Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa

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ABSTRACT

We present a molecular phylogenetic analysis of caenophidian (advanced) snakes using sequences from two mitochondrial genes (12S and 16S rRNA) and one nuclear (c-mos) gene (1681 total base pairs), and with 131 terminal taxa sampled from throughout all major caenophidian lineages but focussing on Neotropical xenodontines. Direct optimization parsimony analysis resulted in a well-resolved phylogenetic tree, which corroborates some clades identified in previous analyses and suggests new hypotheses for the composition and relationships of others. The major salient points of our analysis are: (1) placement of Acrochordus, Xenodermatids, and Pareatids as successive outgroups to all remaining caenophidians (including viperids, elapids, atractaspidids, and all other “colubrid” groups); (2) within the latter group, viperids and homalopsids are successive sister clades to all remaining snakes; (3) the following monophyletic clades within crown group caenophidians: Afro-Asian psammophiids (including Mimophis from Madagascar), Elapidae (including hydrophiines but excluding Homoroselaps), Pseudoxyrhophiinae, Colubrinae, Natricinae, Dipsadinae, and Xenodontinae. Homoroselaps is associated with atractaspidids. Our analysis suggests some taxonomic changes within xenodontines, including new taxonomy for Alsophis elegans, Liophis amarali, and further taxonomic changes within Xenodontini and the West Indian radiation of xenodontines. Based on our molecular analysis, we present a revised classification for caenophidians and provide morphological diagnoses for many of the included clades; we also highlight groups where much more work is needed. We name as new two higher taxonomic clades within Caenophidia, one

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new subfamily within Dipsadidae, and, within Xenodontinae five new tribes, six new genera and two resurrected genera. We synonymize Xenoxybelis and Pseudablubes with Philodryas; Erythrolamprus with Liophis; and Lystrophis and Waglerophis with Xenodon.

**KEYWORDS:** Serpentes; Colubridae; Caenophidia; Phylogeny; Classification; Systematics; Xenodontinae; Dipsadinae; New genus; Elapoidea; Colubroidea; South America; West Indies.

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**INTRODUCTION**

The phylogenetic affinities and classification of caenophidian (“advanced”) snakes have been a matter of debate for decades. The great diversity of living species (> 3000 species), the limited range of morphological characters investigated thoroughly within the group, and the limited taxonomic and genomic sampling in molecular phylogenetic studies, have been the main deterrents to significant advances in understanding caenophidian phylogeny. Rieppel (1988a,b) provided useful historical reviews of progress in understanding snake phylogeny and classification. Recent studies, building upon the foundations established in classical works such as Duméril (1853), Jan (1863), Cope (1895, 1900), Dunn (1928), Hoffstetter (1939, 1955), Bogert (1940), and Underwood (1967), have amplified and extended the morphological evidence for particular caenophidian clades and succeeded in defining some monophyletic units at the familial and infra-familial levels (e.g., McDowell, 1987; Dowling & Duellman, “1974-1978” [1978]; Ferrarezzi, 1994a,b; Meirete, 1992; Underwood & Kochva, 1993; Zaher, 1999).

More recently, molecular studies have provided new insights on the higher-level phylogeny of caenophidians, corroborating some long-held views and suggesting new hypotheses for evaluation (e.g., Alfaro et al., 2008; Cadle, 1984a,b, 1988, 1994; Crother, 1999a,b; Glaw et al., 2007a,b; Gravlund, 2001; Heise et al., 1995; Kelly et al., 2003, 2008, 2009; Keogh, 1998; Kraus & Brown, 1998; Lawson et al., 2005; Mulcahy, 2007; Nagy et al., 2003, 2005; Pinou et al., 2004; Vidal et al., 2000, 2007, 2008; Vidal & Hedges, 2002a,b). Some of these contributions were designed to evaluate higher-level relationships, while others focus on more restricted assemblages (e.g., homalopines, xenodontines, pseudoxyrhophines, elapids, psammophiines, lamprophiines). The principal molecular phylogenetic studies examining broader relationships among caenophidian are summarized in Table 1. All of these efforts have resulted in increasing consensus on the content of many snake clades and the relative branching order among some of them. Improved knowledge of morphology is helping diagnose and characterize clades at all levels of their evolutionary history. However, there is as yet little compelling evidence supporting any particular branching order among many caenophidian clades. The family Colubridae, long suspected to be paraphyletic, has especially defied partition into well defined and strongly supported clades and a nested hierarchy of their evolution, although molecular data in particular have been especially helpful in understanding the evolution of this group.

Both molecular and morphological data sets will ultimately be necessary to develop a comprehensive phylogeny of snakes and each data source can make a unique contribution. On one hand, molecular methods can provide large quantities of phylogenetically

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**TABLE 1:** Comparison among the principal molecular phylogenetic studies of Colubroidea.

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informative data. Although data have been plentiful, colubroid molecular phylogenies have been unstable due to their inherent sensitivity to taxon sampling (Kelly et al., 2003; Kraus & Brown, 1998). On the other hand, only few morphological complexes have been analyzed thoroughly within snakes, and the paucity of broadly sampled morphological characters has prevented the compilation of a large morphological data matrix. We prefer a combination of the two data sources.

Zaher (1999) synthesized available morphological evidence, primarily from hemipenes, and allocated all “colubrid” genera into subfamilies, based in part on lists published by Dowling & Duellman (1978), McDowell (1987), Williams & Walach (1989), and Meirte (1992). Zaher (1999) recognized the putatively monophyletic Atractaspidae and an ostensibly paraphyletic Colubridae including twelve subfamilies: Xenodermatinae, Pareatinae, Calamariinae, Homalopsinae, Boodontinae, Psammophiinae, Pseudoxyrhophiinae, Natricinae, Dipsadinae, and Xenodontinae. In Zaher’s taxonomy, Xenodermatinae, Homalopsinae, Boodontinae, and Pseudoxyrhophiinae were explicitly recognized (using enclosing quotation marks) as possibly non-monophyletic working hypotheses requiring validation. The other subfamilies were supported by at least one putative morphological synapomorphy.

Kraus & Brown (1998), in one of the earliest comprehensive studies of snakes employing DNA sequences, provided molecular evidence for the monophyly of the Viperidae, Elapidae, Xenodermatinae, Homalopsinae, Pareatinae, Thamnophiini, Xenodontinae, Colubrinae, and Boodontinae. They were the first to recognize the basal rooting of the Xenodermatinae on the basis of molecular data, although various authors (e.g., Boulenger, 1894) had long recognized their relative basal position within caenophidians. Corrections and modifications to Zaher’s (1999) generic arrangement followed in several molecular studies, which concentrated on the “boodontine” and psammophiine lineages, and in the placement of the North American xenodontines (Pinou et al., 2004; Lawson et al., 2005; Vidal et al., 2007, 2008). Most importantly, the paraphyletic family Colubridae was redefined as a much more restrictive group, and most of the subfamilies recognized by Zaher (1999) were rearranged among various families and superfamilies (Pinou et al., 2004; Lawson et al., 2005; Vidal et al. 2007, 2008).

Lawson et al. (2005) revised the allocation of many genera based on a molecular phylogeny of 100 caenophidians representing all subfamilies recognized by Zaher (1999). They recognized families Colubridae, Elapidae, Homalopsidae, Pareatidae, and Viperidae, and resolved Acrochordus as the sister taxon of all other caenophidians. However, their maximum parsimony analysis (MP) did not resolve well supported deeper nodes among the five “colubrid” families, apart from Pareatidae, which was the sister taxon of a clade including the remaining four. Within that clade, Viperidae + Homalopsidae was the sister clade of Colubridae (their Clade B, including Calamariinae, Colubrinae, Natricinae, Pseudoxyenodontinae, Xenodontinae) + Elapidae (their Clade A, including Atractaspidinae, Booodontinae, Elapinae, Hydrophiinae, Psammophiinae, Pseudoxyrhophiinae, and Oxyrhinodesmus). Subsequently, Pinou et al. (2004) applied the resurrected name “Elapoidea” to a clade comprising Atractaspis + Elapidae. “Elapoidea” has subsequently been used for “Clade A” of Lawson et al. (2005) in several molecular phylogenetic studies (Vidal et al., 2007, 2008; Kelly et al., 2009; see also our results below). Clade B of Lawson et al. (2005) was referred to as “Colubroida” by Pinou et al. (2004) and subsequent authors.

Vidal et al. (2007, 2008) studied broad patterns of phylogenetic relationships among caenophidians based on an analysis of sequences from approximately 25-30 taxa, primarily from Africa, and revised some of the taxonomy of snakes based on their analyses. However, we feel that some of their formally recognized taxa are only weakly supported by their molecular data, or receive conflicting phylogenetic signals in different data sets. These authors made little attempt to analyze the effects of taxon sampling and long branch attraction (Felsenstein, 1978) or repulsion (Siddall & Whiting 1999) in small molecular data matrices, problems that were acknowledged by Kraus & Brown (1998) and Kelly et al. (2008), and supported by simulation and other studies (e.g., Goertzen & Theriot, 2003; Salisbury & Kim, 2001). Vidal et al. (2007) argued that the problem of long branch attraction (and repulsion) in more basal nodes was better addressed through gene sampling rather than taxon sampling, but this will only partially solve the issue. Increasing gene sampling in a reduced taxon sample can actually reinforce long branch attraction (or repulsion), and increasing the taxon sampling density will at least help reveal unstable clades within a phylogenetic analysis. We comment in more detail on certain aspects of their analyses and taxonomy at appropriate points in our discussion below.

In this study we address the phylogenetic relationships of caenophidians with an increased taxonomic sample over all previous studies (131 species).
In particular, we emphasize the vast radiation of South American “xenodontine” snakes. Although this analysis forms the most comprehensive sampling of caenophidian species analyzed thus far, ours has the same deficiency of other studies: a small sample for most previously recognized colubroid lineages, with the exception of the South American xenodontines (77 species representing most major groups within this radiation). Nonetheless, we believe it represents a significant advance to our present knowledge of caenophidian snake relationships, particularly xenodontines.

Based on our phylogenetic analysis, we revise the classification of caenophidians, paying special attention to morphological diagnoses for particular clades. Although we are able to provide diagnostic morphological characters for most clades (see exceptions below), the characters diagnosing some of the clades are few in number. We believe this reflects the lack of a broad comparative morphological perspective for snakes, rather than weak support for any particular clade (some of the clades that have weak morphological support are strongly supported by molecular data). This should serve to highlight areas needing additional research.

**MATERIAL AND METHODS**

**Terminal taxa and Genes Sampled**

Our molecular matrix comprised 132 terminal taxa and sequences for two mitochondrial and one nuclear gene: 12S, 16S and c-mos respectively (Table 2). We used sequences deposited in GenBank and combined them with our own sequences to sample broadly among caenophidians (Table 2). The caenophidian tree was rooted using a boine, *Boa constrictor*, as an outgroup. 184 sequences were downloaded from GenBank (68 sequences for 12S, 69 for 16S, and 47 for c-mos) and 180 sequences were generated by us (63 sequences for 12S, 60 for 16S and 57 for c-mos); the sequences we generated were primarily from Neotropical xenodontines since these were the lineages of most immediate interest. A list of voucher specimens for the new sequences we present is available from the authors. In all cases our taxon selection was based on the criterion of completeness of gene sequence data; only a few species that represent distinctive and phylogenetically unknown groups were included within fewer than three genes.

The higher clades of caenophidians represented by the terminal taxa in our study are the following (using more or less classical higher taxonomic categories): Boinae (1 species); Acrochordidae (1 species); Atractaspididae (3 species); Boodontinae (2 species); Calamariinae (1 species); Colubrinae (5 species); Elapidae (including Laticaudinae and Hydrophiinae) (5 species); Homalopsinae (2 species); Natricinae (5 species); Paretinae (2 species); Psammophiinae (2 species); Pseudoxenodontinae (1 species); Pseudoryphophiinae (2 species); Viperidae (including Azemiopinae and Crotalinae) (5 species); Xenodermatinae (2 species) and Xenodontinae “sensu lato” (93 species).

Our 180 sequences represent most of the molecular data for the 93 species of Xenodontinae from North, Central, and South America in our matrix, comprising the principal clades (tribes) for this taxon. We sampled 10 species (representing 7 genera) for Central American xenodontines (Dipsadinae) and 77 species (representing 40 genera) for South American xenodontines (Xenodontinae sensu stricto).

We assume the monophyly for the specific category to construct our matrix, so we combined sequences from different specimens to compose our specific terminals (Table 2). Only in two taxa we combined two different species as terminals (Table 2), these are: *Calamaria pavimentata* (c-mos) + *C. yunnanensis* (12S and 16S) as one terminal taxon, and *D. rufozonatum* (12S and c-mos) + *D. semicarinatus* (16S) as another terminal taxon.

**DNA extraction, amplification and 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 following primers: for 12S rRNA: L1091mod (5’ CAA ACT AGG ATT AGA TAC CCT ACT AT 3’; modified from Kocher et al., 1989) and H1557mod (5’ GTA CRC TTA CCW TGT TAC GAC TT 3’; modified from Knight & Mindell, 1994); for 16S rRNA: L2510mod (also named as “16sar”; 5’ CCG ACT GTT TTG TMA CAA AAA CA 3’) and H3056mod (also named as “16shr”; 5’ CTC CGG TCT GAA CTC AGA TCA CGT RGG 3’), both modified from Palumbi et al. (1991); and for c-mos: S77 (5’ CAT GGA CTG GGA TCA GTT AGT 3’) and S78 (5’ CCT TGG GTG TGA TTT TCT CAC CT 3’), both from Lawson et al. (2005). PCRs protocols were used as described in the original work, with some adjustments aimed to increase the amplification efficiency (addition of 0.4% of Triton 100, and annealing temperature for 12S and 16S of 54°C and for c-mos of 56°C).
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Amplicons were purified with shrimp alkaline phosphatase and exonuclease I (GE Healthcare) and sequenced using the DYEnamic ET Dye Terminator Cycle Sequencing Kit (GE Healthcare) in a MegaBACE 1000 automated sequencer (GE Healthcare) following the manufacturer's protocols. Chromatograms were checked and, when necessary, were manually edited using Bioedit version 7.0.9.0 (Hall, 1999).

Alignment and phylogenetic approach

Phylogenetic analyses of the sequence data were conducted using the method of direct optimization (Wheeler, 1996), as implemented in the program POY, version 4 (Varón et al., 2008). This approach simultaneously estimates the nucleotide alignment and the phylogenetic tree based on the algorithm described by Sankoff (1975). Homologies among base pairs are inferred as a dynamic process in which the alignment is optimized upon a tree and the best alignment and tree are chosen by the same optimality criterion. Our criterion for direct optimization was Maximum Parsimony (Varón, et al., 2008). Parsimony analysis under direct optimization is distinct from most molecular phylogenetic analyses of snakes done so far, which have used model-based analyses (e.g., maximum-likelihood and Bayesian inferences).

For the non-coding sequences (rRNAs) we conducted a pre-alignment step using the default parameters implemented in Clustal X (Thompson et al. 1997). After that, we identified the regions which were unambiguously homologous (probably the stem regions) by virtue of having high levels of sequence similarity and without insertions and deletions. These regions were used to split both sequences (12S and 16S) into six fragments, each of them comprising approximately 100 base pairs and acting as regions of homology constraint for the alignment search.

