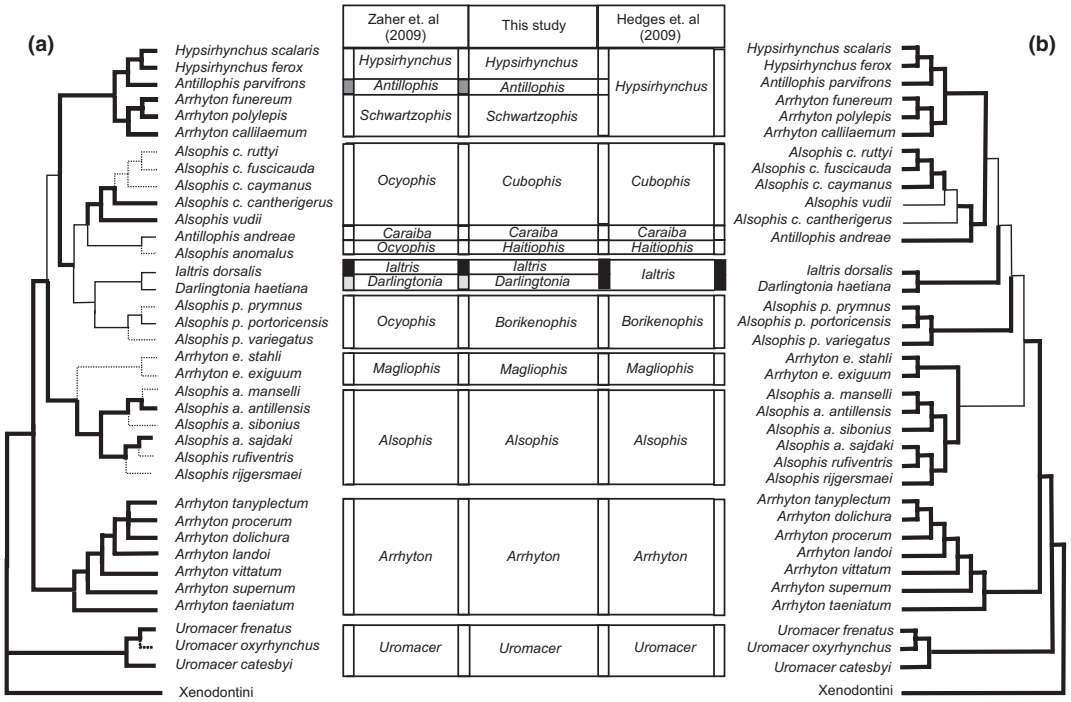

Fig. 2. Comparison of the taxonomies (central box) and phylogenies for the West Indian xenodontines based on the results of Zaher et al. (2009), Hedges et al. (2009) and the current analysis. (a) Phylogenetic relationship derived from Fig. 1. Thick branches represent relationships also recovered in Zaher et al. (2009); dotted branches represent taxa not sampled by Zaher et al. (2009). (b) Phylogenetic relationships extracted from Hedges et al. (2009). Thick branches represent relationships also recovered herein. Terminal names followed by an asterisk are from Hedges et al. (2009).

We recover a moderately supported clade composed of *Haitiophis*, *Caraiba* and *Cubophis* (90/8/< 70), as did Hedges et al. (2009). Within this clade, *Haitiophis* and *Caraiba* are resolved as sister taxa, with high support in MP/DH (90/4) but low support in ML/MA (< 70). We agree with Hedges et al. (2009) that both *Ha. anomalus* and *Ca. andreae*, while being sister taxa, are better assigned to different genera because of differences in scalation and morphology of the hemipenis, skull and tooth elements (Maglio, 1970; Zaher, 1999; Fig. 3).

In both MP/DH and ML/MA analyses, the genera *Magliophis* and *Alsophis* form a poorly supported clade (< 70/2) that is the sister group of the clade formed by the remaining genera of Alsophiini excluding *Arrhyton* and *Uromacer* (i.e. *Antillophis*, *Hypsirhynchus*, *Schwartzophis*, *Darlingtonia*, *Ialtris*, *Borikenophis*, *Caraiba*, *Haitiophis* and *Cubophis*). The latter clade also is poorly supported in both MP/DH and ML/MA analyses (< 70/2). Relationships within the genera *Alsophis*, *Schwartzophis*, *Borikenophis* and *Cubophis* are well established and identical to those found by Hedges et al. (2009).

