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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 sucessive 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* Pseudablabes *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.

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; Meirte, 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.,* homalopsines, xenodontines, pseudoxyrhophiines, elapids, psammophiines, lamprophiines). The principal molecular phylogenetic studies examining broader relationships among caenophidians 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

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

References	Focused in	Number of taxa	Genes	base pairs
Kraus & Brown (1998)	Serpentes	37	ND4	694
Gravlund (2001)	Caenophidia	43	12S, 16S	722
Vidal & Hedges (2002)	Xenodontinae	29	12S, 16S, ND4, c-mos	1968
Kelly *et al.* (2003)	Caenophidia	61	12S, 16S, ND4, Cyt-b	2338
Pinou *et al.* (2004)	Xenodontinae	85	12S, 16S	613
Lawson *et al.* (2005)	Colubroidea	100	cyt-b, c-mos	1670
Vidal *et al.* (2007)	Caenophidia	24	c-mos, RAG1, RAG2, R35, HOXA13, JUN, AMEL	3621
Vidal *et al.* (2008)	Lamprophiinae	90	12S, 16S, cyt-b, c-mos, RAG1	3950
Kelly *et al.* (2009)	Elapoidea	96	cyt-b, ND1, ND2, ND4, c-mos	4345
Present study	Xendontinae	132	12S, 16S, c-mos	1681

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 Atractaspididae 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 "colubroid" 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, Pseudoxenodontinae, Xenodontinae) + Elapidae (their Clade A, including Atractaspidinae, Boodontinae, Elapinae, Hydrophiinae, Psammophiinae, Pseudoxyrhophiinae, and *Oxyrhabdium*). 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 "Colubroidea" 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 with 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); Pareatinae (2 species); Psammophiinae (2 species); Pseudoxenodontinae (1 species); Pseudoxyrhophiinae (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 TAM CAA AAA CA 3') and H3056mod (also named as "16Sbr"; 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 ATG 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).

TABLE 2: List of taxa and sequences analyzed in this study.

	Terminal	12S	Cmos	16S
1	*Acrochordus granulatus*	AB177879	AF471124	AB177879
2	*Agkistrodon piscivorus*	AF259225	AF471096	AF057278
3	*Alsophis antiguae*	AF158455	—	AF158524
4	*Alsophis antillensis*	AF158459	—	AF158528
5	*Alsophis cantherigerus*	AF158405	AF544694	AF158475
6	*Alsophis elegans*	AF158401	—	AF158470
7	*Alsophis portoricensis*	AF158448	AF471126	AF158517
8	*Alsophis vudii*	AF158443	—	AF158512
9	*Antillophis andreae*	AF158442	—	AF158511
10	*Antillophis parvifrons*	AF158441	—	AF158510
11	*Aparallactus capensis*	FJ404129	AY187967	AY188045
12	*Aplopeltura boa*	AF544761	AF544715	AF544787
13	*Apostolepis assimilis*	**this study**	**this study**	**this study**
14	*Apostolepis dimidiata*	**this study**	**this study**	**this study**
15	*Arrhyton calliaemum*	AF158440	—	AF158509
16	*Arrhyton dolichura*	AF158438	—	AF158507
17	*Arrhyton funereum*	AF158451	—	AF158520
18	*Arrhyton landoi*	AF158439	—	AF158508
19	*Arrhyton polylepis*	AF158450	—	AF158519
20	*Arrhyton procerum*	AF158452	—	AF158521
21	*Arrhyton supernum*	AF158436	—	AF158505
22	*Arrhyton taeniatum*	AF158453	—	AF158522
23	*Arrhyton tanyplectum*	AF158446	—	AF158516
24	*Arrhyton vittatum*	AF158437	—	AF158506
25	*Atractaspis micropholis*	AF544740	AF544677	AF544789
26	*Atractus albuquerquei*	**this study**	**this study**	**this study**
27	*Atractus trihedrurus*	**this study**	**this study**	**this study**
28	*Azemiops feae*	AF512748	AF544695	AY352713
29	*Bitis nasicornis*	DQ305411	AF471130	DQ305434
30	*Boa constrictor*	AB177354	AF544676	AB177354
31	*Boiruna maculata*	**this study**	**this study**	**this study**
32	*Bothriechis schlegelii*	AF057213	AF544680	AF057260
33	*Bothrophthalmus lineatus*	FJ404146	AF471129	FJ404198
34	*Bungarus fasciatus*	U96793	AY058924	Z46501
35	*Calamaria yuannanensis/pavimentata*	**this study**	AF471103	**this study**
36	*Calamodontophis paucidens*	**this study**	**this study**	**this study**
37	*Carphophis amoenus*	AY577013	DQ112082	AY577022
38	*Causus resimus*	AY223649	AF544696	AY223662
39	*Clelia bicolor*	**this study**	**this study**	**this study**
40	*Clelia clelia*	AF158403	—	AF158472
41	*Coluber constrictor*	AY122819	AY486938	L01770
42	*Conophis lineatus*	**this study**	—	**this study**
43	*Contia tenuis*	AY577021	AF471134	AY577030
44	*Darlingtonia haetiana*	AF158458	—	AF158527

TABLE 2: Continued.