On the other hand, for the coding gene (c-mos) we used the retro-alignment approach, which permits the inclusion of the biological information in codon triplets. We used the information on translation sequence available in NCBI GenBank and the frame-shift of the sequences to define the starting position for the codon according to which we translated all DNA sequences to amino-acid sequences. Amino-acid sequences were aligned with Clustal X, using the standard parameters of the Gonnet series matrix. These were subsequently retro-translated to DNA in order to be analyzed in the POY search as static homology matrix.

Search strategy and support indexes

Our search strategy involved three routines designed to explore the space of hypotheses for trees and alignments:

1 – We constructed 200 Random Addition Sequences (RAS) followed by branch swapping using the Tree Bisection Reconnection algorithm (TBR). All best trees and suboptimal trees with fewer than five extra steps were stored. These stored trees were submitted to a round of tree fusing with modified settings for swapping, in which a consensus tree was constructed based on the trees stored in memory, and used as a constraint for the following rounds. After that, the best tree was perturbed using 50 interactions of ratchet with a re-weighing of 20% of the data matrix using a weight of three. One tree per interaction was stored and an additional step of tree fusing was conducted;

2 – Based on previous taxonomies and hypotheses of relationships among taxa, we constructed ten predefined trees as starting trees, thus guaranteeing that these topologies were evaluated, after that we followed the same steps used in routine one;

3 – The last routine was a step of TBR, followed by a tree fusing using the resultant trees from both previous routines as starting trees.

Finally, we conducted a round of TBR using an interactive pass algorithm (Wheeler, 2003), which applies the information of the three adjacent nodes to perform a three dimensional alignment optimization for the target node. The resultant dynamic homologies were transformed into static homologies and the implied alignment was exported in Hennig86 format. The phylogenetic results were then checked using the TNT (Tree analysis using New Technology, version 1.1) software (Goloboff et al., 2008). For TNT Maximum Parsimony search we used the “new technology” algorithms, mixing rounds of TBR, SPR (Sub-tree Pruning and Regrafting), Drift, Ratchet, Sectorial search, and tree fusing. Searches were stopped after the consensus was stabilized for five rounds. To access the corroboration values and support values (sensu Grant & Kluge, 2003) for clades in our best tree, we conducted 1000 site re-sampling in POY, with a static approximation transformed matrix for bootstrap, and we used all visited trees for our analysis routine to infer Bremer support.
RESULTS

Sequence characterization

The implied alignment of the 12S and 16S rRNA sequences resulted in 492 and 688 sites, respectively, whereas the c-mos sequences comprised 501 sites (for a total of 1681 sites among the three genes). Our c-mos sequences had an indel of three base pairs at positions 272-274 in Acrochordus, Bitis, Calamaria, Colubrinae, Natricinae, Pseudoxenodon, and Xenodontinae; this indel is equivalent to that reported in these same groups by Lawson et al. (2005). However it is a deletion of an arginine AA, in an area of the sequence that frequently shows three consecutive arginines, rendering it difficult to determine whether Acrochordus and Bitis show a deletion at the same site as the other monophyletic group (Calamaria, Colubrinae, Natricinae, Pseudoxenodon, Xenodontinae) or a deletion at one of the subsequent arginines. An additional indel of three base pairs at positions 266-268 was found in the sequence of Pseudoeryx. This deletion is one additional arginine indel that occurred in the same three-arginine region.

We found a frame-shift mutation, a deletion of one nucleotide, at position 299 for the monophyletic group Lystrophis hystricus, Lystrophis dorhignyi and Waglerophis merremi (Xenodon newwiedi was not sequenced for c-mos). In L. hystricus we found one additional indel, an insertion of five nucleotides at position 373-377. To deal with these frame-shift mutations in our alignment approach we conducted the alignment using AA sequences in Clustal X, without this monophyletic group. After that, we retro-translated to DNA and aligned the sequences for this group over the aligned matrix using the default parameters in Clustal X. We do not have a clear explanation for this frame-shift mutation, because the first deletion inserts a stop codon at position 101 (AA sequence), probably disabling the c-mos protein. However, mechanisms such as post-transcriptional modifications and RNA editing (Brennicke et al., 1999), could be involved to correct the frame changing of the RNA sequence before translation. This type of frame-shift mutation was also found in snakes for the ornithine decarboxylase gene (ODC, Noonan & Chippindale, 2006). Another possible explanation is the amplification of a paralogous gene for this group of species. However, the sequence trace did not show any signal that could indicate a pseudogene contamination (sequence ambiguities, double peaks, noise, etc). Therefore, more studies are needed to completely understand this new mutational event in such a broadly employed gene as the c-mos.

Phylogenetic analysis: broad patterns of relationships

Direct optimization parsimony analysis of the data set using POY resulted in one most parsimonious tree with 5130 steps (Fig. 1). Further independent analysis of the results from POY was obtained by analyzing the optimal implied alignment in TNT, which identified 53 optimal topologies of 5124 steps, one of which is identical to our Figure 1. The strict consensus of the 53 trees generated by TNT produced a polytomy at node 19 (Fig. 1) including clades Colubridae, (Xenodontinae + Dipsadinae), Carphophiinae, (Natriciteres + Rhabdophis + Xenochrophis), Heterodon, Calamaria, Pseudoxenodon, Sinonatrix, Natrix, and Farancia. The remaining topology of the strict consensus was completely concordant with the best tree found in POY. We further used the pruned tree method in TNT to resolve the polytomy at node 19 and found that the position of Pseudoxenodon is the principal cause of different trees found in TNT. Only one gene sequence, c-mos, was available for Pseudoxenodon and this may be responsible for the lability of its position in different trees. Using the 53 parsimony trees as starting trees in one more round of TBR, tree fusing and Ratchet in POY did recover the same most parsimonious tree shown in Figure 1, which is consistent with our results in POY. Thus Figure 1 represents our preferred tree that will be discussed below.

In discussing our results we use informal designations for clades that follow generally recognized familial or subfamilial categories for caenophidians (e.g., subfamilies, as in Lawson et al., 2005). For example, ‘viperids’ and ‘elapids’ refer to the classically recognized families Viperidae and Elapidae, whereas ‘homalopsines’, ‘pareatines’, and ‘colubrines’ refer to Homalopsinae, Pareatinae, and Colubrinae, respectively. Discussion of the application of these names in our new taxonomy is deferred to the section on classification. In our discussion we refer to individual clades by the identifying numbers at each node of our tree (Fig. 1).

The broad pattern of relationships indicated by our analysis includes the following main points. Clade 1 (Fig. 1) corresponds to the clade equivalent to the Colubroidea, as used in most recent literature for the caenophidian sister clade to Acrochordus and containing viperids, elapids, and all ‘colubrid’ groups (e.g., Lawson et al., 2005; but see discussion of this name in the classification section); this clade is robustly supported (bootstrap 94%; Bremer 14). There is strong support for the successive positioning of Acrochordus, xenodermatids, and pareatids as
FIGURE 1: Best Phylogenetic tree based on molecular matrix (12S, 16S and c-mos) found by Directed optimization under Maximum Parsimony analyses (implemented in POY 4.1). Numbers above branches are bootstrap support values; numbers below branches are Bremer supports. The asterisk (*) corresponds to nodes with bootstrap values less than 60%.
successive sister taxa to all remaining caenophidians (Clade 5; vipers, elapids, sea snakes, atractaspidids, homalopsines, and all other caenophidians). Within Clade 5, viperids and homalopsines are successive sister taxa to all other caenophidians (Clade 9). All of the basal clades (Clades 1-9) are strongly supported, with Bremer support ≥ 9 and/or bootstrap support ≥ 94%. Within Clade 9, two major branches are supported. The first includes elapids and an array of primarily African lineages (Clade 10, bootstrap support 85%, Bremer support 2; psammophiines, aparallactines, atractaspidids, lamprophiines, pseudodoxyrhophiines). Within Clade 10, psammophiines (Clade 11) and elapids (Clade 13) are successive sister groups to the remaining African lineages, but these relationships are only moderately supported (bootstrap 81-85%, Bremer support 1-2). The second (Clade 19, bootstrap support 98%, Bremer support 10) includes the widespread colubrine and natricine lineages, New World xenodontines (sensu lato), and several smaller Asian groups represented by Calamaria and Pseudoxenodon. Within Clade 19, colubrines (Clade 21) + Calamaria, Pseudoxenodon, and natricines (Clade 24) are successive outgroups to xenodontines sensu lato (Clade 25), but basal branches within Clade 19 generally have poor support. Clade 20 (Bootstrap 75%, Bremer support 11) indicates a monophyletic group comprising Calamaria + Colubrinae (Clade 21; bootstrap 97%, Bremer support 7).

Many historically recognized taxa are monophyletic in our analysis insofar as our taxon sampling dictates (see further comments in the classification). These include: Xenodermatidae (Clade 2), Pareatidae (Clade 4), Viperidae (Clade 6), Homalopsidae (Clade 8), Psammophiinae (Clade 11), Elapidae (Clade 13), Lamprophiidae (Clade 17), Pseudodoxyrhophiinae (Clade 18), Colubrinae (Clade 20), Natricinae (Clade 24), and “xenodontines” in the broad sense, with a monophyletic North American group (Clade 26), Dipsadinae (Clade 31), and Xenodontinae (Clade 34). With the exception of some basal branches within Clade 19 (Clades 21, 22, and 24) and within “xenodontines” (Clades 25, 29, 34), these clades are generally well-supported, as measured by bootstrap and Bremer support (Fig. 1).

Our study thus indicates strong support for the non-monophyly of Colubridae in the classical sense of caenophidians that are not viperids or elapids. Viperids are nested within the successive outgroups of pareatines and xenodermatines, whereas elapids are nested higher in the tree among some primarily-African ‘colubrid’ clades.

### Relationships within clades

Our sampling within clades apart from xenodontines is not dense relative to the diversity within these clades, but the following relationships are indicated in our tree (Fig. 1).

Within Viperidae (Clade 6) Causus appears as the basal-most viperid genus while Bitis and Azemiops are the two successive sister-taxes to a well-supported crotaline clade represented by Bothriechis and Agkistrodon (bootstrap 100%; Bremer 9). All nodes within Viperidae are supported by high bootstrap values.

Within elapids (Clade 13; bootstrap 98%, Bremer support 9), our results show strong support for the monophyly of Australopapuan terrestrial elapids (here represented by Notechis + sea snakes (represented by Laticauda) (bootstrap 97%, Bremer support 7) relative to other Old- and New World elapids (Naja, Micrurus, Bungarus). Support for a monophyletic Elapinae for the last group (bootstrap 81%, Bremer support 3) is less but we recognize our limited sampling within this group.

Clade 15 (bootstrap 94%, Bremer support 6) comprises three genera whose relationships have been controversial (Homoroselaps, Atractaspis, and Aparallactus). These represent an extended “atracaspidine” or “aparallactine” clade (Bourgeois, 1968; McDowell, 1968; Underwood & Kochva, 1993). Within this group, clustering of Homoroselaps and Atractaspis relative to Aparallactus receives strong support (bootstrap 90%, Bremer support 7).

Clade 16 (bootstrap 74%, Bremer support 1) comprises representatives of two large Afro-Madagascan clades that are sister taxa, lamprophiines (Lycophidion and Bothrophthalmus) and pseudodoxyrhophiines (Pseudoxyrhopus and Leioheterodon). Although Clade 16 is not strongly supported, both of the sub-clades are strongly supported by high bootstrap values (94% and 96%, respectively) and moderate Bremer support values (3 and 8, respectively).

### Relationships among ‘xenodentine’ lineages

Our results provide weak bootstrap support (< 60%) but strong Bremer support (9) for the monophyly of xenodontines sensu lato (Clade 25). Within Clade 25, three subclades are identified: Clade 26 (North American xenodontines), Clade 31 (Central American xenodontines, or dipsadines), and Clade 34 (South American xenodontines, or xenodontines sensu stricto). These clades receive poor bootstrap support (60-74%) but moderate Bremer support...
We have not sampled intensively within either the North American or Central American groups, but we note in passing that with the last group, our results show moderate support for a Leptodeirini (Clade 32; Leptodeira + Imantodes) and a Dipsadini (Dipsas, Sibynomorphus, Sibon, but also including the selected species of Nina and Atractus). However, no internal nodes within Dipsadini are strongly supported. The nesting of Nina and Atractus within Dipsadini is novel, and suggests that additional work with denser taxonomic sampling should be carried out within this group (see also Mulcahy, 2007).

Within South American xenodontines (Clade 34), our results show a series of dichotomous basal branches that receive poor support (Clades 37, 39, 42, 47, 49), whereas many of the internal clades toward the tips of the tree are more strongly supported. Monophyletic clades within South American xenodontines include Elapomorphini (Clade 38; bootstrap support 86%, Bremer support 6), Tachymenini (Clade 41; bootstrap support 92%, Bremer support 9), Pseudoboini (Clade 46; bootstrap support 99%, Bremer support 21), Philodryadini (Clade 48; bootstrap support 93%, Bremer support 6), Hydropsini (Clade 53; bootstrap support 97%, Bremer support 8), Xenodontini (Clade 55; bootstrap support 100%, Bremer support 10), and Alsophiini (West Indian radiation) (Clade 60; bootstrap support 89%, Bremer support 4).

Alsophis: Alsophis has included a large assemblage in the West Indies, one species in mainland western South America, and several species in the Galapagos Islands (Maglio, 1970; Thomas, 1997). Our results show that Alsophis is polyphyletic, with the species of western Peru (A. elegans) a basal lineage (Clade 35), only remotely related to West Indian species of Alsophis (Clade 64). Within the West Indian radiation, Alsophis antillensis + A. antiquae are a sister group to a clade including species of Darlingtonia, Antillophis, Ialtris, Alsophis, Arrhyton, and Hypsirrhynchus.

Liophis and Xenodontini: Liophis is an assemblage of more than 60 species, making it one of the most diverse genera of South American colubrids. A core of species has been associated with the tribe Xenodontini (see Myers, 1986) but the genus has also been a repository for generalized colubrids whose affinities with other snakes are unclear (e.g., Myers, 1969, 1973). Consequently, its taxonomic history has been subject to considerable fluctuation. Our results show that Liophis is polyphyletic, with Liophis amatali, a species of southeastern Brazil, a sister taxon (Clade 45) to Pseudoboini. Within Xenodontini (Clade 55), Liophis is paraphyletic with respect to Erythrolamprus and to a clade (Clade 59) containing Waglerophis, Xenodon, and Lystrophis. Our results are not surprising given the complicated taxonomic history of these snakes.

Clade 59 (Waglerophis + Xenodon + Lystrophis) is strongly supported (bootstrap support 95%, Bremer support 6). The two species of Lystrophis we examined (bistricus and dorbignyi) are strongly supported as a clade, but as a terminal clade nested within successive outgroups of Xenodon and Waglerophis as represented by the two species of those genera included here (see further discussion in the section on classification).