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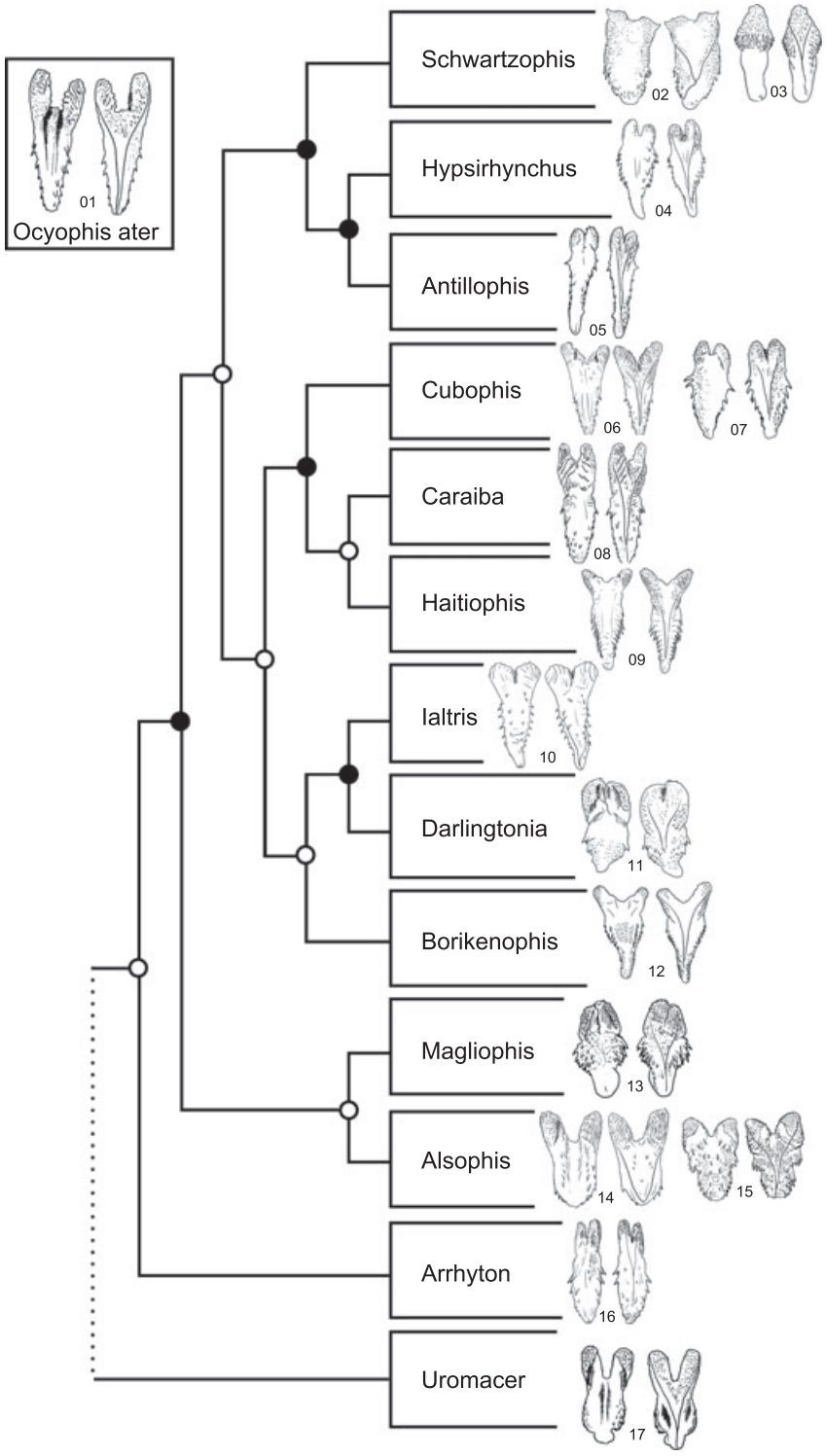