	Terminal	12S	Cmos	16S
45	*Diadophis punctatus*	AY577015	AF471122	AF544793
46	*Dinodon rufozonatum/semicarinatus*	AF233939	AF471163	AB008539
47	*Dipsas indica*	**this study**	**this study**	**this study**
48	*Dipsas neivai*	**this study**	**this study**	**this study**
49	*Drepanoides anomalus*	**this study**	**this study**	**this study**
50	*Elaphe quatuorlineata*	AY122798	AY486955	AF215267
51	*Elapomorphus quinquelineatus*	**this study**	**this study**	**this study**
52	*Enhydris enhydris*	AF499285	AF544699	AF499299
53	*Erythrolamprus aesculapii*	**this study**	**this study**	**this study**
54	*Farancia abacura*	Z46467	AF471141	AY577025
55	*Gomesophis brasiliensis*	**this study**	—	**this study**
56	*Helicops angulatus*	**this study**	**this study**	**this study**
57	*Helicops gomesi*	**this study**	**this study**	**this study**
58	*Helicops infrataeniatus*	**this study**	**this study**	**this study**
59	*Helicops pictiventris*	**this study**	**this study**	**this study**
60	*Heterodon nasicus*	**this study**	**this study**	AY577027
61	*Heterodon simus*	AY577020	AF471142	AY577029
62	*Hierophis spinalis*	AY541508	AY376802	AY376773
63	*Homalopsis buccata*	AF499288	AF544701	AF544796
64	*Homoroselaps lacteus*	FJ404135	AY611901	AY611843
65	*Hydrodynastes bicinctus*	**this study**	**this study**	**this study**
66	*Hydrodynastes gigas*	**this study**	**this study**	**this study**
67	*Hydrops triangularis*	**this study**	**this study**	**this study**
68	*Hypsirhynchus ferox*	AF158447	—	AF158515
69	*Hypsirhynchus scalaris*	AF158449	—	AF158518
70	*Ialtris dorsalis*	AF158456	—	AF158525
71	*Imantodes cenchoa*	**this study**	**this study**	**this study**
72	*Laticauda colubrina*	U96799	AY058932	EU547138
73	*Leioheterodon madagascariensis*	AF544768	AY187983	AY188061
74	*Leptodeira annulata*	**this study**	**this study**	**this study**
75	*Liophis amarali*	**this study**	**this study**	**this study**
76	*Liophis elegantissimus*	**this study**	**this study**	**this study**
77	*Liophis jaegeri*	**this study**	**this study**	**this study**
78	*Liophis meridionalis*	**this study**	**this study**	**this study**
79	*Liophis typhlus*	**this study**	**this study**	**this study**
80	*Lycophidion laterale*	FJ404179	FJ404280	FJ404197
81	*Lystrophis dorbignyi*	**this study**	**this study**	**this study**
82	*Lystrophis histricus*	**this study**	**this study**	**this study**
83	*Micrurus surinamensis*	AF544770	EF137422	AF544799
84	*Naja naja*	Z46453	AF435020	Z46482
85	*Natriciteres olivacea*	AF544772	AF471146	AF544801
86	*Natrix natrix*	AY122682	AF471121	AF158530
87	*Ninia atrata*	**this study**	**this study**	—
88	*Notechis ater*	EU547131	EU546944	EU547180

TABLE 2: Continued.

	Terminal	12S	Cmos	16S
89	*Oxybelis aeneus*	AF158416	AF471148	AF158498
90	*Oxyrhopus clathratus*	**this study**	**this study**	**this study**
91	*Oxyrhopus rhombifer*	**this study**	**this study**	**this study**
92	*Pareas carinatus*	AF544773	AF544692	AF544802
93	*Phalotris lemniscatus*	**this study**	**this study**	**this study**
94	*Phalotris nasutus*	**this study**	**this study**	**this study**
95	*Philodryas aestiva*	**this study**	**this study**	**this study**
96	*Philodryas mattogrossensis*	**this study**	**this study**	**this study**
97	*Philodryas patagoniensis*	**this study**	**this study**	**this study**
98	*Phimophis guerini*	**this study**	**this study**	**this study**
99	*Psammophis condanarus*	Z46450	AF471104	Z46479
100	*Pseudablabes agassizi*	**this study**	**this study**	**this study**
101	*Pseudoboa coronata*	**this study**	**this study**	**this study**
102	*Pseudoboa nigra*	**this study**	**this study**	**this study**
103	*Pseudoeryx plicatilis*	**this study**	**this study**	**this study**
104	*Pseudotomodon trigonatus*	**this study**	**this study**	**this study**
105	*Pseudoxenodon karlschmidti*	—	AF471102	—
106	*Pseudoxyrhopus ambreensis*	FJ404188	AY187996	AY188074
107	*Psomophis genimaculatus*	**this study**	**this study**	**this study**
108	*Psomophis joberti*	**this study**	**this study**	**this study**
109	*Ptychophis flavovirgatus*	**this study**	**this study**	**this study**
110	*Rhabdophis subminiatus*	AF544776	AF544713	AF544805
111	*Rhamphiophis oxyrhynchus*	Z46443	AF544710	Z46738
112	*Sibon nebulatus*	AF544777	AF544736	AF544806
113	*Sibynomorphus garmani*	**this study**	**this study**	**this study**
114	*Sibynomorphus mikanii*	**this study**	**this study**	**this study**
115	*Sinonatrix annularis*	AF544778	AF544712	AF544807
116	*Siphlophis compressus*	**this study**	**this study**	**this study**
117	*Siphlophis pulcher*	**this study**	**this study**	**this study**
118	*Stoliczkia borneensis*	AF544779	AF544721	AF544808
119	*Tachymenis peruviana*	**this study**	**this study**	**this study**
120	*Taeniophallus affinis*	**this study**	**this study**	**this study**
121	*Taeniophallus brevirostris*	**this study**	**this study**	**this study**
122	*Thamnodynastes nattereri*	**this study**	—	**this study**
123	*Thamnodynastes rutilus*	**this study**	**this study**	**this study**
124	*Tomodon dorsatus*	**this study**	**this study**	**this study**
125	*Tropidodryas striaticeps*	**this study**	—	**this study**
126	*Uromacer catesbyi*	AF158454	—	AF158523
127	*Uromacer frenatus*	AF158444	—	AF158513
128	*Waglerophis merremi*	**this study**	**this study**	—
129	*Xenochrophis flavipunctatum*	AF544780	AF544714	AF544809
130	*Xenodermus javanicus*	AF544781	AF544711	AF544810
131	*Xenodon neuwiedi*	**this study**	—	**this study**
132	*Xenoxybelis argenteus*	**this study**	**this study**	**this study**