West Indian Xenodontines: Clade 60 includes all of the West Indian alsophines we examined and has moderately strong support (bootstrap support 89%, Bremer support 4). Within that clade, Uromacer (Clade 61) and a clade containing Cuban species of Arrhyton (Clade 63) are successive sister groups to Clade 64, which contains all remaining West Indian alsophines (Alsophis, Darlingtonia, Antillophis, Ialtris, Jamaican species of Arrhyton, and Hypsirrhynchus). Several clades within the West Indian radiation receive strong support from both bootstrap and Bremer measures of support: Uromacer (Clade 61), one clade of Cuban Arrhyton (procerum-tanyplectum-dolichora), Guadeloupe-Antigua Alsophis (Clade 65), Bahamas-Cuban Alsophis (vudii-cantherigerus), Jamaican Arrhyton (Clade 68), and Hypsirrhynchus (Clade 69). Most other internal nodes within the West Indian radiation have strong Bremer support but poor support from bootstrap measures.

DISCUSSION

Many of our results corroborate those found in earlier molecular studies, but it should be noted that some of our results were based on the same sequences used in earlier studies (those obtained from GenBank; Table 2). Our results corroborate Lawson et al. (2005) in positioning Acrochordus as the sister group to all other caenophidians. A sister-group relationship between Acrochordus and other caenophidians is a well-supported hypothesis in all recent morphological phylogenetic analyses (Tchernov et al., 2000; Lee & Scanlon, 2002; Apesteguía & Zaher, 2006), as well as other molecular studies and combined molecular/morphological analyses (Gravlund, 2001; Lee et al., 2004; and references therein). In contrast, Kelly et al. (2003) and Kraus & Brown (1998) found Acrochord-


dus to cluster with Xenodermus-Achalinus (Xenodermatinae); in addition, Kraus & Brown (1998) found their Acrochordus-xenodermatine clade to cluster well within other caenophidians. We suspect that these differences between Kelly et al. (2003) and Kraus & Brown (1998) and other molecular/morphological studies are due to taxonomic sampling issues, as all studies with greater representation of clades within caenophidians support a basal position for Acrochordus. We fully expect that this topology with respect to Acrochordus will be recovered as sampling improves. Nonetheless, an association between Acrochordus and xenodermatines is an old hypothesis, as, for example, expressed in Boulenger (1894).

The Xenodermatinae (Clade 2; represented by Xenodermus and Stoliczkia) is a basally diverging clade among caenophidians in our study, as well as Kelly et al. (2003), Vidal & Hedges (2002a,b), and Vidal et al. (2008). Some other molecular studies (e.g., Lawson et al., 2005; Kelly et al., 2009) found a radically different phylogenetic position for xenodermatines based on molecular sequences for Oxyrhabdium, which is typically included within this group. Xenodermatinae is supported by a putative synapomorphy: a concave nasal shield that accommodates the nostril (McDowell, 1987). This character is only weakly developed in Oxyrhabdion and does not unambiguously support its relationship to other xenodermatines. Thus, rather than indicating an ambiguous phylogenetic placement for Xenodermatinae, the molecular and morphological data for Oxyrhabdium suggest to us only that this genus is not phylogenetically associated with other Xenodermatinae (as represented by Xenodermus and Stoliczkia in our study and Vidal et al., 2008, and, in addition, by Achalinus in Kelly et al., 2003), which is a basally-diverging clade in several studies.

Within Viperidae the basal position of the genus Causus has been suggested by many workers (e.g., Haas, 1952; Bourgeois, 1968; Marx & Rabb, 1965, and Groombridge, 1984, 1986) on the basis of comparative morphology of the venom apparatus and head circulatory systems. Azemiops is consistently placed as the sister-group of the Crotalinae in most molecular studies (Cadle, 1992; Knight & Mindell, 1993; Parkinson, 1999). Our results are consistent with these studies on both Causus and Azemiops. Kelly et al. (2003) and Pinou et al. (2004) found topological relationships within vipers different from ours and other studies. In particular, these authors found Causus nested within Viperinae (as represented by Bitis and Vipera). Azemiops was a sister clade to Viperinae in the study of Kelly et al. (2003), whereas it was a sister group to Viperinae + Crotalinae in the study of Pinou et al. (2004). We suspect that differences among these studies reflect differences in taxonomic and gene sampling, and different methods of tree construction. Resolving the differences among these studies will require more comprehensive samples for all major lineages within vipers, which was not an objective in this study.

Homalopsines (Clade 8) are a strongly supported clade in all molecular studies, and this clade is usually positioned basally among a large assemblage containing most “colubrids” + elapids (Clade 9 in our study; Clades A + B of Lawson et al., 2005: Fig. 1; Kelly et al., 2003: Figs. 4 and 5; Vidal et al., 2007: Fig. 1). In our study homalopsines are strongly supported as a sister clade to Clade 9 (Fig. 1). We found no support for a sister group relationship between homalopsines and Homoroselaps (Kelly et al., 2003), nor with viperids (Gravlund, 2001); however, these associations were not strongly supported in either of these last studies.

Clade 9, representing crown-group caenophidians, is well supported in our analysis (bootstrap 98%; Bremer 4), and was recovered (with a reduced taxonomic sample) by Pinou et al. (2004) and by Lawson et al. (2005). We are unaware of any characters that diagnose this clade morphologically. Within Clade 9, our phylogeny recovered two major groups (Clades 10 and 19) that include the most diverse assemblages of caenophidians. Clade 10 is supported by a high bootstrap value (85%) but a low Bremer value (2). This is mostly due to the fact that the position of the psammophiines (Clade 11; Psammophis + Rhamphophis) is unstable, being sometimes the sister-group of Clade 19 and sometimes clustering with Clade 13 (Elapidae) in suboptimal trees. Clade 10 was recovered in the albumin immunological data of Cadle (1988, 1994), although the lineages in Clade 19 were an unresolved polytomy (Cadle, 1994: Fig. 2). Clades 10 and 19 were recovered by Lawson et al. (2005), who referred to these as Clade A and Clade B, respectively, and Pinou et al. (2004), who referred to these clades as Elapoida and Colubroidea, respectively (their Fig. 1; thus implicitly redefining the meaning of ‘Colubroidea’, as discussed below). Vidal et al. (2007, 2008) followed Pinou et al.’s (2004) arrangement and recognized the crown-clade superfamilies Elapoidae and Colubroidea for these clades.

Lawson et al. (2005) classified all snakes in Clade 10 (their Clade A with the exclusion of Xenodermatinae) into a single family, Elapidae, with subfamilies Psammophiinae, Elapinae, Hydrophiinae, Atractaspidinae, Lamprophiinae, and Pseudoxyrhophiinae.
Our analysis found strong support for the monophyly of all of these subfamilies, as well as for Clade 13, which corresponds to the traditional family Elapidae (including Hydrophiinae) (bootstrap 98%, Bremer 9), and Clade 14, which includes Atractaspidae, Lamprophiinae, and Pseudoxhydrophiinae (bootstrap 91%, Bremer 3).

Snakes in Clade 15 (Aparallactus, Atractaspis, Homoroselaps), usually referred to as “aparallactines” or atractaspids, have had among the most controversial relationships of any caenophidians (see reviews and references in Underwood & Kochva, 1993, and Cadle, 1994). This clade is moderately supported in our analysis (bootstrap 84%, Bremer support 6), and several other studies have shown some unity to this group. The taxonomically most comprehensive studies of this group, Nagy et al. (2005) and Vidal et al. (2008) (both studies based on the same sequences) recovered two monophyletic sister groups, Aparallactinae (Macrelaps, Xenocalamus, Amblyodipsas, Aparallactus, Polemon) and Atractaspidae (Atractaspis, Homoroselaps). This result is consistent with the placement of Aparallactus, Atractaspis, and Homoroselaps in our study with respect to one another. However, neither Nagy et al. (2005), Vidal et al. (2008), nor our study was able to link Aparallactinae + Atractaspidae to other clades of caenophidian snakes with strong support. This is reflected in low support values in all three studies and conflicting placements for the entire assemblage with respect to other major caenophidian clades (sister group to Elapidae in Nagy et al., 2005; sister group to Pseudoxhydrophiinae + Lamprophiinae in our study and that of Vidal et al., 2008).

For xenodontines sensu lato (Clade 25) we defer many of our comments to the section on classification. However, we note that virtually all molecular and morphological studies since Cadle (1984a,b; 1985) have recovered evidence for three main clades within this group, although the degree of support for these clades varies, as indicated in Results: a North American clade (Clade 26), a Central American clade (Clade 31), and a South American clade (Clade 34); see especially Pinou et al., 2004, Vidal et al. (2000), and Zaher (1999). The topological relationships for major clades within each of these groups are broadly concordant among these studies insofar as clades that are strongly supported. However, as ours is the taxonomically most comprehensive study of these groups, the placement of many taxa is here elucidated for the first time. In particular, we call attention to the placements of Alsophis elegans and Promophis (Clades 35 and 36), Taeniophallus (Clade 44), Liophis amarali (Clade 45), and the polyphyly of Arrhyton, Alsophis, and Antilophis within the West Indian radiation (Clade 60; see Results). These taxa clearly require further taxonomic revision, which we initiate and discuss in our classification.

CLASSIFICATION OF ADVANCED SNAKES

Our approach to caenophidian classification

Prior to presenting our classification of advanced snakes, we make some preliminary comments regarding our approach to formal recognition of clades represented by our phylogeny, and on several recent “readjustments” to the classification of caenophidians. We fully recognize that there are still many details of snake phylogeny to be resolved, that results for particular taxa can conflict with one another in different studies, and that branches in a phylogenetic tree may receive no significant support for various reasons. Many taxa are of uncertain relationships, either because of disagreements among studies due to analytical or sampling issues, unstable phylogenetic position in multiple most parsimonious trees, or simple lack of data.

All of these factors have influenced the manner in which we translate the information contained in our phylogeny into a classificatory scheme. As a first principle, we recognize as formal taxonomic categories those clades that have received broad support from either morphological or molecular phylogenetic studies. In general, these are clades that appear repeatedly in different studies directed at the appropriate level, an example being Caenophidia. In many cases, these are clades with strong statistical support in a particular study, given sufficient taxonomic sampling (specific details given below). Secondly, we do not give formal names to clades whose composition varies widely among different trees or which receive poor support in a phylogeny. We have resisted giving formal names to taxa solely because their phylogenetic position cannot be estimated with any precision or robustness. Instead, we prefer to simply list these taxa at incertae sedis within the least inclusive taxon with which they appear to be associated. This approach simultaneously reduces the unnecessary proliferation of formal taxonomic names and flags these taxa for further study. Finally, we prefer to integrate morphological data into our taxonomy insofar as possible. However, morphological data for caenophidians are scant for many taxa and in general is widely scattered. Morphological diagnoses for taxa can highlight areas for research, predict relationships in the absence
of molecular analyses, and complement molecular data. With these working approaches, we recognize that our classification includes a few named clades which we expect will require modification with additional study. An example is Atractaspididae, for which we feel that the morphological evidence adduced is weak (primarily due to taxonomic sampling issues), and for which molecular studies conflict to some extent and often (as ours) have limited taxonomic sampling. We have retained a few such named taxa because they have some currency in usage. We provide commentary where necessary to highlight some of the problems. However, we do not create new formal taxa for such controversial groups, preferring instead to leave them unnamed.

Commentary on recent use of the names Colubroidea, Prosymnidae, Pseudapididae, and Grayiinae

Several recent studies have addressed the classification of caenophidians based on molecular studies (reviewed in the Introduction). In virtually no case has any attempt been made to integrate morphological data into the classification schemes. We disagree with portions of the taxonomies used in some of these studies and here comment on the nature of our disagreements, and why we do not use a few previously named taxa in our classification.

Colubroidea: The name “Colubroidea” has a long history in snake classificatory literature as the name applied to the sister clade of Acrochordidae within Caenophidia. In other words, “Colubroidea” has had long-standing use as the name of the clade comprising viperids, elapid snakes and all “colubrid” snakes and their derivatives (hydrophiines, atractaspidids, etc.). We were surprised to find that this widely used and universally understood name was applied in an entirely new way, without so much as a comment, in a much more restrictive sense by Dowling & Jenner (1988) and Pinou et al. (2004). These authors applied “Colubroidea” to a clade (Pinou et al., 2004: Fig. 1) that included only a few lineages of “colubrid” snakes, namely colubrines, natricines, and North American and Neotropical xenodontines (Dipsadinae + Xenodontinae of some authors, e.g., Zaher, 1999). Other than a strongly supported clade in their molecular phylogeny, neither Pinou et al. (2004) nor Dowling & Jenner (1988) attempted to diagnose their concept of “Colubroidea”; in fact, they did not even mention their entirely novel use of the name and its contravening years of historical precedent! Subsequent to Pinou et al. (2004), Vidal et al. (2007, 2008) used “Colubroidea” as a name for the same clade, with the addition of Pseudoxenodon. Again, these authors attempted no diagnosis or definition of the group.

This new application of a long-standing taxonomic name clouds an already murky and confusing taxonomy, particularly as it was seemingly done very casually. Examples of works using “Colubroidea” in its near-universally understood sense, but by no means an exhaustive list, include the following: Cadle, 1988; Cundall & Greene, 2000; Cundall & Irish, 2008; Dowling & Duellman, 1978; Ferrarezzi, 1994a,b; Greene, 1997; Kelly et al., 2003; Kraus & Brown, 1998; Lawson et al., 2005; Lee et al., 2004; McDarmid et al., 1999; McDowell, 1986, 1987; Nagy et al., 2005; Rieppel, 1988a,b; Romer, 1956; Smith et al., 1977; Vidal, 2002; Vidal & Hedges, 2002a,b; and Zaher, 1999. A radical shift in the meaning of a well-established taxonomic name, in our view, should be explicit and not simply implicit in the presentation of results of a phylogenetic analysis. It is also true that the name Colubroidea has had several meanings since Oppel (1811) first erected the family-group name Colubrini (for Bungarus and Coluber). Fitzinger (1826) explicitly used “Colubroidea” as a family-group name almost in its modern sense. Romer (1956) formally recognized Colubroidea as a superfamilial and his use was followed in most subsequent works.

Nonetheless, we recognize that some names will require changes in definition with improved knowledge of phylogeny, particularly among “colubroid” snakes (sensu Romer, 1956). When making taxonomic changes we maintain current usage of names as far as possible and opted for conservative adjustments to meanings of long-standing names. In any case, when we change the meaning of long-standing names, we provide commentary about the change and our reasons for doing so. Although we do not fully adopt the philosophy and procedures elaborated by Frost et al. (2006: 141-147), we do share some of their concerns about names and ranks. Consequently, for names above the family-group, which are unregulated by the International Code of Zoological Nomenclature, we do not incorporate an explicit concept of rank but we maintain ranks (and comply with the Code’s rules for name formation) at the family-group and below. Thus, we apply the name Colubridae new name as a formal taxonomic name above the family level for the sister taxon to Acrochordidae within Caenophidia; this new
name replaces Colubroidea Oppel as the name for this clade. We use and re-define Colubroidea Oppel for a reduced clade comprising natricines, calamariines, pseudoxenodontines, colubrines, and xenodontines sensu lato, as explained below.