Fig. 3. Variation in the hemipenial morphology and the phylogenetic relationships used to construct the taxonomy of the West Indian xenodontids. Illustrations of the sulcated (right) and asulcated (left) hemipenial faces, based on Zaher (1999). 01, *Ocyophis ater*; 02, *Schwartzophis callilaemum*; 03, *Schwartzophis polylepis*; 04, *Hypsirhynchus ferox*; 05, *Antillophis parvifrons*; 06, *Cubophis cantherigerus*; 07, *Cubophis vudii*; 08, *Caraiba andreae*; 09, *Haitiophis anomalus*; 10, *Ialtris dorsalis*; 11, *Darlingtonia haetiana*; 12, *Borikenophis portoricensis*; 13, *Magliophis exiguum*; 14, *Alsophis rijgersmaei*; 15, *Alsophis sibonius*; 16, *Arrhyton taeniatum*; 17, *Uromacer catesbyi*. Black and open circles on the nodes represent strongly and poorly supported clades, respectively, for maximum parsimony analysis using dynamic homology. Dotted branches do not necessarily represent the phylogenetic relationships recovered herein.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of taxa and GenBank accession numbers of specimens used in this study.

Appendix S2. Strict consensus of 8568 most parsimonious trees found using TNT based on the multiple alignment.

Appendix S3. Tree estimated from the maximum-likelihood analysis.

Appendix S4. Implied alignment derived from POY 4.

Appendix S5. Concatenated static alignment generated by MAFFT and Clustal X.

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Appendix 1

On the use of the name Heterodontinae Bonaparte, 1845

Higher taxonomic names are, at times, controversial, and the use of some names may lead to unnecessary taxonomic confusion. For example, although the subdivision of Dipsadidae into three subfamilies represents a significant improvement with respect to previous schemes (Cadle, 1985), it does not resolve the long-lasting conundrum as to the use of the family group name Heterodontidae, which has two independent origins and applications. The shark family Heterodontidae (based on the genus *Heterodontus* Blainville, 1816) dates from Gray (1851: 65), but its use as the snake family Heterodontidae (based on the genus *Heterodon* Latreille, 1801) dates from Bonaparte (1845) and it has not been used in the literature since. Thus both the genus and family names for snakes have priority over the sharks. However, resurrection of the family name Heterodontidae for snakes (subfamily Heterodontinae in Vidal et al., 2007) causes unnecessary confusion owing to the long-standing use of the name for sharks (e.g. Compagno, 2002; Baldwin, 2005). Consequently, Rossman and Wilson (1965) and Zaher et al. (2009) argued that the family name should be applied only to sharks in the interest of maintaining nomenclatorial stability, a position that contrasts strongly with that of Vidal et al. (2007, 2010). According to Art. 52.2 of the Code, when two names "are homonyms, only the senior, as determined by the Principle of Priority, may be used as a valid name". We believe that if this clade of snakes continuously appears in phylogenetic studies, then it is desirable to petition the International Commission on Zoological Nomenclature to set aside use of the family name for the snakes in favour of the sharks in the interest of nomenclatorial stability. An alternative nomenclature would be to change the spelling of the shark family to Heterodontusidae. In any case, we suggest the North American relictual Xenodontinae (*sensu* Pinou, 1993; Pinou et al., 2004) should not be referred to as the subfamily Heterodontinae until a well defined nomenclatural resolution is obtained.

New taxa and taxonomic arrangements derived from the analysis

Philodryas Wagler, 1830

Type-species: Coluber Olfersii Lichtenstein, 1823.

Diagnosis: No exclusive morphological synapomorphy known so far.

Content: Philodryas aestiva (Duméril, Bibron and Duméril, 1854); *Philodryas agassizii* (Jan, 1863); *Philodryas argentea* (Daudin, 1803); *Philodryas arnaldoi* (Amaral, 1932); *Philodryas baroni* Berg, 1895; *Philodryas chamissonis* (Wiegmann, 1835); *Philodryas cordata* Donnelly and Myers, 1991; *Philodryas georgeboulengeri* (Procter, 1923) **new replacement name** for *Oxybelis boulengeri* Procter, 1923; *Philodryas laticeps* Werner, 1900; *Philodryas livida* (Amaral, 1923); *Philodryas mattogrossensis* Koslowsky, 1898; *Philodryas nattereri* Steindachner, 1870; *Philodryas olfersii* (Lichtenstein, 1823); *Philodryas patagoniensis* (Girard, 1858); *Philodryas psammophidea* Günther, 1872; *Philodryas simonsii* Boulenger, 1900; *Philodryas tachymenoides* (Schmidt and Walker, 1943); *Philodryas trilineata* (Burmeister, 1861); *Philodryas varia* (Jan, 1863); *Philodryas viridissima* (Linnaeus, 1758).