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 frameshift 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 arginine, 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 dorbignyi* and *Waglerophis merremi* (*Xenodon neuwiedi* 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

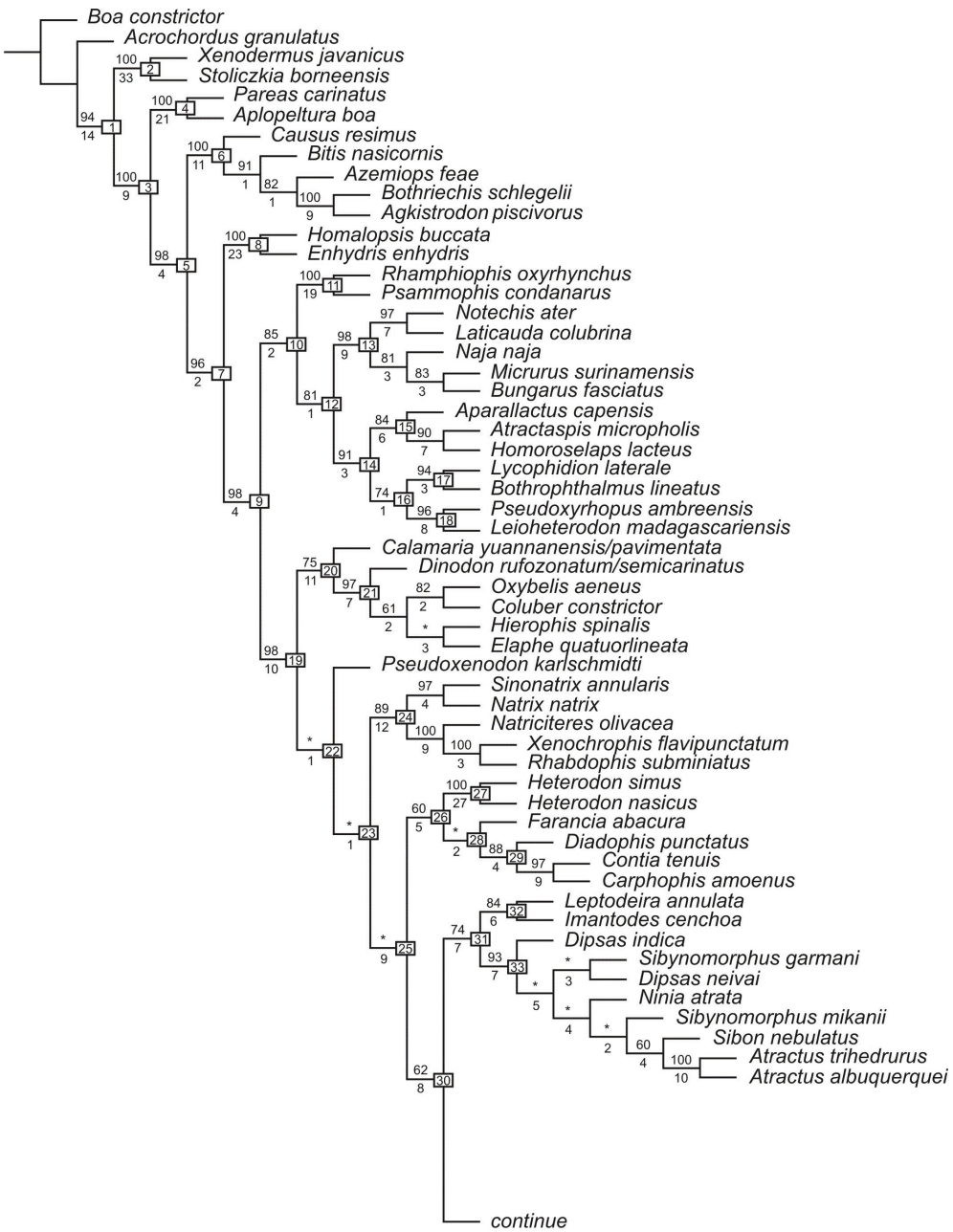

FIGURE 1: Best Phylogenetic tree based on molecular matrix (12S, 16S and c-mos) found by Directed optimization under Maximum Parsimony analyses (implemented in POY 4.1). Numbers above branches are bootstrap support values; numbers below branches are Bremer supports. The asterisk (*) corresponds to nodes with bootstrap values less than 60%.