Prosymnidae and Pseudaspididae: Kelly et al. (2009) proposed new names for several “clades” within Elapoidea (see below). They recognized a new family, Prosymnidae, including only the genus Prosymna based on the fact that Prosymna appeared in all their analyses “at the same hierarchical level as other major clades” and thus should be accommodated in a distinct family. They used a similar argumentation for recognizing a family Pseudaspididae (including Pseudaspis and Pythonodipsas). On the other hand, Vidal et al. (2008) considered Prosymna, Pseudaspis, Pythonodipsas, Buhoma, Psammodynastes, Micrelaps, and Oxyrhhabdium to represent elapid lineages with unresolved affinities, and suggested that additional sequencing was needed to better resolve their affinities. Indeed, Prosymna falls into radically different phylogenetic positions in the studies of Vidal et al. (2008), in which it clusters with Atractaspidae + Pseusoxyrhophiidae + Lamprophiidae, and Kelly et al. (2009), in which it is nested within the Ptyasmiidae + Pseusoxyrhophiidae. In neither analysis does the position of Prosymna receive significant support. Similarly, although Kelly et al. (2009) provided strong support for a clade (Pseudaspis + Pythonodipsas), the relationship of that clade to other elapid groups was ambiguous. In the taxonomically broader phylogenetic analysis by Lawson et al. (2005), the strict consensus parsimony tree shows Prosymna + Oxyrhhabdium as a sister clade to the Elapidae; Psammodynastes as the sister group of Atractaspis; and Pseudaspis + Pythonodipsas as a clade more closely related to the Lamprophiidae than to any other elapid group.

The conflicting results among these studies might be due to the different strategies of outgroup and ingroup sampling used in these analyses. However, none of these hypotheses show significant statistical support. For these reasons we prefer not to recognize Prosymnidae and Pseudaspididae. Rather, we consider Prosymna, Pythonodipsas, and Pseudaspis as well as Buhoma, Psammodynastes, and Oxyrhhabdium as Elapoidea incertae sedis.

Grayinae Meirte, 1992: Vidal et al. (2007) erroneously thought they were erecting a new family-group name, Grayinae, but this name should actually be attributed to Meirte (1992). Both Meirte (1992) and Vidal et al. (2007) included only the genus Grayia Günther, 1858 in this taxon. We did not include Grayia in our analysis but its phylogenetic affinities have been found to lie with the Colubrinae by Cadle (1994), Pinou et al. (2004), and Vidal et al. (2007), and with the Natricinae by Kelly et al. (2009). The genus was associated with Colubrinae in the maximum parsimony tree of Lawson et al. (2005), although with no significant statistical support, essentially forming a basal polytomy with both Natricinae and Colubrinae. Since there seems to be no compelling evidence that would support an unambiguous position of Grayia within Colubroidea, we here refrain to include the genus in a separate subfamily and place it in Colubridae incertae sedis.

Taxonomy of caenophidians, with a focus on xenodontines

The present taxonomic arrangement refers only to the “colubroid” radiation, with special emphasis on the “New World xenodontine” radiation of snakes. We recognize taxonomically all clades that can be characterized morphologically and display either a high bootstrap value (more than 70%) or a high Bremer support (superior to 5). We avoided suggesting new taxonomic arrangements for nodes that are poorly supported in our molecular analysis and that lack any putative morphological synapomorphy. However, in a few cases we recognize a clade taxonomically for which no morphological synapomorphies are known; we discuss these at the appropriate places in the text.

Before each diagnosis we parenthetically present the bootstrap support (expressed as a percentage) and Bremer support for each node discussed. For example, the first clade discussed (Clade 1) is denoted by “(94%, 19)”, which reflects a bootstrap value of 94% and a Bremer support of 19. An asterisk (*) denotes bootstrap support < 70%. All clade numbers refer to those indicated in Fig. 1. A few named taxa in our taxonomic hierarchy (e.g., Calamariinae) are represented by only a single terminal taxon in our study. For these, we denote their placement in the tree (Fig. 1) by the name of the terminal taxon rather than a node number (these consequently lack “node support” statistics).

The following summarizes our classification to tribe level as an aid in following the text. We also note here the new higher taxa and genera described (certain genera are placed incertae sedis in many of the higher taxa, as explained below):
Caenophidia
   Acrochordidae
   Colubroides, new taxon
   Xenodermatidae
   Colubridae
   Pareatidae
   Endogyptodonta, new taxon
   Viperidae
   Homalopsidae
   Elapidae
   Psammophiidae
   Elapoida
   Pseudoxenodontidae
   Natricidae
   Dipsadidae
   Psamophiini, new tribe
   Alsophiini
   Ocyophis Cope (resurrected)
   Conophiini, new tribe
   Hydrodynastini, new tribe
   Xenodontinae
   ‘Pseudalf disti’ – (Latin, “snake”) + oides (Greek, “having the form of”).

Diagnosis: (94%, 19). A clade that can be diagnosed by at least eight putative morphological synapomorphies: loss of the right carotid artery; intercostal arteries arising from the dorsal aorta throughout the trunk at intervals of several body segments; specialized expanded costal cartilages; presence of a muscle protractor laryngeus; separate muscle protractor quadrati; separate spinalis and semispinalis portion in the epaxial trunk; spines or spines covering the hemipenial body.

Content: Colubroides new taxon is a monophyletic group composed of Xenodermatidae Gray, 1849 and Colubridae.

Comments: The following genera are included as incertae sedis because we are unaware of any compelling evidence associating them with other clades recognized in the present study: Blythia Theobald, 1868; Ceraspis Wagler, 1830; Cyclocorus Duméril, 1853; Dolicophis Gistel, 1868; Elapoidis H. Boie (in F. Boie), 1827; Gongylomorpha Fitzinger, 1843; Haplocercus Günther, 1858; Helophis de Witte & Laurent, 1942; Ignagnathus Boulenger, 1898; Miodon Duméril, 1859; Myersophis Taylor, 1963; Omoadiaphia Köhler, McCranie & Wilson, 2001; Oreocalamus Boulenger, 1899; Poechophis Boulenger, 1903; Rhadinops Boulenger, 1893; Rhadinophis Vogt, 1922; Terelepis Boettger, 1892; Trachichium Günther, 1858.

Colubroides new taxon is equivalent to a clade long recognized by the name “Colubroidae” for the clade of all Caenophidia exclusive of Acrochordidae (see above discussion for application of the name Colubroidae).

FAMILY XENODERMATIDAE Gray, 1849 (Clade 2)

Xenodermatidae Gray, 1849:40.

Type-genus: Xenodermus Reinhardt, 1836.

Diagnosis: (100%, 33). Putative synapomorphies for the group are: maxilla suspended, in part, from a lateral process of the palatine; loose ligamentous connection between maxilla and prefrontal; and vertebral zygapophyses and neural spines with broad lateral expansions (Bogert, 1964; McDowell, 1987; Ferrarezz, 1994a,b).

Content: Achalinus Peters, 1869; Fimbrios Smith, 1921; Stoliczkia Jerdon, 1870; Xenodermus Reinhardt, 1836; Xylophis Beddome, 1878.
Comments: Lawson et al. (2005) and Kelly et al. (2009) showed that *Oxyrhambdium* Boulenger, 1893 belongs to the Elapoidea, instead of being related to the Xenodermatidae, i.e., nested much higher in the caenophidian phylogenetic tree than is indicated by *Xenodermus* and *Stoliczkia* (this study). No molecular study, including ours, has sampled more than one or two species of xenodermatids. Expanded vertebral zygapophyses and neural spines have appeared convergently among dipsadids (e.g., *Ninia*, *Xenopholis*, *Synophis*) (Bogert, 1964). We are not convinced by the few morphological characters adduced by Dowling & Pinou (2003) for a greatly expanded Xenodermatidae. In their concept, the Xenodermatidae comprises “more than 20 genera (…) distributed from Japan, China, and India to Australia, Africa, and South America” (Dowling & Pinou, 2004: 20). Although the reader is referred to a “Table 1” that apparently lists these genera, no such table exists in the published paper. However, at least some of the genera they mention as xenodermatids (*Mehelya*, *Pseudaspis*, *Xenopholis*) are shown in other works to have phylogenetic affinities elsewhere. We expect Xenodermatidae will ultimately prove to be a much more restricted clade than conceived by Dowling & Pinou (2004). Vidal et al. (2007) erected a superfamily Xenodermatoidea including only the family Xenodermatidae, so these terms carry redundant information.

**FAMILY PAREATIDAE** Romer, 1956

(Pareinae Romer, 1956: 583.)

Type-genus: *Pareas* Wagler, 1830.

**Diagnosis:** (100%, 21). Preorbital portion of maxilla reduced (Cundall & Irish 2008); anterior part of the maxilla edentulous; teeth long and narrow; pterygoids not articulating with the quadrates or mandibles (Brongersma 1956, 1958); muscle levator anguli oris inserting directly on the infralabial gland and acting as a compressor glandulae (Haas 1938, Zaher 1999); hemipenes deeply bilobed and with an unusual ring of tissue encircling each lobe (Zaher, 1999).

**Content:** *Aplopeltura* Duméril, 1853; *Asthenodipsas* Peters, 1864; *Pareas* Wagler, 1830.

Comments: Some of the morphological characters of the jaw apparatus are convergent between Pareatidae and Dipsadini (Brongersma 1956, 1958; Peters 1960), probably because many synapomorphies of both groups are associated with a specialized diet of gastropods. Vidal et al. (2007) erected a superfamily Pareatoidea including only the family Pareatidae, so these terms carry redundant information.

**ENDOGLYPTODONTA, new taxon**

(Clade 5)

**Etymology:** Endo- (Greek, “within, inside”) + Glyptos- (Greek, “carved”) + Odontos (Greek, “tooth”), in reference to the sulcate maxillary teeth.

**Diagnosis:** (98%, 4). This clade is supported by a single putative morphological synapomorphy: sulcate maxillary dentition.

**Content:** Endoglyptodonta *new taxon* is a monophyletic group composed of Viperidae Laurenti, 1768, Homalopsidae Bonaparte 1845, Elapoidea Boie 1827, and Colubroidea Oppel 1811 (Clade 5).
Comments: A sulcate maxillary dentition is present unambiguously in the two most basal groups of Endoglyptodonta (Viperidae and Homalopsidae); it reverses in several less inclusive lineages (e.g., Colubridae, Natricidae, Lamprophiidae, several Pseudoxyrhophiidae and within Dipsadidae).

FAMILY VIPERIDAE Oppel, 1811
(Clade 6)

Viperini Oppel, 1811: 50.

Type-genus: Vipera Laurenti, 1768.

Diagnosis: (100%, 11). Maxilla extremely shortened and bearing a single tooth; tooth modified into a fang with a central hollow canal (McDowell, 1987); well-differentiated venom gland with a large central lumen; secretory tubules of venom gland developing from the posterior portion of the gland primordium; accessory mucous gland located anteriorly on the venom duct; part of muscle adductor mandibulae externus medialis, pars posterior, acting as the compressor of the veno gland (Haas, 1938, 1962; Kochva, 1963, 1978; Zaher, 1994a); presence of well-developed, strongly anterovertrally directed (anteriorly directed in Causes), paraphyseal processes on the vertebrae; calyces present on the hemipenial lobes.

Content: Adenorhinos Marx & Rabb, 1965; Agkistrodon Palisot de Beauvois, 1799; Atheris Cope, 1862; Atropoides Werman, 1992; Azemiops Boulenger, 1888; Bitis Gray, 1842; Bothriechis Peters, 1859; Bothriopsis Peters, 1861; Bothrocophias Guberlet & Campbell, 2001; Bothrops Wagler (in Spix), 1824; Calloselasma Cope, 1860; Causus Wagler, 1830; Cerastes Laurenti, 1768; Cerrophidion Campbell & Lamar, 1992; Crotalus Linnaeus, 1758; Cryptelytrops Cope, 1860; Daboia Gray, 1842; Deinagkistrodon Gloyd, 1979; Echis Merrem, 1820; Eristicophis Alcock (in Alcock & Finn), 1896; Garthius Malhotra & Thorpe, 2004; Gloydius Hoge and Romano-Hoge, 1981; Himalayophis Malhotra & Thorpe, 2004; Hypnale Fitzinger, 1843; Lachesis Daudin, 1803; Macrovipera Reuss, 1927; Montatheris Broadley 1996; Ophryacus Cope, 1887; Ovophis Burger (in Hoge and Romano-Hoge), 1981; Parias Gray, 1849; Peltopelor Günther, 1864; Popeia Malhotra & Thorpe 2004; Porthidiun Cope, 1871; Proatheris Broadley 1996; Protobothrops Hoge & Romano-Hoge, 1983; Pseudocerastes Boulenger, 1896; Sistrurus Garman, 1884; Triceratolepidophis Ziegler, Herrmann, David, Orlov & Plauvels 2000; Trimeresurus Lacépède, 1804; Tropidolaemus Wagler, 1830; Vipera Laurenti, 1768; Viridovipera Malhotra & Thorpe, 2004; Zhaeremia Gumprecht & Tillack, 2004.

Comments: The monophyly of the family Viperidae has never been seriously questioned. Well-developed, strongly anterovertrally directed, paraphyseal processes on the vertebrae are also present in Natricidae (Auffenberg, 1963; Zaher, 1999). Calyces have been independently derived in Colubroidea.

Intra-viperid relationships have been studied by numerous workers and we have little to add to these other works given our deliberate de-emphasis on this group other than its placement broadly within Caenophidia. Because the relationships of New and Old World vipers are under active investigation, we expect revisions to the taxonomy to proceed apace. A recent checklist (McDiarmid et al., 1999) recognized four subfamilies: Causinae (Causus only), Azemiopinae (Azemiops only), Crotalinae (pitvipers), and Viperinae (Old World pitless vipers). Subclades within the last two subfamilies have been recognized as tribes. Comprehensive summaries and reviews of some of this literature can be found in McDiarmid et al. (1999), Schuett et al. (2002), and Thorpe et al. (1997).

The rattlesnakes, Crotalus and Sistrurus, recently underwent a taxonomic revision by Hoser (2009). Hoser largely used the molecular phylogeny of Murphy et al. (2002) to resurrect older names from synonyms and designate a number of new genera and subgenera. In doing so, he recognized nine genera including three new genera. Some taxonomic arrangements are certainly in error. For example, genus Cammingea Hoser 2009 contains three species, none of which have been included in a phylogenetic study and at least one of which we now know is incorrectly placed in this group (Murphy, unpublished data). Bryson, Murphy et al. (unpublished data) have DNA sequence data for several hundred specimens of the triseriatus complex of Klauber (1972); the phylogenetic relationships among these taxa changed substantially as a consequence of far greater sampling. Hoser placed Sistrurus raui in a new monotypic genus and thus obscured its phylogenetic relationships. Until a well-supported phylogeny is obtained, we recommend against recognizing Hoser’s new taxonomy.

FAMILY HOMALOPSIDAE Bonaparte, 1845
(Clade 8)

Homalopsina Bonaparte, 1845.
Type-genus: *Homalopsis* Kuhl & van Hasselt, 1822.

Diagnosis: (100%, 23). Synapomorphies include: viviparity; external nares and eyes located dorsally on the snout and head, respectively; nostril closure by narial muscles in combination with swelling of cavernous tissue in the nasal chamber (Santos-Costa & Hofstadler-Deiques, 2002); glottis and choanal folds modified for subaquatic breathing; and hemipenial lobes covered with minute, densely arranged spinules (Zaher, 1999).