Comments: According to Article 53.3 of the Code, *Philodryas boulengeri* Werner 1909, a junior synonym of *Philodryas mattogrossensis* Koslowsky, 1898 and *Philodryas boulengeri* (Procter, 1923) are secondary homonyms because both meet the criterion of availability (see Articles 10.6 and 11 of the Code). According to the Principle of Priority (Article 23), *Philodryas boulengeri* (Procter, 1923) is the junior secondary homonym. Considering that both names do not fall into any of the exceptions listed in Articles 23.7.3, 23.8 and 23.9, and that *Philodryas boulengeri* (Procter, 1923) has no known available and potentially valid junior synonyms, its specific epithet must be replaced by a new substitution name (Articles 57.3.1. and 59.1).

Therefore we propose *georgeboulengeri* as a replacement name for the species. The replacement name intends to keep the homage originally made by Procter to George A. Boulenger.

Erythrolamprus Boie, 1926

Type-species: Coluber venustissimus Wied-Neuwied, 1821.

Diagnosis: No exclusive morphological synapomorphy known so far.

Content: *Erythrolamprus aesculapii* (Linnaeus, 1766); *Erythrolamprus albertguentheri* **new replacement name** for *Liophis guentheri* Peracca, 1897; *Erythrolamprus almadensis* (Wagler, 1824) **new combination**; *Erythrolamprus andinus* (Dixon, 1983) **new combination**; *Erythrolamprus atraventer* (Dixon and Thomas, 1985) Forlani, Bernardo, Haddad and Zaher, 2010; *Erythrolamprus bizona* (Jan, 1863); *Erythrolamprus breviceps* (Cope, 1860) **new combination**; *Erythrolamprus carajasensis* (Cunha, Nascimento and Ávila-Pires, 1985) **new combination**; *Erythrolamprus ceii* (Dixon, 1991) **new combination**; *Erythrolamprus cobella* (Linnaeus, 1758) **new combination**; *Erythrolamprus cursor* (Lacépède, 1789) **new combination**; *Erythrolamprus dorsocorallinus* (Esqueda, Natera, La Marca and Ilija-Fistar, 2007) **new combination**; *Erythrolamprus epinephelus* (Cope, 1862) **new combination**; *Erythrolamprus festae* (Peracca, 1897) **new combination**; *Erythrolamprus frenatus* (Werner, 1909) **new combination**; *Erythrolamprus guentheri* (Garman, 1883); *Erythrolamprus ingeri* (Roze, 1958) **new combination**; *Erythrolamprus jaegeri* (Gunther, 1958) Forlani, Bernardo, Haddad and Zaher, 2010; *Erythrolamprus janaleeae* (Dixon, 2000) **new combination**; *Erythrolamprus juliae* (Cope, 1879) **new combination**; *Erythrolamprus leucogaster* (Jan, 1863) **new combination**; *Erythrolamprus longiventris* (Amaral, 1925) **new combination**; *Erythrolamprus maryellenae* (Dixon, 1985) **new combination**; *Erythrolamprus melanotus* (Shaw, 1802) **new combination**; *Erythrolamprus mertensi* (Roze, 1964) **new combination**; *Erythrolamprus miliaris* (Linnaeus, 1758) Forlani, Bernardo, Haddad and Zaher, 2010; *Erythrolamprus mimus* (Cope, 1868); *Erythrolamprus ocellatus* Peters, 1869; *Erythrolamprus oligolepis* (Boulenger, 1905) **new combination**; *Erythrolamprus ornatus* (Garman, 1887) **new combination**; *Erythrolamprus perfuscus* (Cope, 1862) **new combination**; *Erythrolamprus poecilogyrus* (Wied, 1825) Forlani, Bernardo, Haddad and Zaher, 2010; *Erythrolamprus problematicus* (Myers, 1986) **new combination**; *Erythrolamprus pseudocorallus* (Roze, 1959); *Erythrolamprus pyburni* (Markezich and Dixon, 1979) **new combination**; *Erythrolamprus pygmaeus* (Cope, 1868) **new combination**; *Erythrolamprus reginae* (Linnaeus, 1758) **new combination**; *Erythrolamprus sagittifer* (Jan, 1863) Scrocchi, Abdala, Nori and Zaher, 2010; *Erythrolamprus semiaureus* (Cope, 1862); *Erythrolamprus steinbachi* (Boulenger, 1905) **new combination**; *Erythrolamprus subocularis* (Boulenger, 1902) **new combination**; *Erythrolamprus taeniogaster* (Jan, 1863) **new combination**; *Erythrolamprus taeniurus* (Tschudi, 1845) **new combination**; *Erythrolamprus torrenicola* (Donnelly and Myers, 1991) **new combination**; *Erythrolamprus trebbaui* (Roze, 1958) **new combination**; *Erythrolamprus triscalis* (Linnaeus, 1758) **new combination**; *Erythrolamprus typhlus* (Linnaeus, 1758) Forlani, Bernardo, Haddad and Zaher, 2010; *Erythrolamprus viridis* (Günther, 1862) **new combination**; *Erythrolamprus vitti* (Dixon, 2000) **new combination**; *Erythrolamprus williamsi* (Roze, 1958) **new combination**.