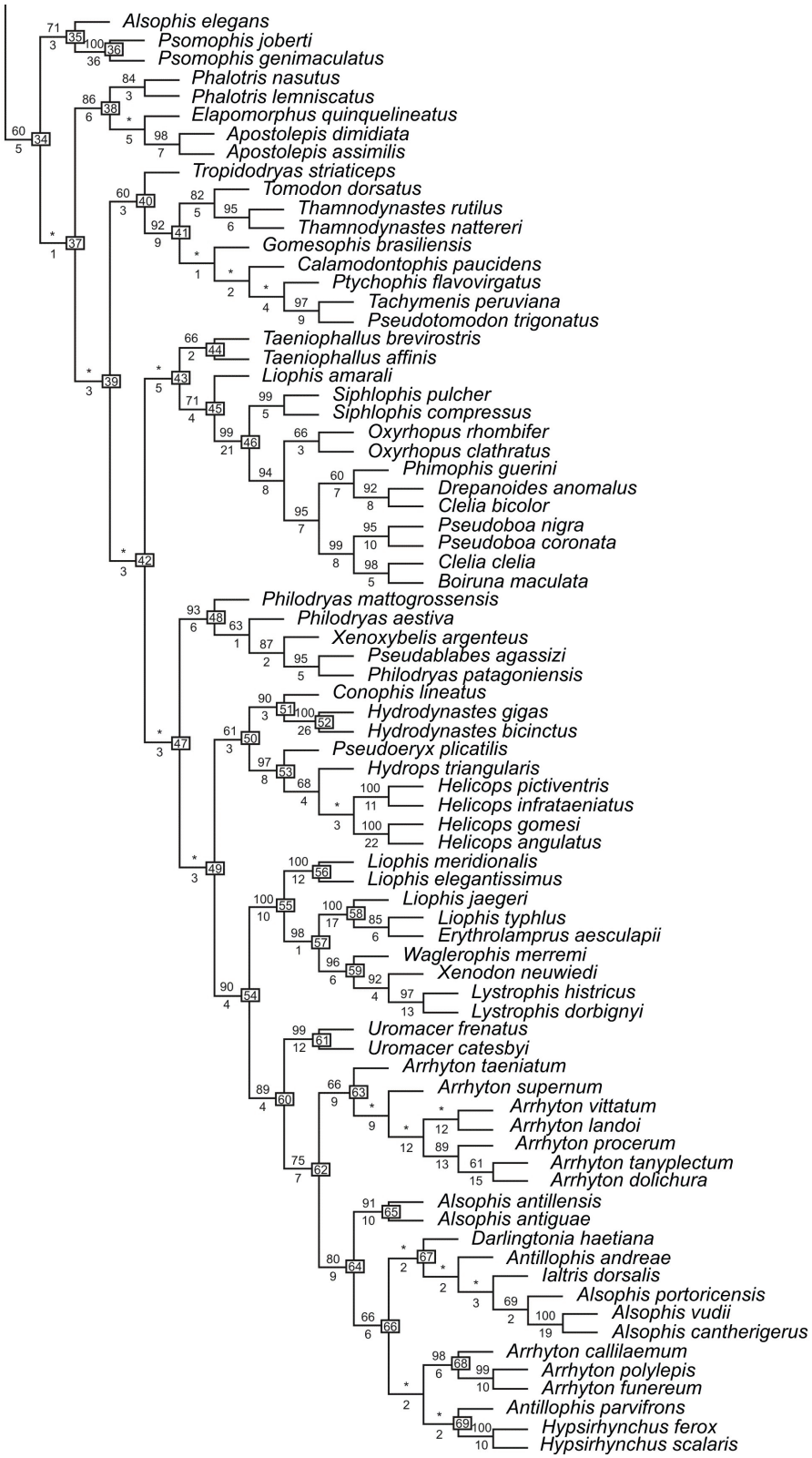

FIGURE 1: Continued.

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, pseudoxyrhophiines). 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), Pseudoxyrhophiinae (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-taxa to a well-supported crotaline clade represented by *Bothriechis* and *Agkistrodon* (bootstrap100%; 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 "atractaspidine" 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 pseudoxyrhophiines (*Pseudoxyrhopus* and *Leioheterodon*). Although Clade 16 is not strongly supported, both of the subclades are strongly supported by high bootstrap values (94% and 96%, respectively) and moderate Bremer support values (3 and 8, respectively).