Content: *Bitia* Gray, 1842; *Brachyorrhos* Kuhl (in Schlegel), 1826; *Cantoria* Girard, 1857; *Cerberus* Cuvier, 1829; *Enhydris* Latreille (in Sonnini & Latreille), 1801; *Erpeton* Lacépède, 1800; *Fordonia* Gray, 1842; *Gerarda* Gray, 1849; *Heurnia* de Jong, 1926; *Homalopsis* Kuhl & van Hasselt, 1822; *Myron* Gray, 1849.

Comments: The level of generality of the character “viviparity” is unclear, as it has evolved repeatedly among snakes (Blackburn, 1985) and is present widely in the immediate outgroup to endoglyptodonts (Viperidae). The derived hemipenial feature cited herein as a synapomorphy of the family Homalopsidae is also homoplasically present in several Madagascan genera (Zaher, 1999; Cadle, 1996). Vidal et al. (2007) erected a superfamily Homalopsoidea including only the family Homalopsidae, so these terms carry redundant information. We follow McDowell (1987) in including *Brachyorrhos* Kuhl (in Schlegel), 1826 in the homalopsids.

SUPERFAMILY ELAPOIDEA Boie, 1827
(Clade 10)

Diagnosis: (85%, 2). No known morphological synapomorphy.


Comments: The name Elapoidea was used by Pinou et al. (2004) for a clade comprising *Atractaspis* + Elapidae. Subsequently, the name has been applied to a clade first identified by Lawson et al. (2005; their “clade A”) including Psammophiidae + Elapidae + Atractaspidae + Lamprophiidae (Vidal et al., 2007, 2008; Kelly et al., 2009; this study). The monophyly of the Elapoidea is currently supported exclusively by molecular data and further inquiry on its composition is needed. Most especially, the position of the Psammophiidae is unstable and might render the Elapoidea, as presently understood, parapleletic. We tentatively maintain Elapoidea in the present classification, pending further testing, and we include several genera *incertae sedis* because of conflicting or ambiguous phylogenetic placements in various studies. Genera considered as Elapoidea *incertae sedis* are as follow (see also discussion above): *Buhoma* Ziegler, Vences, Glaw & Bohme, 1997; *Oxyrhabdium* Boulenger, 1893; *Prosymna* Gray, 1849; *Psammodyastes* Günther, 1858; *Pseudaspis* Fitzinger, 1843; *Pythonodipsas* Günther, 1868.

FAMILY PSAMMOPHIIDAE Bonaparte, 1845
(Clade 11)

Psammophiidae Bonaparte, 1845:5.

Type-genus: *Psammophis* H. Boie (in Fitzinger), 1826.

Diagnosis: (100%, 19). Hemipenes extremely reduced, threadlike (Bogert, 1940); sulcus spermaticus undivided and in centrolineal orientation; differentiated maxillary and mandibular dentition (Bogert, 1940; Bourgeois, 1968); loss of hypapophyses on posterior trunk vertebrae.

Content: *Dipsina* Jan, 1863; *Hemirhabdus* Boettger, 1893; *Malpolon* Fitzinger, 1826; *Mimophis* Günther, 1868; *Psammophis* H. Boie (in Fitzinger), 1826; *Psammodylox* Fitzinger, 1843; *Rhamphiophis* Peters, 1854.

Comments: *Dromophis* Peters, 1869 was recently synonymized with *Psammophis* (Kelly et al., 2008). Hypapophyses have been lost repeatedly in the evolution of caenophidians but all immediate outgroups to Psammophiidae retain them on the posterior trunk vertebrae. De Haan (1982, 2003a,b) identified some peculiarities in the infralabial glands associated with a rubbing (“polishing”) behavior in *Dromophis, Malpolon, Mimophis*, and *Psammophis*, as well as parietal pits (perhaps sensory in nature) in the same genera (see also Steehouder, 1984). If these features are discovered more generally in psammophiids, they may provide additional morphological and behavioral corroboraton for the monophyly of this clade.

FAMILY ELAPIDAE Boie, 1827
(Clade 13)

Elapidae Boie, 1827: 510.
**Type-genus:** Elaps Schneider, 1801.

**Diagnosis:** (98%, 9). Maxilla bearing an enlarged anterior tooth modified into a hollow fang (proteroglyphous maxillary dentition), venom gland with a central lumen; accessory mucous gland elongated and surrounding the venom duct; venom gland compressor divided and derived from the superficial external adductor muscle (Kochva & Wollberg, 1970; McCarthy, 1985; Underwood & Kochva, 1993; Zaher, 1994a, 1999).

**Content:** Acalyptophis Boulenger, 1896; Acanthophis Daudin, 1803; Aipysurus Lacépède, 1804; Apistocala mus Boulenger, 1898; Aspidelaps Fitzinger, 1843; Aspidomorphus Fitzinger, 1843; Astrotia Fischer, 1855; Austrelaps Worrel, 1963; Boulengerina Dollo,1886; Bunyurus Daudin, 1803; Cacophis Günther, 1863; Calliophis Gray, 1835; Demansia Gray (in Gray), 1842; Dendroaspis Schlegel, 1848; Denisonia Krefft, 1869; Distere Lacépède, 1804; Drysdalia Worrel, 1961; Echiopsis Fitzinger, 1843; Elapognathus Bou lenger, 1896; Elapooidea Bocage, 1866; Enydocophalus Krefft, 1869; Enhydrina Gray, 1849; Épalophilis Smith, 1931; Furina Duméril, 1853; Hemachatus Fleming, 1822; Hemispis Fitzinger, 1861; Hemit bungarus Peters, 1862; Hoplocephalus Wagler, 1830; Hydrelaps Boulenger, 1896; Hydrophis Lateulle (in Sonnini & Latreille), 1801; Kerilia Gray, 1849; Kol pophis Smith, 1926; Lapemis Gray, 1835; Laticauda Laurenti, 1768; Loveridgelaps McDowell, 1970; Macicora Gray, 1835; Micropechis Boulenger, 1896; Micruroides Schmidt, 1928; Micurus Wagler (in Spix), 1824; Naja Laurenti, 1768; Narophis Worrel, 1961; Neelaps Günther, 1863; Notechis Boulenger, 1896; Ognodon Peters, 1864; Ophiopagus Günther, 1864; Ox yuranus Kinghorn, 1923; Parademansia Kinghorn, 1955; Parahydrophis Burger & Natsumo, 1974; Parana bia Loveridge, 1944; Parapistocalamus Roux, 1934; Pelamis Daudin, 1803; Polyodontognathus Wall, 1921; Praescutata Wall, 1921; Pseudechis Wagler, 1830; Pseu dohaje Günther, 1858; Pseudolaticauda Kharin 1984; Pseudonaja Günther, 1858; Rhinopocephalus Müller, 1885; Salomonelaps McDowell, 1970; Simoselaps Jan, 1859; Sinomicrourus Slowinski, Boundy & Lawson 2001; Smithohydrophis Kharin, 1981; Suta Worrel, 1961; Thalassophis Schmidt, 1852; Toxicocalamus Boulenger, 1896; Tropidechis Günther, 1863; Uenechis Worrel, 1961; Vernicella Gray (in Günther), 1858; Walterinnesia Lataste, 1887.

Comments: Molecular studies demonstrate the monophyly of marine elapids + Australopapuan terrestrial elapids + some Melanesian elapids, all of which were referred to the Hydrophiinae by Keogh (1998) and Keogh et al. (1998). The remaining African, Asian, and American elapids are a series of clades basal to this monophyletic group (see Keogh 1998). Interrelationships within the elapid radiation still needs to be clarified and, apart from Hydrophiinae, we refrain here to recognize a formal hierarchical taxonomy for subgroups within this family.

Lawson et al. (2005) greatly expanded the Elapidae to include Atractaspidae, “Boodontinae” (=Lamprophiidae), Pammorphiinae, Pseudoxylrhophiinae, and Xenodermatinae; this group is roughly equivalent to Elapoidea herein (with removal of Xenodermatidae). Elapid relationships are under active investigation and recent work is summarized by Castoe et al. (2007), Keogh (1998), Keogh et al. (1998), and Sowinski & Keogh (2000).

**FAMILY ATRACTASPIDIDAE Günther, 1858**  
(Clade 15)

Atractaspidae Günther, 1858: 239.

**Type-genus:** Atractaspis A. Smith, 1849.

**Diagnosis:** (84%, 6). Spines of the hemipenial lobes connected basally by tissue, forming flounce-like structures surrounding the lobes.

**Content:** Amblyodipsas Peters, 1857; Aparallactus A. Smith, 1849; Atractaspis A. Smith, 1849; Brachyophis Mocquard, 1888; Chilorhinophis Werner, 1907; Elapopus Jan, 1862; Homoroselaps Jan, 1858; Hypotophis Bouleger, 1908; Macrelaps Boulenger, 1896; Micrelaps Boettger, 1880; Polemon Jan, 1858; Xenocalamus Günther, 1868.

Comments: Spinulate flouc-like structures have been confirmed only in Polemon, Macrelaps, Amblyodipsas, and most Aparallactus (not present in Atractaspis fallax); they are yet to be confirmed in the other genera. This character is also present in Pammorphinae, which has been shown to be closely related to the Atractaspidae in one molecular phylogenetic study (Lawson et al., 2005). A similar character exists in some Lamprophiidae, but in this case the flounces extend to the hemipenial body. The atractaspid hemipenis differs from the lamprophiid hemipenis by the condition of the sulcus spermaticus (centripetal in the former and centrifugal in the latter).
The content and relationships of Atractaspidae has been among the most controversial of any clade within advanced snakes (for reviews, see Cadle, 1988, and Underwood & Kochva, 1993), and we recognize its composition here primarily as one of convenience and historical legacy. The hemipenial synapomorphies we list have appeared in very similar form elsewhere within caenophidians. Furthermore, most of the morphological characters adduced for this group (e.g., Underwood & Kochva, 1993) are in reality only found in particular subsets of taxa within it. Even the derived venom apparatuses of two of the included taxa (Atractaspis and Homoroselaps) show trencant differences that are difficult to reconcile with one another and with those of less-derived members of the assemblage.

FAMILY LAMPROPHIIDAE Fitzinger, 1843
(Clade 16)

Diagnosis: (74%, 1). Sulcus spermaticus centrifugal and dividing on the mid-region of the hemipenial body (Zaher, 1999).

Content: Lamprophiinae Fitzinger, 1843; Pseudoxyrhophiinae, Dowling, 1975.

Comments: Although it has a poor bootstrap and Bremer support, this clade is diagnosed by a significant hemipenial feature. Our clade 16 has also been retrieved again with poor support by Vidal et al. (2008). Alternatively, Kelly et al. (2009) retrieved a poorly supported clade that includes pseudoxyrhophiines and psammophiids.

SUBFAMILY LAMPROPHIINAE Fitzinger, 1843
(Clade 17)

Lamprophis Fitzinger, 1843: 25

Type-genus: Lamprophis Fitzinger 1843.

Diagnosis: (94%, 3). Spines of the hemipenial body arrayed in transverse rows connected basally by tissue, forming spinulate flounce-like structures (less developed in some taxa such as Bothrolycus) (Zaher, 1999).

Content: Bothrolycus Günther, 1874; Bothroptalmus Peters, 1863; Chamaelycus Bou勒enger, 1919; Dendrolycus Laurent, 1956; Genionotophis Bou勒enger, 1893; Hormonotus Hallowell, 1857; Lamprophis Fitzinger, 1843; Lycodonomorphus Fitzinger, 1843; Lycophidion Fitzinger, 1843; Mehelya Csiki, 1903; Pseudoboodon Peracca, 1897.

Comments: Spinulate flounce-like structures are also present on the hemipenial lobes of some atractaspidid genera (Zaher, 1999), and might represent a synapomorphy uniting this family with the Lamprophiinae. However, flounce-like spinulate structures on the hemipenial body are unique to the Lamprophiinae.

SUBFAMILY PSEUDOXYRHOPHIIINAE Dowling, 1975
(Clade 18)

Type-genus: Pseudoxyrhopus Günther, 1881.

Diagnosis: (96%, 8). Spines reduced to spinules on the hemipenial lobes (Zaher, 1999).

Content: Alluaudina Mocquard, 1894; Amplorhinus A. Smith, 1847; Bryophis Domergue & Bour, 1989; Compsophis Mocquard, 1894; Dityphops Günther, 1881; Dromicodryas Bou勒enger, 1893; Duberria Fitzinger, 1826; Exallodontophis Cadle, 1999; Heteroliodon Boettger, 1913; Ichthyophis Günther, 1873; Langaha Bonnaterre, 1790; Leioheterodon Jan, 1863; Liophidium Bou勒enger, 1896; Liopholidophis Mocquard, 1904; Lycoðryas Günther, 1879; Madagascarophis Mertens, 1952; Micropisthodon Mocquard, 1894; Montaspis Bourquin 1991; Pararhadinaea Boettger, 1898; Pseudoxyrhopus Günther, 1881; Stenophis Bou勒enger, 1896; Thamnosophis Jan, 1863.

Comments: The hemipenial synapomorphy of Pseudoxyrhophiinae is also present homoplastically in Homalopsidae. Geodipsas Bou勒enger, 1896 was placed in the synonymy of Compsophis by Glaw et al. (2007a). Bibilibava Glaw, Nagy, Franzen & Vences, 2007 was synonymized with Thamnosophis (Cadle & Ineich, 2008). The broader phylogenetic analyses of Lawson et al. (2005) and Kelly et al. (2009) demonstrated convincingly that Duberria and Amplorhinus were more closely related to the Pseudoxyrhophiinae than to any other elapid or colubroid lineage; a similar relationship of Amplorhinus (but not Duberria) to pseudoxyrhophiids was previously suggested by Cadle (1994). Bourquin (1991) suggested, on the basis of skull morphology, that Montaspis is closely related to the Pseudoxyrhothiidae. We recognize both Stenophis and Lycodyras
as valid, but the systematics of these snakes needs revision (Cadle, 2003: 1000-1001); furthermore, Kelly et al. (2009) found that the two species of Stenophis they examined were not monophyletic relative to other pseudoxyrhophids. Species and generic level taxonomy of pseudoxyrhophids needs more research.

SUPERFAMILY COLUBROIDEA Oppel, 1811
(Clade 19)

Diagnosis: (98%, 10). Colubroids can be diagnosed by the presence of well-developed calyces present on the hemipenial lobes, a centrifugal sulcus spermaticus that divides on the proximal or central region of the hemipenial body and an aglyphous dentition.

Content: Calamariidae Bonaparte, 1838; Colubridae Oppel, 1811; Pseudoxenodontidae McDowell, 1987; Natricidae Bonaparte, 1838; Dipsadidae Bonaparte, 1838.

Comments: Zaher (1999) discussed the variation regarding the sulcus spermaticus in colubroid snakes. Well-developed calyces on the hemipenial lobes are considered to be lost secondarily by the Natricidae. See above discussion on the new use of this name.

Family Calamariidae Bonaparte, 1838
(terminal taxon: Calamaria yunnanensis-pavimentata)

Calamaria Bonaparte, 1838: 392.