Comments: Zaher et al. (2009) erroneously synonymized *Erythrolamprus* into *Liophis* and they did so while showing the correct dates for the generic epithets: "*Liophis* Wagler, 1830 (includes *Erythrolamprus* Boie, 1826)…" (Zaher et al., 2009: 146). Following the rule of priority (article 23.1 of the International Code of Zoological Nomenclature, 1999), *Erythrolamprus* should be recognized (Curcio et al., 2009). We follow Article 51G of the Code when citing new combinations made by previous authors (Forlani et al., 2010; Scrocchi et al., 2010). *Erythrolamprus guentheri* (Garman, 1883) and *Erythrolamprus guentheri* (Peracca, 1897) are secondary homonyms. According to Articles 57.3 and 60.3 of the Code, *Erythrolamprus guentheri* (Peracca, 1897) is the junior homonym and, having no known available and potentially valid junior synonym, its specific epithet must be replaced by a new substitution name. We propose *albertguentheri* as a replacement name for the species, an epithet that intends to keep the homage originally made by Peracca to Günther. We follow Frota et al. (2005) and Giraudo et al. (2006), and recognize *Liophis oligolepis* and *L. semiaureus*, respectively, as valid species.

Paraphimophis Zaher, Grazziotin, Murphy, Scrocchi, Altamirano Benavides, Zhang and Bonatto, **new genus**

Type-species: Oxyrrhopus rusticus Cope, 1878.

Etymology: From the Greek "para" and *Phimophis*, meaning near the genus *Phimophis*.

Diagnosis: Anterolaterally divergent anterior tips of the nasals and enlarged nasal processes of the premaxillae, but no specialized spatulate rostral scale; young specimens with a dark head, a faint pale whitish or orange nuchal collar, a dark vertebral band and reddish flanks; adults with a uniform brown dorsum.

Content: *Paraphimophis rusticus* (Cope, 1878) **new combination**.

Rodriguesophis Zaher, Grazziotin, Murphy, Scrocchi, Altamirano Benavides, Zhang and Bonatto, **new genus**

Type-species: Rhinostoma iglesiasi Gomes, 1915.

Etymology: A patronym honouring Miguel T. Rodrigues, who discovered and described the highly diverse psammophilous herpetofauna of the São Francisco River.

Diagnosis: Loreal absent, specialized, spatulate straight rostral scale present (i.e. not upcurved to form a shovel-like structure), bright red dorsal colour pattern, and dark nuchal collar of juveniles retained in adult specimens, except for *R. scriptorcibatus* that looses the red colour but tends to retain an unconspicuous nuchal collar.

Content: Rodriguesophis iglesiasi (Gomes, 1915) **new combination**; *Rodriguesophis chui* (Rodrigues, 1993) **new combination**; *Rodriguesophis scriptorcibatus* (Rodrigues, 1993) **new combination**.

Comments: Pending further testing, *R. chui* and *R. scriptorcibatus* are tentatively allocated in this genus due to their external similarities with *R. iglesiasi*.

Tribe Alsophiini Fitzinger, 1843

Type-genus: Alsophes Fitzinger, 1843: 25.

Diagnosis: No exclusive morphological synapomorphy known so far.