Relationships among 'xenodontine' 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

(5-7). We have not sampled intensively within either the North American or Central American groups, but we note in passing that within 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 *Ninia* and *Atractus*). However, no internal nodes within Dipsadini are strongly supported. The nesting of *Ninia* 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. antiguae* are a sister group to a clade including species of *Darlingtonia, Antillophis, Ialtris, Alsophis, Arrhyton,* and *Hypsirhynchus.*

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 amarali,* 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 (*histricus* 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 alsophiines 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 alsophiines (*Alsophis, Darlingtonia, Antillophis, Ialtris,* Jamaican species of *Arrhyton,* and *Hypsirhynchus*). 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-dolichura*), Guadeloupe-Antigua *Alsophis* (Clade 65), Bahamas-Cuban *Alsophis* (*vudii-cantherigerus*), Jamaican *Arrhyton* (Clade 68), and *Hypsirhynchus* (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 *Acrochor-*

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* + *Rhamphiophis*) 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 Elapoidea 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 Elapoidea 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 Atractaspidinae, Lamprophiinae, and Pseudoxhyrophiinae (bootstrap 91%, Bremer 3).

Snakes in Clade 15 (*Aparallactus, Atractaspis, Homoroselaps*), usually referred to as "aparallactines" or atractaspidids, 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 Atractaspidinae (*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 + Atractaspidinae to other clades of caenophidians 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 Pseudoxyrhophiinae + 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 *Psomophis* (Clades 35 and 36), *Taeniophallus* (Clade 44), *Liophis amarali* (Clade 45), and the polyphyly of *Arrhyton, Alsophis,* and *Antillophis* 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 as *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, Pseudaspididae, 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, elapids, 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; McDiarmid *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 superfamily 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 Colubroides **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 *Oxyrhabdium* to represent elapoid 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 Atractaspididae + Pseudoxyrhophiidae + Lamprophiidae, and Kelly *et al.* (2009), in which it is nested within the Psammophiidae + Pseudoxhyrhophiidae. 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 elapoids was ambiguous. In the taxonomically broader phylogenetic analysis by Lawson *et al.* (2005), the strict consensus parsimony tree shows *Prosymna* + *Oxyrhabdium* 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 elapoid 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 *Oxyrhabdium* as Elapoidea *incertae sedis*.

Grayiinae Meirte, 1992: Vidal *et al.* (2007) erroneously thought they were erecting a new family-group name, Grayiinae, 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
  - Colubriformes
    - Pareatidae
    - Endoglyptodonta, new taxon
      - Viperidae
      - Homalopsidae
      - Elapoidea
        - Psammophiidae
        - Elapidae
        - Atractaspididae
        - Lamprophiidae
      - Colubroidea
        - Calamariidae
        - Colubridae
        - Pseudoxenodontidae
        - Natricidae
        - Dipsadidae
          - Dipsadinae
          - Carphophiinae, new subfamily
          - Xenodontinae
            - Saphenophiini, new tribe
              - *Pseudalsophis,* new genus
            - Psomophiini, new tribe
            - Elapomorphini
            - Tropidodryadini
            - Tachymenini
            - Echinantherini, new tribe
            - Caaeteboiini, new tribe
              - *Caaeteboia,* new genus
            - Pseudoboini
              - *Mussurana,* new genus
            - Conophiini, new tribe
            - Hydrodynastini, new tribe
            - Hydropsini
            - Xenodontini
              - *Lygophis* Fitz. (resurrected)
            - Alsophiini
              - *Ocyophis* Cope (resurrected)
              - *Caraiba,* new genus
              - *Schwartzophis,* new genus
              - *Magliophis,* new genus

COLUBROIDES, new taxon (Clade 1)

Etymology: Colubri- (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; spinules or spines covering the hemipenial body.

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

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; *Cercaspis* Wagler, 1830; *Cyclocorus* Duméril, 1853; *Dolichophis* Gistel, 1868; *Elapoidis* H. Boie (in F. Boie), 1827; *Gongylosoma* Fitzinger, 1843; *Haplocercus* Günther, 1858; *Helophis* de Witte & Laurent, 1942; *Iguanognathus* Boulenger, 1898; *Miodon* Duméril, 1859; *Myersophis* Taylor, 1963; *Omoadiphas* Köhler, McCranie & Wilson, 2001; *Oreocalamus* Boulenger, 1899; *Poecilopholis* Boulenger, 1903; *Rhabdops* Boulenger, 1893; *Rhadinophis* Vogt, 1922; *Tetralepis* Boettger, 1892; *Trachischium* Günther, 1858.

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

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; Ferrarezzi, 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 *Oxyrhabdium* 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.

COLUBRIFORMES, Günther, 1864 (Clade 3)

Etymology: Coluber- (Latin, "snake") + formes (Greek, "shaped like").

Diagnosis: (94%, 14). Colubriformes can be diagnosed by the following putative morphological synapomorphies: septomaxilla broadly contacts the frontal ventrally (McDowell, 1987; Cundall & Irish, 2008; see also Cundall & Shardo, 1995); optic foramen bordered ventrally by the parasphenoid due to the loss of contact between frontals and parietals ventral to the optic foramen (Underwood, 1967).