Type-genus: Calamaria H. Boie (in F. Boie), 1826.

Diagnosis: Frontals and sphenoid forming ventral border of the optic foramen (excluding entirely, or nearly so, the parietales); hemipenial body nude; hemipenial body bearing a pair of longitudinal ridges (Zaher, 1999).

Content: Calamaria H. Boie (in F. Boie), 1826; Calamorhabdium Boettger, 1898; Collorhabdium Smedley, 1932; Eberidgeum Wallach, 1988; Macrocalamus Günther, 1864; Pseudorabdion Jan, 1862; Rabdion Duméril, 1853.

FAMILY COLUBRIDAE Oppel, 1811
(Clade 21)

Colubrini Oppel, 1811:50.

Type-genus: Coluber Linnaeus, 1758.

Diagnosis: (97%, 7). Sulcus spermaticus simple, derived from the right branch of a primitively divided sulcus (see Comments).

Content: Aeluroglena Boulenger, 1898; Abacetulla Link, 1807; Argyrogena Werner, 1924; Arizona Kennicott (in Baird), 1859; Bogertopis Dowling and Price, 1988; Boiga Fitzinger, 1826; Cenophora Cope, 1860; Chilomeniscus Cope, 1860; Chionactis Cope, 1860; Chironius Fitzinger, 1826; Chrysopelea H. Boie (in Schlegel), 1826; Coelognathus Fitzinger, 1843; Coluber Linnaeus, 1758; Conopsis Günther, 1858; Coronella Laurenti, 1768; Crotaphopeltis Fitzinger, 1843; Cryptophidion Wallach and Jon 1992; Cyclophiops Boulenger, 1888; Dasyptelis Wagler, 1830; Dendrelaphis Boulenger, 1890; Dendrophidion Fitzinger, 1843; Dinodon Duméril, Bibron & Duméril, 1854; Dipsadoboa Günther, 1858; Dispholidus Duvernoy, 1832; Drymarchon Fitzinger, 1843; Drymobius Fitzinger, 1843; Drymoluber Amaral, 1930; Dryocalamus Günther, 1858; Dryophiops Boulenger, 1896; Eirenis Jan, 1863; Elachistodon Reinhardt, 1863; Elapho Fitzinger (in Wagler), 1833; Euprepiophis Fitzinger, 1843; Ficinia Gray, 1849; Gastrophis Cope, 1861; Geogras Cope, 1875; Gonyophis Boulenger, 1891; Gonyosoma Wagler, 1828; Gyalopion Cope, 1860; Hapsidophrys Fischer, 1856; Hemerophis Schätti & Utiger, 2001; Hemorrhois F. Boie, 1826; Hierophis Fitzinger (in Bonaparte), 1834; Lampropeltis Fitzinger, 1843; Leptodrymus Amaral, 1927; Leptophis Bell, 1825; Lepturopsis Boulenger, 1900; Liochlorophis Oldham & Smith, 1991; Liopeltis Fitzinger, 1843; Lyodon Boie (in Fitzinger), 1826; Lytorhynchus Peters, 1862; Macroprotodon Duméril & Bibron (in Guichenot), 1850; Maculophilus Burbrink & Lawson, 1997; Masticophis Baird (in Baird & Girard), 1853; Mastigodryas Amaral, 1934; Mezodon Fischer, 1856; Oligodon H. Boie (in Fitzinger), 1826; Oocatochus Helfenberger, 2001; Opheodrys Fitzinger, 1843; Oreocryptophis Utiger, Schätti & Helfenberger, 2005; Oreophis Utiger, Helfenberger, Schätti, Schmidt, Ruf & Ziswiler, 2002; Orthriophis Utiger, Helfenberger, Schätti, Schmidt, Ruf & Ziswiler, 2002; Oxybelis Wagler, 1830; Pantherophis Fitzinger, 1843; Philothamnus A. Smith, 1847; Phyllorhynchos Stejneger, 1890; Pituophis Holbrook, 1842; Platycercus Blyth, 1860; Pseudelaphe Mertens & Rosenberg, 1943; Pseudocyclophis Boettger, 1888; Pseudoficimia Bocourt, 1883; Pseustes Fitzinger, 1843; Ptyas Fitzinger, 1843; Rhannophis Günther, 1862; Rhinechis Michahelles, 1833; Rhinobothryum Wagler, 1830;

Diagnosis: Hemipenis deeply bilobed, with each lobe separately calculate on the distal half and nude on the medial half; fringes of large papillae separating the nude region from the calculate area (Zaher, 1999).

Comments: He et al. (2009) demonstrated that Pliopelis is indeed closely related to Pseudoxenodon.

FAMILY NATRICIDAE Bonaparte, 1838 (Clade 24)

Natrix Bonaparte, 1838: 392.

Type-genus: Natrix Laurenti, 1768.

Diagnosis: (89%, 12). Sulcus spermaticus single and highly centripetal, forming a nude region on the medial surfaces of the hemipenial lobes; hemipenial calyces absent (evolutionary loss).

Comments: Among Natricidae, the New World natricids are a monophyletic tribe (Thamnophiini) supported by molecular and morphological evidence (Rossman & Eberle 1977; Alfaro & Arnold 2001; De Queiroz et al. 2002). Relationships among African and Eurasian species are largely unresolved. See Comments under Colubridae concerning differences between the simple sulci spermatici of natricids and colubrids.

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Rhinocelis Girard (in Baird & Girard), 1853; Rhynchochelamus Günther, 1864; Rhynchophis Mocquard, 1897; Salvadora Baird (in Baird & Girard), 1853; Scaphiodontophis Taylor & Smith, 1943; Scaphiophis Peters, 1870; Scolecopis Fitzinger, 1843; Senticolis Dowling & Fries, 1987; Sibynophis Fitzinger, 1843; Simophis Peters, 1860; Sonora Girard (in Baird & Girard), 1853; Spalerosophis Jan (in De Filippi), 1865; Spilotes Wagler, 1830; Stegtonotus DuméRIL, Bibron & DuméRIL, 1854; Stenorrhina DuméRIL, 1853; StilooSoma Brown, 1890; Symphimus Cope, 1870; Sympholis Cope, 1862; Tantilla Girard (in Baird & Girard), 1853; Tantillita Smith, 1941; Telescopus Wagler, 1830; Thelotornis A. SMith, 1849; Thrasops Hallowell, 1857; Toxicodryas Hallowell 1857; Trimorphodon Cope, 1861; Xenelaphis Günther, 1864; Xyelodontophis Broadley & Wallach 2002; Zamenis Bonaparte, 1838; Zaocsys Cope, 1861.

Comments: Use of the name “Colubridae” for this clade is a much more restricted use of this name than its long-standing use in the literature on caenophidian systematics, in which “Colubridae” generally referred to all caenophidians that were not acrochordids, elapids, or vipersids. The single sulcus spermaticus of colubrids and natricids is considered to have derived from a centrifugally divided sulcus, but in different ways in the two groups (McDowell 1961). On unilobed organs of colubrids the sulcus extends centrolineally to the distal end of the hemipenis, whereas on some distally bilobed organs the sulcus always extends to the right lobe. On the other hand, in natricids when the sulcus extends to only one of the lobes of a bilobed organ, it is always to the left lobe (see also Rossman & Eberle, 1977; and Zaher, 1999: 25-26). Lawson et al. (2005) have shown that Macroprotodon lies within the family Colubridae, but without clear affinities within that group. The phylogenetic affinities of Scaphiophis Peters, 1870 has been disputed (Zaher, 1999; Vidal et al., 2008). Recently, Kelly et al. (2008) included the genus in their molecular analysis, in which it appears nested within colubrines. For this reason, we include this genus in the family Colubridae.

FAMILY PSEUDOXENODONTIDAE

McDowell, 1987

(terminal taxon: Pseudoxenodon karlschmidtii)


Type-genus: Pseudoxenodon Boulenger, 1890.
FAMILY DIPSADIDAE Bonaparte, 1838  
(Class 25)

**Diagnosis:** (*, 9). A row of enlarged lateral spines on each side of the hemipenis; hemipenial lobes with distinct differentially ornamented regions (a sulcate capitulum and an asulcate nude or weakly calyculate region) (Zaher, 1999).

**Content:** Dipsadinae Bonaparte 1838, Carphophiinae new subfamily, and Xenodontinae Bonaparte 1845.

**Comments:** The diagnosis we give here for Dipsadidae includes those synapomorphies previously considered for the more restricted group Xenodontinae (sensu Zaher, 1999). We present them here for Dipsadidae because the North American *Farancia* and *Heterodon* also have these characters. Thus, these characters could have separately evolved in *Farancia* and *Heterodon*, and South American xenodontines (with subsequent loss in *Carphophis*, *Contia*, and *Diadophis*); or, the interpretation we adopt here, the characters could be synapomorphic at the level of Dipsadidae, with subsequent transformations (losses) in the clade including *Carphophis*, *Contia*, and *Diadophis* on one hand, and in Dipsadinae on the other. This question must be resolved with further research. In any case, we note that there is evidence from the present study and from the immunological comparisons of Cadle (1984a,b,c) for three major clades within the Dipsadidae as we conceive it, namely a North American clade, a Dipsadinae clade, and a Xenodontinae clade (see also Pinou et al., 2004). However, Pinou et al. (2004) found the North American xenodontines (their North American relicts) paraphyletic with respect to dipsadines, xenodontines, and natricids. The monophyly of the North American xenodontines was also unstable in the present analysis, with a low bootstrap support on Clades 23, 25, and 30 due to the variable positions of *Heterodon* and *Farancia* with respect to these nodes in suboptimal trees. Thus, further revisions on that issue may be warranted. On the other hand, *Carphophis*, *Contia*, and *Diadophis* form a well-supported clade (Clade 29; 88%, 4) corroborated by putative hemipenial synapomorphies. Those synapomorphies also support the clade Dipsadinae (Clade 31; 74%, 7) and are here viewed as having evolved homoplastically in these two groups. The optimization of these characters on the tree depends on a better understanding of the position of *Heterodon* and *Farancia* that are here included in Dipsadidae incertae sedis.

The genus *Xenopholis* Peters, 1869, not included in the present analysis, has been recently associated with the Xenodermatidae by Dowling & Pinou (2003). However, its dipsadid hemipenial morphology, the presence of a well-developed septomaxillary-frontal articulation, and previous immunological studies do not support the latter hypothesis (Cadle, 1984a), suggesting dipsadid affinities instead (see also discussion above in Xenodermatidae). Since the position of *Xenopholis* within the Dipsadidae is still unknown, we opted to include it in the family as incertae sedis, but we have no reservations at all about its placement within this group. We also assume, following Zaher (1999), that the other Neotropical genera *Crisantophis*, *Diaphorolepis*, *Emmochliophis*, *Enulophis*, *Enulius*, *Hydromorphus*, *Nothopsis*, *Rhadinophanes Synophis*, and *Tantalophis* which have a dipsadid hemipenial morphology, belong within Dipsadidae, and we place them here incertae sedis.

Guo et al. (2009) and He et al. (2009) have shown convincingly that the genus *Thermophis* Malnate, 1953 is more closely related to the Dipsadidae than it is to any other colubroid clade. However, a more thorough analysis of the phylogenetic affinities of *Thermophis* is still needed in order to clearly place this genus in respect to the Dipsadidae. Meanwhile, we include *Thermophis* Malnate, 1953 in the Dipsadidae as incertae sedis. Finally, the poorly known genera *Cercophis*, *Lioboterophis*, *Sordellina*, and *Uromacerina* that present a dipsadid hemipenial morphology and were considered by Zaher (1999) as being Xenodontinae incertae sedis are here included in the Dipsadidae incertae sedis.

**Dipsadidae incertae sedis:** *Cercophis* Fitzinger, 1843; *Crisantophis* Villa, 1971; *Diaphorolepis* Jan, 1863; *Emmochliophis* Fritts & Smith, 1969; *Enulophis* McCranie & Villa, 1971; *Enulius* Cope, 1871; *Farancia* Gray, 1842; *Heterodon* Latreille (in Sonnini & Latreille), 1801; *Hydromorphus* Peters, 1859; *Lioboterophis* Amaral, 1934; *Nothopsis* Cope, 1871; *Rhadinophanes* Myers & Campbell, 1981; *Sordellina* Procter, 1923; *Synophis* Peracca, 1896; *Tantalophis* Duellman, 1958; *Thermophis* Malnate, 1953; *Uromacerina* Amaral, 1930; *Xenopholis* Peters, 1869.

**SUBFAMILY CARPHOPHIINAE new subfamily**  
(Class 29)

**Diagnosis:** (88%, 4). Hemipenes slightly bilobed to unilobed and noncapitate; sulcus spermaticus dividing distally, within the capitulum (Myers, 1974; Cadle, 1984b; Zaher, 1999).
Content: *Carphophis* Gervais (in D’Orbigny), 1843 (type-genus of the subfamily); *Contia* Girard (in Baird & Girard), 1853; *Diadophis* Girard (in Baird & Girard), 1853.

Comments: Because *Carphophis*, *Contia* and *Diadophis* form a strongly supported clade that is also corroborated by derived hemipenial evidence, we here include them in a new subfamily Carphophiinae. Whether *Farancia* and *Heterodon* belong to this subfamily is a question that needs further investigation (see also comments under Dipsadidae). The hemipenial morphology of Carphophiinae **new subfamily** resembles the one of Dipsadinae, but differs in an important detail, namely the lack of capitation on the lobes.

For the sake of stability of the shark family name Heterodontidae Gray, 1851, the name Heterodontinae Bonaparte, 1845, used by Vidal et al. (2007) for the North American xenodontines (including *Heterodon* and *Farancia*), should be avoided (Rossman & Wilson, 1964).

**SUBFAMILY DIPSADINAE** Bonaparte, 1838

(Clade 31)

Dipsadina Bonaparte, 1838: 392.

Type-genus: *Dipsas* Laurenti, 1768.

Diagnosis: (74%, 7). Hemipenes unilobed or with strongly reduced bilobation; hemipenes unicapitate; sulcus spermaticus dividing distally, either at the base of, or within, the capitulum (Myers, 1974; Cadle, 1984b; Zaher, 1999).

Content: *Adelphicos* Jan, 1862; *Amastridium* Cope, 1861; *Atractus* Wagler, 1828; *Chapinophis* Campbell & Smith, 1998; *Chersodromus* Reinhardt, 1860; *Coniophanes* Hallowell (in Cope), 1860; *Cryptophis* Bogert & Duellman, 1963; *Dipsas* Laurenti, 1768; *Eridiphas* Leviton & Tanneker, 1960; *Geophis* Wagler, 1830; *Hypsiglena* Cope, 1860; *Imantodes* Duméril, 1853; *Leptodeira* Fitzinger, 1843; *Ninia* Girard (in Baird & Girard), 1853; *Pleiodipsas* Harvey, Fuenmayor, Portilla & Rueda-Almonacid, 2008; *Pliocercus* Cope, 1860; *Pseudoleptodeira* Taylor, 1938; *Rhadinaea* Cope, 1863; *Sibon* Fitzinger, 1826; *Sibynomorphus* Fitzinger, 1843; *Tretanorhinus* Duméril, Bibron & Duméril, 1854; *Trimetopon* Cope, 1885; *Tropidodipsas* Günther, 1858; *Urotheca* Bibron (in de la Sagra), 1843.