Content: Alsophis Fitzinger, 1843; *Antillophis* Maglio, 1970 **resurrected**; *Arrhyton* Günther, 1858; *Borikenophis* Hedges and Vidal, 2009; *Caraiba* Zaher, Grazziotin, Cadle, Murphy, Moura-Leite and Bonatto, 2009; *Cubophis* Hedges and Vidal, 2009; *Darlingtonia* Cochran, 1935 **resurrected**; *Haitiophis* Hedges and Vidal, 2009; *Hypsirhynchus* Günther, 1858; *Ialtris* Cope, 1862; *Magliophis* Zaher, Grazziotin, Cadle,

Murphy, Moura-Leite and Bonatto, 2009; *Ocyophis* Cope, 1886 **resurrected**; *Schwartzophis* Zaher, Grazziotin, Cadle, Murphy, Moura-Leite and Bonatto, 2009 **resurrected**.

Hypsirhynchus Günther, 1858

Type species: Hypsirhynchus ferox Günther, 1858.

Diagnosis: Enlarged teeth; hemipenis moderately bilobed, proximal region of each lobe with a bulbous projection ornamented by a row of small papillae.

Content: Hypsirhynchus ferox Günther, 1858, *Hypsirhynchus scalaris* Cope, 1863.

Antillophis Maglio, 1970, **resurrected**

Type species: Dromicus parvifrons Cope, 1862.

Diagnosis: Asulcate surfaces of hemipenial lobes completely nude except for a row of two to three enlarged papillae aligned vertically on the lobular crotch and proximal region of the lobes; hemipenes long and slender (hemipenial body at least 4–5× length of lobes).

Content: A. parvifrons (Cope, 1862).

Comments: Antillophis was synonymized with *Hypsirhynchus* by Hedges et al. (2009). However, these two genera have remarkably different hemipenial morphologies (Fig. 3). *Hypsirhynchus* has a moderately bilobed, slightly bicalyculate and semicapitate hemipenis with enlarged lateral spines arranged in several parallel rows. In contrast, *Antillophis* has a long, slender, semicalyculate hemipenis with relatively small and almost completely nude lobes, with basal pockets in the proximal region of the hemipenial body, and relatively larger and calcified papillae that ornament the edge of the capitulum.

Darlingtonia Cochran, 1935, **resurrected**

Type species: Darlingtonia haetiana Cochran, 1935.

Diagnosis: Strongly bilobed, semicalyculated and semicapitated hemipenis with the capitulum restricted to the sulcate and lateral surface of the lobes, formed by papillate calyces; relatively long lobes, representing almost half the total length of the organ.

Content: D. haetiana Cochran, 1935.

Comments: The synonymization of *Darlingtonia* with *Ialtris* (Hedges et al., 2009) is not justified given the significantly distinct, external and hemipenial morphologies of these genera (Fig. 3). Synonymization is based on the genera being sister taxa and in having seven supralabials. The organ of *Darligtonia* is semicalyculated and the capitulum is restricted to the sulcate and lateral surfaces of the lobes and formed by papillate calyces. In contrast, *Ialtris* completely lacks calyces and the lobes that are ornamented with flounces in a typical "bicalyculate" position (Zaher, 1999). Further, *Darlingtonia* differs from *Ialtris* in having eight infralabials (nine in *Ialtris*), 132–144 ventrals (vs. 160–192) and 40–54 subcaudals (vs. 57–115), an entire anal scale (vs. divided), no loreal scale (vs. present) and ungrooved teeth (vs. grooved) (data from Cochran, 1941; Schwartz and Rossman, 1976; and Schwartz and Henderson, 1991).

Schwartzophis Zaher, Grazziotin, Cadle, Murphy, Moura-Leite and Bonatto, 2009, **resurrected**

Type species: Arrhyton callilaemum Gosse, 1851.

Diagnosis: Complete loss of capitular calyces; presence of an apical awn (secondarily lost in *S. funereum* owing to reduction of the distal region of the lobes); reduction or loss of hemipenial lobes.

Content: S. callilaemum (Gosse, 1851), *S. funereum* (Cope, 1863) and *S. polylepis* (Buden, 1966).

Comments: Hedges et al. (2009) ignored the striking uniqueness in the hemipenial morphology of *Schwartzophis*, an omission that disserves morphological evidence (Fig. 3). Zaher (1999) noted hemipenial particularities in all three species of *Schwartzophis* (as the *Arrhyton callilaemum* Group); the almost unilobed hemipenis is unique among West Indian Xenodontinae (WIX). Among mainland components, it only occurs in Elapomorphini and *Xenopholis*. In contrast, all other xenodontines have bilobed hemipenes. *Schwartzophis* also differs from *Hypsirhynchus* and *Antillophis* in lacking calyces on the capitulum. The recognition of *Schwartophis* allows the hemipenes to serve as a valuable diagnostic character.