Content: Colubriformes is a monophyletic group composed of Pareatidae Romer, 1956 and Endoglyptodonta **new taxon.**

Comments: The character of the optic foramen is reversed in a few phylogenetically diverse Colubriformes (Underwood, 1967; Cundall & Irish, 2008; personal observations). Günther (1864) included a diverse array of snakes in his "Colubriformes Non-venenosi" (including virtually all non-viperid and non-elapid snakes) and "Colubriformes venenosi" (elapids, including sea snakes). We therefore equate Günther's concept of "Colubriformes" with our definition of Colubriformes.

FAMILY PAREATIDAE Romer, 1956 (Clade 4)

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 venom gland (Haas, 1938, 1962; Kochva, 1962, 1978; Zaher, 1994a); presence of well-developed, strongly anteroventrally directed (anteriorly directed in *Causus*), parapophyseal 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* Gutberlet & 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; *Porthidium* 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; *Zhaoermia* Gumprecht & Tillack, 2004.

Comments: The monophyly of the family Viperidae has never been seriously questioned. Well-developed, strongly anteroventrally directed, parapophyseal 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 viperids 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 synonomies 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 *Cummingea* 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 ravus* 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 homoplastically 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.

Content: Psammophiidae Dowling, 1967, Elapidae Boie, 1827, Atractaspididae Günther, 1858, Lamprophiidae Fitzinger, 1843.

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 + Atractaspididae + 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, paraphyletic. 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; *Psammodynastes* Günther, 1858; *Pseudaspis* Fitzinger, 1843; *Pythonodipsas*, Günther, 1868.

FAMILY PSAMMOPHIIDAE Bonaparte, 1845 (Clade 11)

Psammophidae 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; *Hemirhagerrhis* Boettger, 1893; *Malpolon* Fitzinger, 1826; *Mimophis* Günther, 1868; *Psammophis* H. Boie (in Fitzinger), 1826; *Psammophylax* 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 corroboration 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; *Apistocalamus* Boulenger, 1898; *Aspidelaps* Fitzinger, 1843; *Aspidomorphus* Fitzinger, 1843; *Astrotia* Fischer, 1855; *Austrelaps* Worrel, 1963; *Boulengerina* Dollo,1886; *Bungarus* Daudin, 1803; *Cacophis* Günther, 1863; *Calliophis* Gray, 1835; *Demansia* Gray (in Gray), 1842; *Dendroaspis* Schlegel, 1848; *Denisonia* Krefft, 1869; *Disteira* Lacépède, 1804; *Drysdalia* Worrel, 1961; *Echiopsis* Fitzinger, 1843; *Elapognathus* Boulenger, 1896; *Elapsoidea* Bocage, 1866; *Emydocephalus* Krefft, 1869; *Enhydrina* Gray, 1849; *Ephalophis* Smith, 1931; *Furina* Duméril, 1853; *Hemachatus* Fleming, 1822; *Hemiaspis* Fitzinger, 1861; *Hemibungarus* Peters, 1862; *Hoplocephalus* Wagler, 1830; *Hydrelaps* Boulenger, 1896; *Hydrophis* Latreille (in Sonnini & Latreille), 1801; *Kerilia* Gray, 1849; *Kolpophis* Smith, 1926; *Lapemis* Gray, 1835; *Laticauda* Laurenti, 1768; *Loveridgelaps* McDowell, 1970; *Maticora* Gray, 1835; *Micropechis* Boulenger, 1896; *Micruroides* Schmidt, 1928; *Micrurus* Wagler (in Spix), 1824; *Naja* Laurenti, 1768; *Narophis* Worrell, 1961; *Neelaps* Günther, 1863; *Notechis* Boulenger, 1896; *Ogmodon* Peters, 1864; *Ophiophagus* Günther, 1864; *Oxyuranus* Kinghorn, 1923; *Parademansia* Kinghorn, 1955; *Parahydrophis* Burger & Natsuno, 1974; *Paranaja* Loveridge, 1944; *Parapistocalamus* Roux, 1934; *Pelamis* Daudin, 1803; *Polyodontognathus* Wall, 1921; *Praescutata* Wall, 1921; *Pseudechis* Wagler, 1830; *Pseudohaje* Günther, 1858; *Pseudolaticauda* Kharin 1984; *Pseudonaja* Günther, 1858; *Rhinoplocephalus* Müller, 1885; *Salomonelaps* McDowell, 1970; *Simoselaps* Jan, 1859; *Sinomicrurus* Slowinski, Boundy & Lawson 2001; *Smithohydrophis* Kharin, 1981; *Suta* Worrel, 1961; *Thalassophis* Schmidt, 1852; *Toxicocalamus* Boulenger, 1896; *Tropidechis* Günther, 1863; *Unechis* Worrel, 1961; *Vermicella* 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 Atractaspidinae, "Boodontinae" (=Lamprophiidae), Psammophiinae, Pseudoxyrhophiinae, 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 Slowinski & Keogh (2000).

FAMILY ATRACTASPIDIDAE Günther, 1858 (Clade 15)

Atractaspididae 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; *Elapotinus* Jan, 1862; *Homoroselaps* Jan, 1858; *Hypoptophis* Boulenger, 1908; *Macrelaps* Boulenger, 1896; *Micrelaps* Boettger, 1880; *Polemon* Jan, 1858; *Xenocalamus* Günther, 1868.