Comments: Hemipenial morphology varies among this diverse group and the level of generality of the hemipenial synapomorphies we cite should be reviewed as more taxa are surveyed (see Zaher, 1999 for discussion). A simple sulcus spermaticus is present in some dipsadines as a further derived condition.

We refrain from defining tribes within Dipsadinae in the present analysis since we have sampled little of the diversity within this large group. However, there are indications from both molecular (Cadle, 1984b; Mulcahy, 2007) and morphological (Peters, 1960; Myers, 1974; Cadle, 1984b, 2007; Oliveira et al., 2008; Vidal et al., 2000) data for a monophyletic Leptodeirini including at least the genera *Leptodeira* and *Imantodes* and a monophyletic Dipsadini including at least *Dipsas*, *Sibon*, *Sibynomorphus*, and *Tropidodipsas*. However, much more work will be required to confidently resolve the relationships among the other species of this diverse group (> 200 species).

**SUBFAMILY XENODONTINAE**

Bonaparte, 1845

(Clade 34)

Diagnosis: (60%, 5). No known morphological synapomorphies.


Comments: The clade Xenodontinae (Clade 34) is here recognized tentatively, in spite of its poor measures of support (only 60% and 5) for three main reasons: 1) we still do not have a strong case with respect to the exact optimization of the hemipenial characters here associated with Dipsadidae (Clade 25, see above discussion), that might turn over to be synapomorphies of Clade 34 as suggested previously by Zaher (1999); 2) the name Xenodontinae Bonaparte, 1845 has a long standing association with this group of snakes and therefore is widely understood as such; 3) not recognizing Xenodontinae for the mainly South American xenodontine radiation would require the allocation of its constituent monophyletic subgroups to a higher taxonomic level, i.e., subfamily, thus greatly
changing the well-established taxonomic hierarchy for this group. Such reallocation might be needed in the future, although it still needs further research and clarification on the higher-level interrelationships between these parts.

Our analysis reveals very strong support for several previously known Xenodontinae tribes (Zaher, 1999): Elapomorphini (86%, 6), Tachymenini (92%, 9), Pseudoboini (99%, 21), Philodryadini (93%, 6); Hydrosini (97%, 8), Xenodontini (100%, 10), Alsophiini (89%, 4). These tribes are here formally recognized. However, except for the sister group relationship between Xenodontini and Alsophiini that shows some measure of support (69%, 4), interrelationships between well-established tribes are highly unstable, showing no significant measure of support in our analysis. We thus refrain to further comment on these nodes (Clades 37, 39, 42, 47, 49). Alsophis elegans and Liophis amarali fall in our analysis well outside their generic allocation and have been here assigned to new tribes and genera. Additionally, the genera Pseudomphis, Tropidodryas, Taeniophallus, Conophis, and Hydrodynastes are here placed in separate new tribes due to their isolated phylogenetic position in the tree, clustering only weakly with well-supported tribes for which they have no known morphological affinities. Conophis and Hydrodynastes form a monophyletic group in our analysis (Clade 51) that shows a high bootstrap (90%) but a low Bremer support (3). However, similarly to our reasoning above for the recognized tribes, we decided to allocate these two genera in separate tribes because they do not share any known morphological synapomorphy.

TRIBE SAPHENOPHIINI new tribe
(Terminal taxon: Alsophis elegans)

Diagnosis: Reduction or loss of ornamentation on the asulcate and medial surfaces of the hemipenial lobes; papillate ridge on medial surface of hemipenial lobes in a lateral-to-medial orientation from proximal to distal, and confluent proximally with the enlarged lateral spines (Zaher, 1999).

Content: Sphenophis Myers, 1973 (type-genus of the tribe); Pseudalsophis, new genus.

Comments: The papillate ridge on the hemipenial lobes in Saphenophiini is here considered non-homologous to a ridge in a similar position in Alsophiini (see below). The non-homology of the two structures is indicated by their different orientations proximal to distal. See also Comments under Pseudoboini.

Alsophis elegans is clearly set apart from the other species of the genus Alsophis in our analysis, being more closely related to the genus Pseudomphis (although with a low Bootstrap support of 71% and Bremer of 3) than to any of the West Indian xenodontine snakes. Zaher (1999) pointed out important hemipenial differences between Alsophis elegans and species of West Indian Alsophis, suggesting that its affinities would lie with the Galapagos species of xenodontines, allocated by Thomas (1997) to the genera Philodryas (P. boudensis), Alsophis (A. occidentalis, A. biseriatus), and Antillophis (A. slevini, A. steindachneri). Zaher (1999) also elevated all the subspecies of Galapagos snakes recognized by Thomas (1997) to species status. The Galapagos snakes have a hemipenial morphology that is not only closer in most respects to that of Alsophis elegans, but it also departs significantly from the hemipenial patterns shown by the West Indian species of Alsophis and the genera Philodryas and Antillophis. On the other hand, the Galapagos xenodontines and Alsophis elegans share with the Ecuadorian genus Saphenophis a characteristic hemipenial morphology (see Zaher, 1999).

Based on this hemipenial evidence and in order to render the genera Alsophis, Philodryas, and Antillophis monophyletic, we allocate Alsophis elegans and the Galapagos xenodontine species in a new genus. The Galapagos species are presently under study and will be dealt in more detail elsewhere.

Pseudalsophis new genus

Type-species: L.[Lygophis (Lygophis)] elegans Tschudi, 1845.

Etymology: Pseudo- (Greek, “false, erroneous”) + Alsophis, in allusion to the morphological similarity with Alsophis Fitzinger sensu stricto, gender masculine.

Diagnosis: Hemipenis generally deeply bilobed, bicalyculate, semicapitate, with a forked sulcus spermaticus dividing on the proximal half of the body, with branches extending centrol ineally until the base of the capitula, here it takes a centrifugal position on the lobe, ending in the distal region; intrasulcal region mostly nude, without spines; enlarged lateral spines of moderate size and numerous; capitula formed by diminutive papillate calyces and are most restricted to
the sulcate side; asulcate and medial surfaces of the lobes almost completely nude, except for the presence of a medial papillate and inflated crest or ridge that runs from the lobular crotch to the distal edge of each capitulum; vestigial body calyces along all the internal region of the lobes.

Content: *Pseudalsophis elegans* (Tschudi, 1845) new combination; *Pseudalsophis dorsalis* (Steindachner, 1876) *Pseudalsophis hoodensis* (Van Denburgh, 1912) new combination; *Pseudalsophis occidentalis* (Van Denburgh, 1912) new combination; *Pseudalsophis biserialis* (Günther, 1860) new combination; *Pseudalsophis steindachneri* (Van Denburgh, 1912) new combination; *Pseudalsophis slevini* (Van Denburgh, 1912) new combination.

**TRIBE PSOMOPHIINI** new tribe
(Clade 36)

**Diagnosis:** (100%, 36). Hemipenis bicapitate, with pseudocalyces, and with large spinulate papillae on the sulcate sides; premaxillary bone with peculiar expanded lateral flanges (Myers & Cadle, 1994).

Content: *Psomophis* Myers & Cadle, 1994 (type-genus of the tribe by monotypy).

**TRIBE ELAPOMORPHINI** Jan, 1862
(Clade 38)

Elapomorphinae Jan, 1862: 3.

**Type-genus:** *Elapomorphus* Wiegmann (in Fitzinger), 1843.

**Diagnosis:** (86%, 6). Reduced number of supralabial scales (6); nasal plate entire; frontal bones dorsally included by the antero-lateral processes of the parietal, and almost excluded from the reduced optic foramen; exoccipitals in contact on the dorsal surface of the condyle; second supralabial scale contacting the eye; AMES displaced posteriorly to reveal the Harderian gland; hypertrophied muscle retractor quadrati with an extensive insertion zone; U-shaped fronto-parietal suture; reduction or loss of the quadrato-maxillary ligament; no more than two teeth on the palatine process of the pterygoid, anteriorly to the ectopterygoid articulation; dentigerous process of the dentary short (Ferrarezi, 1993, 1994b; Savitzky, 1979; Zaher, 1994b).

Content: *Apostolepis* Cope, 1861; *Elapomorphus* Wiegmann (in Fitzinger), 1843; *Phalotris* Cope, 1862.

**TRIBE TROPIDODRYADINI** new tribe
(Terminal taxon: *Tropidodryas stiaticeps*)

**Diagnosis:** Hemipenis bicalyculate and noncapitate; calycular regions directed laterally; intrasulcal area of hemipenis with two parallel rows of enlarged spines; tip of the tail yellowish with tail-luring posture in young individuals.

Content: *Tropidodryas* Fitzinger, 1843 (type-genus of the tribe by monotypy).

Comments: See Comments under Pseudoboini.

**TRIBE TACHYMENINI** Bailey, 1967
(Clade 41)


**Type-genus:** *Tachymenis* Wiegmann, 1834.

**Diagnosis:** (92%, 9). Viviparity; male-biased sexual dimorphism in ventral scale numbers (Bailey, 1967, 1981); reduced calyces on hemipenial body; relatively distal division of the sulcus spermaticus; vertical or sub-elliptical pupil; Duvernoy's gland attached to m. adductor mandibulae externus superficialis (Franco, 1999).

Content: *Calamodontophis* Amaral, 1963; *Gomesophis* Hoge and Mertens, 1959; *Pseudotomodon* Koslowski, 1896; *Psychophis* Gomes, 1915; *Tachymenis* Wiegmann, 1834; *Thamnodynastes* Wagler, 1830; *Tomodon* Duméril (in Duméril, Bibron & Duméril), 1853.

Comments: Viviparity and male-biased sexual dimorphism have evolved repeatedly in colubroids, but are here considered derived characters of Tachymenini. These characters are otherwise rare in Xenodontinae. Ferrarezi (1994b) questioned the autorship of this Tribe, probably due to the inexistence of a formal diagnosis for the group in the Bailey’s paper (1967). However, as pointed out by Franco (1999), Bailey (1967) characterized adequately the group, justifying thus its authorship of the tribe. Bailey’s (1967) attribution of oviparity to this group is an obvious misprint, which he corrected in Bailey (1981).
TRIBE ECHINANTHERINII new tribe
(Clade 44)

Diagnosis: (66%, 2). Hemipenis unilobed and unincapitate; sulcus spermaticus divides relatively distally, within the calyculate region; large nude region present on asulcate side of the hemipenial body.

Content: Echinanthera Cope, 1894 (type-genus of the tribe); Taeniophallus Cope, 1895.

Comments: Schargel et al. (2005) recognized a close relationship between Taeniophallus and Echinanthera on the basis of hemipenial morphology. Although they concluded that Echinanthera sensu Myers & Cadle (1994) was monophyletic, and that Taeniophallus included at least one monophyletic subgroup (the affinis group of southeastern Brazil), the monophyly of Taeniophallus with respect to Echinanthera s. s. is still an open question.

TRIBE CAAEETOBIINI new tribe
(Terminal taxon: Liophis amarali)

Diagnosis: Transverse processes of premaxilla slender, and the origin of a very small, thin posteriorly directed process lateral to the vomerine processes. We are unaware of any other xenodontines that have such an additional process on the premaxilla.

Content: Caeateboia new genus (type-genus of the tribe by monotypy).

Comments: In our analysis, Liophis amarali is clearly set apart from the species of the genus Liophis, or any other genus of the tribe Xenodontini in which the genus Liophis belongs, being associated instead with the tribe Pseudoboini, although with poor statistical support (71%, 4). Indeed, Liophis amarali does not share the typical Xenodontini hemipenis, but rather has a semicapitate, semicalyculate hemipenial pattern, typical of Xenodontinae. For this reason, we erect a new genus to accommodate Liophis amarali.

Caeateboia new genus

Type-species: Liophis amarali Wettstein, 1930).

Etymology: Caa-etê- (Brazilian indigenous Tupi, “true forest”) + Boia (derived from the Tupi Mboi, “snake”), gender feminine.

TRIBE PSEUDOBOINI Bailey, 1967
(Clade 46)


Type-genus: Pseudoboa Schneider, 1801.

Diagnosis: (99%, 21). A pair of pigmented spots on the palate; posterior region of the palatine bone longer than dental process, behind vomerine process; dorsal region of the vomer with a distinct process in which the ligament of the muscle retractor vomeris is attached; distinct maxillary process of the prefrontal forming a well defined articular area; lateral (nasal) process of the prefrontal hook-like; hemipenis bicalyculate and bicapitate; large lateral spines on the lobular crests; presence of a pair of calycular pockets within the lobular crotch of the hemipenis; enlarged lateral spines of hemipenis extending onto the lobular crests; lobular crests inflated (Zaher, 1994b, 1999).

Content: Boiruna Zaher, 1996; Clelia Fitzinger, 1826; Drepanoides Dunn, 1928; Massurana new genus; Oxyrhynchus Wagler, 1830; Phimophis Cope, 1860; Pseudoboa Schneider, 1801; Rhabidels Boulenger, 1908; Siphlophis Fitzinger, 1843.

Comments: We agree with Myers & Cadle (1994) and Ferrarezzi (1994a,b) in assigning authorship of the tribe Pseudoboini to Bailey (1967) instead of Jenner in Dowling et al. (1983; see Jenner & Dowling, 1985). Although Bailey’s (1967: 157; see also Bailey
1940) use of the name “Pseudoboini” was meant to be informal (“I call informally a tribe, Pseudoboini”), he nonetheless defined the original concept of the tribe in a table on page 158 (without Saphenophis and Tropidodryas, which were included in this group by Jenner & Dowling, but which are not closely related; see Myers & Cadle, 1994, and Zaher, 1999).

Our analysis confirmed the polyphyletic nature of the genus Clelia already suggested by Zaher (1994b; 1999). We thus describe the new genus Mussurana to accommodate Clelia bicolor and two closely related species previously assigned to Clelia (Zaher, 1999).

**Mussurana new genus**

*Type-specie:* Oxyrhopus bicolor, Peracca, 1904).

*Etymology:* From Mosu- (indigenous Tupi, “eel”) + Rana (indigenous Tupi, “like or false”), gender feminine (Amaral, 1974). Mussurana or Muçurana is a very common name in Latin America, applied mostly to the dark adults of pseudoboine snakes.

*Diagnosis:* Presence of ontogenetic changes in color pattern; juveniles with a brick red color, a black longitudinal vertebral band, and an uniformly creamish venter. Adults with dorsum entirely black; Hemipenis with a unique row of larger papillae on the internal face of the lobes; postero-ventral tip of the nasal gland longer than wide; dorsal wall of Duvernoy gland reduced along all its dorsal surface (Zaher, 1994b; 1999).

*Content:* Mussurana bicolor (Peracca, 1904) new combination; Mussurana montana (Franco, Marques & Puerto, 1997) new combination; Mussurana quimi (Franco, Marques & Puerto, 1997) new combination.

**TRIBE PHILONERADINII new tribe**

*(Clade 48)*

*Diagnosis:* Presence of ontogenetic changes in color pattern; juveniles with a brick red color, a black longitudinal vertebral band, and an uniformly creamish venter. Adults with dorsum entirely black; Hemipenis with a unique row of larger papillae on the internal face of the lobes; postero-ventral tip of the nasal gland longer than wide; dorsal wall of Duvernoy gland reduced along all its dorsal surface (Zaher, 1994b; 1999).