Ocyophis Cope, 1886, **resurrected**

Type species: Natrix ater Gosse, 1863.

Diagnosis: Hemipenis (only known for *O. ater*) semicalyculate, semicapitate and deeply bilobed, with few well developed enlarged lateral spines arranged in two parallel rows; large papillate calyces forming the capitula, which are positioned laterally; row of large papilla ornamenting the lobular crotch.

Content: O. ater (Gosse, 1863) and *O. melanichnus* (Cope, 1863).

Comments: Hedges et al. (2009) placed *Ocyophis ater* and *O. melanichnus* (*sensu* Zaher et al., 2009) in *Hypsirhynchus*. These two species are rare and probably extinct; thus neither Zaher et al. (2009) nor Hedges et al. (2009) had tissue or sequence data. However, their allocation of *O. ater* and *O. melanichnus* to *Hysirhynchus* is unjustified. The assignment of *O. ater* to *Hypsirhynchus* is based on the absence of a loreal scale and on skull similarities taken from Maglio (1970). Whereas Maglio (1970) noted strong similarity between *O. ater* and *Hypsirhynchus*, his hypothesis of phyletic relationships (Maglio, 1970, fig. 18) places *O. ater* as the sister group of a lineage formed by *Hypsirhynchus* and *Uromacer*. Zaher (1999) remarked on the puzzling hemipenial morphology of *O. ater* (Fig. 3) and he avoided allocation for this species.

The long-standing composition of *Hypsirhynchus* (as in Zaher et al., 2009) reflects its morphological distinction from *O. ater*, from which it differs in several meristic and anatomical features. Both taxa have distinct, non-overlapping counts in the following suite of characters (*Hypsirhynchus*: *O. ater*): number of subcaudals (71–93 : 144–162), dorsal scale rows (19 : 17), maxillary teeth (13–14 : 18), pterygoid teeth (17–19 : 26–27), palatine teeth (7 : 13–16) and dentary teeth (18–19 : 22–25), apical pits (1 : 2; data from Cochran, 1941; Maglio, 1970; Schwartz and Henderson, 1991). Therefore we resurrect the genus *Ocyophis* Cope, 1886 to include *O. ater*, its type species (*Natrix ater* Gosse, 1863).

Hedges et al. (2009) placed *Ocyophis melanichnus* into *Hypsirhynchus* because of the presence of relatively large posterior supralabial scales and its occurrence in Hispaniola. This species is one of the poorest-known WIX and we must base its taxonomy on morphological data provided by a few specimens. Cochran (1941) observed that this rare species lacks a groove behind the eye between the last upper labials and the temporals. This separates it from *Al. antillensis* and *B. portoricensis*. Maglio (1970) analysed scalation and skull morphol-

ogy. In contrast to Cochran (1941), he positioned *O. melanichnus* as the sister group of a clade formed by the *Al. antillensis* Group and the *B. portoricensis* Group. In assigning *O. melanichnus* to *Hypsirhynchus*, Hedges et al. (2009) ignored the conclusion of Maglio (1970) and based their taxonomy only on the shape pattern of the supralabials and the snake's distribution. The following suite of non-overlapping characters distinguish *Hypsirhynchus* (*sensu* Zaher et al., 2009) from *O. melanichnus* (*Hypsirhynchus*: *O. melanichnus*): number of ventrals (156–182 : 189); number of subcaudals (71–93 : 108); mid-body dorsal scale rows (19 : 17); temporal scale formulae (1 + 2/1 + 2 : 2 + 2/2 + 2); maxillary teeth (13–14 : 20); pterygoid teeth (17–19 : 28); palatine teeth (7 : 16); dentary teeth (18–19 : 24); and number of apical pits (1 : 2; data from Cochran, 1941; Maglio, 1970; Schwartz and Henderson, 1991). Because no morphological or molecular evidence supports the transfer of *O. melanichnus* into *Hypsirhynchus*, we opt to maintain it in *Ocyophis* (Zaher et al., 2009). This genus may still be paraphyletic with respect to the other well established assemblages of WIX, and further studies are necessary in order to clarify its phylogenetic affinities.