Comments: Spinulate flounce-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 *Psammodynastes,* which has been shown to be closely related to the Atractaspididae 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 atractaspidid 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 Atractaspididae 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 trenchant 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)

Lamprophes 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; *Bothrophtalmus* Peters, 1863; *Chamaelycus* Boulenger, 1919; *Dendrolycus* Laurent, 1956; *Gonionotophis* Boulenger, 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 PSEUDOXYRHOPHIINAE Dowling, 1975 (Clade 18)

Pseudoxyrhophini Dowling, 1975.

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; *Brygophis* Domergue & Bour, 1989; *Compsophis* Mocquard, 1894; *Ditypophis* Günther, 1881; *Dromicodryas* Boulenger, 1893; *Duberria* Fitzinger, 1826; *Exallodontophis* Cadle, 1999; *Heteroliodon* Boettger, 1913; *Ithycyphus* Günther, 1873; *Langaha* Bonnaterre, 1790; *Leioheterodon* Jan, 1863; *Liophidium* Boulenger, 1896; *Liopholidophis* Mocquard, 1904; *Lycodryas* Günther, 1879; *Madagascarophis* Mertens, 1952; *Micropisthodon* Mocquard, 1894; *Montaspis* Bourquin 1991; *Pararhadinaea* Boettger, 1898; *Pseudoxyrhopus* Günther, 1881; *Stenophis* Boulenger, 1896; *Thamnosophis* Jan, 1863.

Comments: The hemipenial synapomorphy of Pseudoxyrhophiinae is also present homoplastically in Homalopsidae. *Geodipsas* Boulenger, 1896 was placed in the synonymy of *Compsophis* by Glaw *et al.* (2007a). *Bibilava* 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 elapoid 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 Pseudoxyrhophiidae. We recognize both *Stenophis* and *Lycodryas*

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*)

Calamarina 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 parietals); 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; *Etheridgeum* 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; *Ahaetulla* Link, 1807; *Argyrogena* Werner, 1924; *Arizona* Kennicott (in Baird), 1859; *Bogertophis* Dowling and Price, 1988; *Boiga* Fitzinger, 1826; *Cemophora* 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; *Dasypeltis* 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; *Elaphe* Fitzinger (in Wagler), 1833; *Euprepiophis* Fitzinger, 1843; *Ficimia* Gray, 1849; *Gastropyxis* Cope, 1861; *Geagras* 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; *Lepturophis* Boulenger, 1900; *Liochlorophis* Oldham & Smith, 1991; *Liopeltis* Fitzinger, 1843; *Lycodon* Boie (in Fitzinger), 1826; *Lytorhynchus* Peters, 1862; *Macroprotodon* Duméril & Bibron (in Guichenot), 1850; *Maculophis* Burbrink & Lawson, 1997; *Masticophis* Baird (in Baird & Girard), 1853; *Mastigodryas* Amaral, 1934; *Meizodon* 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; *Phyllorhynchus* Stejneger, 1890; *Pituophis* Holbrook, 1842; *Platyceps* Blyth, 1860; *Pseudelaphe* Mertens & Rosenberg, 1943; *Pseudocyclophis* Boettger, 1888; *Pseudoficimia* Bocourt, 1883; *Pseustes* Fitzinger, 1843; *Ptyas* Fitzinger, 1843; *Rhamnophis* Günther, 1862; *Rhinechis* Michahelles, 1833; *Rhinobothryum* Wagler, 1830;

Rhinocheilus Girard (in Baird & Girard), 1853; *Rhynchocalamus* Günther, 1864; *Rhynchophis* Mocquard, 1897; *Salvadora* Baird (in Baird & Girard), 1853; *Scaphiodontophis* Taylor & Smith, 1943; *Scaphiophis* Peters, 1870; *Scolecophis* 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; *Stegonotus* Duméril, Bibron & Duméril, 1854; *Stenorrhina* Duméril, 1853; *Stilosoma* 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; *Zaocys* 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 viperids. 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 karlschmidti*)

Pseudoxenodontinae McDowell, 1987: 38.

Type-genus: Pseudoxenodon Boulenger, 1890.

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

Content: Plagiopholis Boulenger, 1893; *Pseudoxenodon* Boulenger, 1890.

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

FAMILY NATRICIDAE Bonaparte, 1838 (Clade 24)

Natricina 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).

Content: Adelophis Dugès (in Cope), 1879; *Afronatrix* Rossman & Eberle, 1977; *Amphiesma* Duméril, Bibron & Duméril, 1854; *Amphiesmoides* Malnate, 1961; *Anoplohydrus* Werner, 1909; *Aspidura* Wagler, 1830; *Atretium* Cope, 1861; *Balanophis* Smith, 1938; *Clonophis* Cope, 1888; *Hologerrhum* Günther, 1858; *Hydrablabes* Boulenger, 1891; *Hydraethiops* Günther, 1872; *Limnophis* Günther, 1865; *Lycognathophis* Boulenger, 1893; *Macropisthodon* Boulenger, 1893; *Natriciteres* Loveridge, 1953; *Natrix* Laurenti, 1768; *Nerodia* Baird (in Baird & Girard), 1853; *Opisthotropis* Günther, 1872; *Parahelicops* Bourret, 1934; *Pararhabdophis* Bourret, 1934; *Regina* Baird (in Baird & Girard), 1853; *Rhabdophis* Fitzinger, 1843; *Seminatrix* Cope, 1895; *Sinonatrix* Rossman & Eberle, 1977; *Storeria* Girard (in Baird & Girard), 1853; *Thamnophis* Fitzinger, 1843; *Tropidoclonion* Cope, 1860; *Tropidonophis* Jan, 1863; *Virginia* Girard (in Baird & Girard), 1853; *Xenochrophis* Günther, 1864.