*Content:* Mussurana bicolor (Peracca, 1904) new combination; Mussurana montana (Franco, Marques & Puerto, 1997) new combination; Mussurana quimi (Franco, Marques & Puerto, 1997) new combination.

**TRIBE HYDRODYNASTINI new tribe**

*(Clade 52)*

*Diagnosis:* Hemipenis slightly bilobed, noncapitate, and bicalyculate or semicalyculate; lobes with spinulate calyces distally and spinulate flounces proximally (Zaher, 1999).

*Content:* Hydrodynastes Fitzinger, 1843 (type-genus of the tribe); Manolepis Cope, 1885.

*Comments:* Although not present in our analysis, the genus Manolepis is included here in Conophiini due to its hemipenial similarities with Conophis (Zaher, 1999).
Comments: A similar defensive behavior has appeared in other Xenodontinae (e.g., Xenodontini; see Myers, 1986).

TRIBE HYDROPSENI Dowling, 1975 (Clade 53)

Hydropsini Dowling, 1975.

Type-genus: Hydrops Wagler, 1830.

Diagnosis: (97%, 8). Muscle adductor mandibulae externus superficialis greatly enlarged on its origin site; viviparity.

Content: Helicops Wagler, 1828; Hydrops Wagler, 1830; Pseudoeryx Fitzinger, 1826.

Comments: Roze (1957) first suggested a close relationship between Hydrops, Helicops, and Pseudoeryx. Zaher (1999) hypothesized that Helicops, Hydrops, and Pseudoeryx formed a clade belonging to his Xenodontinae sensu stricto, although the latter two genera did not present the putative hemipenial synapomorphies of Xenodontinae. Vidal et al. (2000) corroborated molecularly Zaher’s (1999) hypothesis by recovering a clade composed by Hydrops and Pseudoeryx as the sister group of Helicops. The present analysis suggests that Pseudoeryx and Hydrops represent two successive outgroups to Helicops. However, this hypothesis is not supported by any measure of support and the interrelationships of Hydropsini remains to be analyzed more thoroughly.

TRIBE XENODONTINI Bonaparte, 1845 (Clade 55)

Xenodontina Bonaparte, 1845: 377.

Type-genus: Xenodon Boie, 1826.

Diagnosis: (100%, 10). Loss of hemipenial calyces and capitular grooves; Paired nude apical disks on hemipenis; Horizontal neck flattening behavior (Myers, 1986).

Content: Liophis Wagler, 1830 (includes Erythrolamprus Boie, 1826), Lygophis Fitzinger, 1843 resurrected; Umbrivaga Roze, 1964; Xenodon Boie, 1826 (includes Lystrophis Cope, 1885 and Waglerophis Romano & Hoge, 1972).

Comments: In a morphological analysis of the group, Dixon (1980) synonymized Lygophis Fitzinger 1843, Dromicus Bibron (in de la Sagra) 1843, and Leimadophis Fitzinger 1843 with Liophis Wagler, as a way of reducing the already chaotic taxonomic situation of the group. However, new approaches using both morphological (osteology, scale microornamentation – Moura-Leite, 2001) and molecular data (the present paper) show at least in part that this position is not supported. Indeed, our phylogenetic analysis shows that the genus Liophis Wagler, 1830, represented here by L. meridionalis, L. elegansimus, L. jaegeri, L. typhlus, and L. amarali, is polyphyletic and needs to be redefined in order to recover a monophyletic status. Liophis amarali shows no close affinities to the genus Liophis or to the tribe Xenodontini (see the new tribe Caaetebobini for more details). Our results support a Xenodontini position for the other representatives of the genus Liophis. However, they form two successive sister groups (nodes 56 and 57) to a clade including the genera Xenodon, Waglerophis, and Lystrophis. The first clade (56) is formed by Liophis elegansimus (Koslowsky, 1896) and L. meridionalis (Schenkel, 1902) while the second clade (58) includes L. jaegeri ( Günther, 1858), L. typhlus (Linnæus, 1758), and Erythrolamprus aesculapii (Linnæus, 1758). The latter is nested within Clade 58 as the more derived terminal.

According to Michaud & Dixon (1987), L. meridionalis (Schenkel, 1902) (Clade 56) belongs to the Liophis lineatus complex, along with L. dilepis (Cope, 1862), L. flavifrenatus (Cope, 1862), L. lineatus (Linnaeus, 1758), and L. paucidens (Hoge, 1953), while L. elegansimus (Koslowsky, 1896) belongs to the Liophis anomalous group that also includes L. anomalus (Günther, 1858) and L. vanzollini Dixon, 1985. Our molecular phylogenetic result is corroborated by morphological evidence that also points to a paraphyletic genus Liophis and retrieves a clade including both anomalous and lineatus groups of Liophis, supported by their unusual color pattern (see Moura-Leite, 2001). We here resurrect Lygophis Fitzinger, 1843 to include these species, which were previously allocated to Liophis Wagler, 1830. We also include in Lygophis three additional species, which also meet the generic concept of Lygophis Fitzinger, 1843 adopted here (see Moura-Leite, 2001).

Furthermore, our analysis revealed that the genera Erythrolamprus, on the one hand, and Waglerophis and Lystrophis on the other hand, are nested within the genera Liophis sensu stricto and Xenodon, respectively. Morphological support for the inclusion of the genera Waglerophis and Lystrophis within Xenodon are
compelling and have been described and discussed by Zaher (1999), Moura-Leite (2001), and Masiero (2006). Therefore, in order to retrieve monophyly of these genera, we synonymize Lystrophis Cope, 1885 and Waglerophis Romano & Hoge, 1972 with Xenodon Boie, 1826.

Erythrolamprus appears firmly nested within Liophis in our analysis, being strongly supported by a bootstrap of 100% and Bremer support of 17 in Clade 58 and appearing as the sister-group of Liophis typhlus (bootstrap 85%, Bremer 6). Although there is no apparently known morphological evidence supporting this grouping, we here synonymize the genus Erythrolamprus Boie, 1826 with Liophis Wagler, 1830 in order to retrieve a monophyletic Liophis Boie, 1826. However, Liophis is a highly speciose and diverse group of snake and we expect a more comprehensive sampling than ours within the whole diversity of Liophis will provide more stable support for the taxonomic decisions taken here.

Lygophis Fitzinger, 1843 resurrected

Type species: Coluber lineatus Linnaeus, 1758.

Diagnosis: dorsal pattern with different arrangements of longitudinal stripes or tending to striation; optic foramen very small; general shape of the hemipenis clavate, with very small lobes; interlobular sulcus reduced or absent; pattern of dorsal scale microornamentation fasciculate (Moura-Leite, 2001).

Content: Lygophis dilepis (Cope, 1862) new combination; Lygophis flavifrenatus (Cope, 1862) new combination; Lygophis lineatus (Linnaeus, 1758) new combination; Lygophis meridionalis (Schenkel, 1902) new combination; Lygophis paucidens (Hoge, 1953) new combination; Lygophis anomalus (Günther, 1858) new combination; Lygophis elegantissimus (Koslowsky, 1896) new combination; Lygophis vanzolini (Dixon, 1985) new combination.

Tribe Alsophiini Fitzinger, 1843 (Clade 60)

Alsophes Fitzinger, 1843: 25.

Type-genus: Alsophis Fitzinger 1843.

Diagnosis: (89%, 4). Papilla present medially (in the crotch) at the base of the hemipenial lobes (lost in some alsophiines, e.g., Ialtris, Uromacer, and Alsophis as redefined herein) (Zaher, 1999).

Content: Alsophis Fitzinger, 1843; Antillophis Maglio, 1970; Arrhyton Günther, 1858; Caraiba new genus; Darlingtonia Cochran, 1935; Hipsirhyncus Günther, 1858; Ialtris Cope, 1862; Magliophis new genus; Ocyophis Cope, 1886 resurrected; Schwartzophis new genus; Uromacer Duméril, Bibron & Duméril, 1854.

Comments: See Comments under Saphenophiini. Our study, as well as earlier molecular studies (e.g., Cadle, 1984a, 1985; Vidal et al., 2000; Pinou et al., 2004), retrieves a monophyletic Alsophiini including all endemic West Indian genera of Xenodontinae (our study used many of the same sequences as the study by Vidal et al., 2000, but our other reference taxa were very dissimilar). The molecular evidence, along with the unusual morphological synapomorphy of this group (Zaher, 1999), strongly supports the monophyly of this clade relative to mainland xenodontines (for a contrary view, see Crother, 1999a,b). We also exclude from Alsophiini the mainland South American species “Alsophis” elegans and the snakes of the Galapagos Islands (contra Maglio, 1970; Thomas, 1997) (see Saphenophiini).

Within Alsophiini, the hierarchy of relationships we find are strongly supported by morphological evidence presented by Zaher (1999). Examples are, Clade 63 (Cuban Arrhyton), Clade 68 (Jamaican Arrhyton), Clade 65 (the primarily Lesser Antillean Alsophis), and, within Clade 66, a polyphyletic Antillophis and a clade of primarily Greater Antillean Alsophis. We therefore name the following new, redefined, and resurrected genera to reflect these relationships:

Ocyophis Cope, 1886 resurrected

Type species: Natrix atra Gosse, 1851, by original designation.

Diagnosis: Lobular crotch and medial surface of hemipenial lobes ornamented with well-developed, horizontally directed papillate flounces; asulate surfaces of lobes completely nude and bearing a large overhanging edge of the capitulum; expanded papillate circular area present on the lobular crotch.

Content: Ocyophis anomalus Peters, 1863; Ocyophis ater Gosse, 1851; Ocyophis cantherigerus Bibron, 1840; Ocyophis melanichnus Cope, 1863; Ocyophis portoricensis Reinhardt & Lütké, 1863; Ocyophis vudii Cope, 1863.
**Alsophis** Fitzinger, 1843

Type species: *Psammophis antillensis* Schlegel, 1837, by original designation.

*Diagnosis*: Hemipenes bicalyculate; enlarged intrasulcal spines present on each side of the sulcal region; lobular crotch and medial surfaces of the lobes almost completely nude; capitular overhanging edge composed of a thin fringe of tissue.

*Content*: *Alsophis antillensis* Schlegel, 1837; *Alsophis antiguae* Schwartz, 1966 (elevated to species rank by Zaher, 1999); *Alsophis danforthi* (elevated to species rank by Zaher, 1999); *Alsophis rijersmai* Cope, 1869; *Alsophis rufiventris* Duméril & Bibron, 1854; *Alsophis sibonius* Cope, 1879 (elevated to species level by Zaher, 1999); *Alsophis sanctaecricus* Cope, 1863.

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**Schwartzophis** new genus

Type species: *Arrhyton callilaemum* Gosse, 1851.

*Etymology*: Named after Albert Schwartz, who made significant contributions to knowledge of West Indian herpetology; gender masculine.

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

*Content*: *Schwartzophis callilaemum* Gosse, 1851 new combination; *Schwartzophis funereum* Cope, 1863 new combination; *Schwartzophis polylepis* Buden, 1966 new combination.

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**Arrhyton** Günther, 1858

Type species: *Arrhyton taeniatum* Günther, 1858.

*Diagnosis*: Medial papillate crest extending from lobular crotch to the edge of the capitulum on each lobe, forming a Y-shaped structure on the distal region of the hemipenial body;


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**Magliophis** new genus

Type species: *Dromicus exiguus* Cope, 1863.

*Etymology*: Named after Vincent J. Maglio, whose 1970 work ushered in the modern era of study of the West Indian xenodontine radiation; gender masculine.

*Diagnosis*: Presence of several large papillae aligned vertically on the lobular crotch and the proximal region of the lobes; enlarged basal nude pocket present with a large associated lobe on the asulcate edge and a much smaller lobe on the sulcate edge.

*Content*: *Magliophis exiguus* (Cope, 1863) new combination.

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**Antillophis** Maglio, 1970

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 four to five times as long as the lobes).

*Content*: *Antillophis parvifrons* Cope, 1862.

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**Caraiba** new genus

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

*Etymology*: Caraiba, in allusion to the “mar das Caraibas,” a Portuguese designation of the Caribbean region, gender feminine.

*Diagnosis*: Long lobes ornamented with spinulate calyces on the sulcate surface; enlarged, transverse papillate flounces on the asulcate surface; papillate flounces decrease in size proximal to distal.

*Content*: *Caraiba andreae* (Reinhardt & Lütken, 1862) new combination.
RESUMO

Este trabalho apresenta uma análise filogenética molecular das serpentes avançadas (Caenophidia), realizada com base na análise de sequências de dois genes mitocôndriais (rRNA 12S e 16S) e de um gene nuclear (c-mos; 1681 pares de bases no total) e com 131 táxons terminais, amostrados a partir das principais linhagens de Caenophidia, com ênfase nos xenodontíneos neotropicais. A análise de parcimônia dos dados mediante otimização direta resultou em uma árvore filogenética bem resolvida que, por um lado, corrobora alguns dos clados identificados em análises anteriores e por outro, estabelece novas hipóteses sobre a composição de outros grupos e do relacionamento entre eles. Os principais resultados obtidos salientam: (1) a alocação de Achrochordus, xenodermatídeos e parentados como grupos externos sucessivos de todos os demais cenefódidos (incluindo viperídeos, elapídeos, atractaspidídeos e todos os grupos de "colubrídeos"); (2) que, em relação ao último grupo, viperídeos e homalopsídeos podem ser considerados como clados irmãos dos demais; (3) a existência, dentro do grande grupo dos cenefódidos, dos seguintes sub‑grupos: psamophídeos afro‑asiáticos (incluindo o gênero Mimophis, de Madagascar), Elapídeos (incluindo os hidrophíneos, mas excluindo Homoroselaps, associado aos atractaspidídeos), Pseudoxyrhophinae, Colubrinae, Natricinae, Dipsadinae e Xenodontinae. A análise sugere algumas alterações de cunho taxonômico dentro dos xenodontíneos, incluindo realocações genéricas para Alsophis elegans, Liophis amarali e modificações substanciais em relação a Xenodontini e à radiação dos xenodontíneos das Antilhas. Também é aqui apresentada uma revisão da classificação de Caenophidia, baseada inicialmente nas análises moleculares, mas provendo diagnoses morfológicas para muitos dos clados incluídos, realçando os grupos que ainda merecem atenção especial no futuro. São aqui nomeados originalmente dois grandes clados dentro de Caenophidia, uma nova subfamília dentro de Dipsadidae e, dentro de Xenodontinae, cinco novas tribos e seis novos gêneros, sendo ainda dois gêneros revalidados. Os gêneros Xenoxybelis e Pseudablades são considerados sinônimos de Philodryas; Erythromamprus, sinônimo de Liophis; Lystrophis e Waglerophis, sinônimos de Xenodon.

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REFERENCES

Bailey, J.R. 1940. Relationships and distributions of the snakes allied to the genus Pseudoboa. (Ph.D. Dissertation), University of Michigan, Ann Arbor, 239p.


(subfamily Hydrophiinae) based on cytochrome b and 16S rRNA sequences. Molecular Phylogenetics and Evolution, 10:67-81.