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.

FAMILY DIPSADIDAE Bonaparte, 1838 (Clade 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 xendontines 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, Enuliophis, 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, Lioheterophis, 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; *Enuliophis* McCranie & Villa, 1971; *Enulius* Cope, 1871; *Farancia* Gray, 1842; *Heterodon* Latreille (in Sonnini & Latreille), 1801; *Hydromorphus* Peters, 1859; *Lioheterophis* 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 (Clade 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** ressembles 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; *Cryophis* Bogert & Duellman, 1963; *Dipsas* Laurenti, 1768; *Eridiphas* Leviton & Tanner, 1960; *Geophis* Wagler, 1830; *Hypsiglena* Cope, 1860; *Imantodes* Duméril, 1853; *Leptodeira* Fitzinger, 1843; *Ninia* Girard (in Baird & Girard), 1853; *Plesiodipsas* 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.

Content: Saphenophiini **new tribe,** Psomophiini **new tribe;** Elapomorphini Jan, 1862; Tropidodryadini **new tribe;** Tachymenini Bailey, 1967; Echinantherini **new tribe;** Caaeteboiini **new tribe;** Pseudoboini Bailey, 1967; Philodryadini Cope, 1886; Conophiini **new tribe;** Hydrodynastini **new tribe;** Hydropsini Dowling, 1975; Xenodontini Bonaparte, 1845; Alsophiini Fitzinger, 1843.

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); Hydropsini (97%, 8), Xenodontini (100%, 10), Alsophiini (89%, 4). These tribes are here formally recognized. However, except fot 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 *Psomophis, 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: Saphenophis 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 *Psomophis* (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. hoodensis*), *Alsophis* (*A. occidentalis, A. biserialis*), 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.[ygophis (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 centrolineally until the base of the capitula, here it takes a centrifugal position on the lobe, ending in the distal region; intrasulcar 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 (Ferrarezzi, 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 b y monotypy).

Comments: See Comments under Pseudoboini.

TRIBE TACHYMENINI Bailey, 1967
(Clade 41)

Tachymenini Bailey, 1967: 160.

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; *Ptychophis* 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. Ferrarezzi (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 ECHINANTHERINI new tribe
(Clade 44)

Diagnosis: (66%, 2). Hemipenis unilobed and unicapitate; 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 CAAETEBOIINI 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: Caaeteboia **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, butrather has a semicapiate, semicalyculate hemipenial pattern, typical of Xenodontinae. For this reason, we erect a new genus to accommodate *Liophis amarali.*

***Caaeteboia* 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.

Diagnosis: Small (much less than 1 m), slender snakes with slender transverse (maxillary) processes of premaxillae bearing a small additional process oriented posteriorly from each transverse process (these are in addition to the vomerine processes); hemipenis typically xenodontine, *i.e.,* bilobed, semicapitate and semicalyculate; sulcus spermaticus divides on the proximal region; branches of the sulcus on the lobes with centrolineal orientation; lobes small, the medial lobe shorter than the lateral one; capitula ornamented with small, ill-defined papillate calyces, restricted to the sulcate and lateral surfaces of the lobes; hemipenial body ornamented with well-defined lateral enlarged spines and smaller spines covering the asulcate and sulcate sides of the organ out of the intrasulcar region; body spines decreasing in length toward the base.

Content: Caaeteboia amarali (Wettstein, 1930) **new combination.**

TRIBE PSEUDOBOINI Bailey, 1967
(Clade 46)

Pseudoboini Bailey, 1967: 157.

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 vomerian 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; *Mussurana* **new genus;** *Oxyrhopus* Wagler, 1830; *Phimophis* Cope, 1860; *Pseudoboa* Schneider, 1801; *Rhachidelus* 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, 1994b).

***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 & Puorto, 1997) **new combination;** *Mussurana quimi* (Franco, Marques & Puorto, 1997) **new combination.**

TRIBE PHILODRYADINI Cope, 1886
(Clade 48)

Philodryadinae Cope, 1886:491

Type-genus: Philodryas Wagler, 1830.

Diagnosis: (93%, 6). Hemipenial body much longer than the lbes (more than twice the length), with the aulcate side of the hemipenial body covered with two parallel rows of enlarged body calyces on most or all its surface.

Content: Philodryas Wagler, 1830 (includes *Pseudablabes* Boulenger 1896, and *Xenoxybelis* Machado 1993); *Ditaxodon* Hoge, 1958.

Comments: Our concept of Philodryadini has a different concept than that used originally by Jenner (1983). The genera *Pseudablables* and *Xenoxybelis* are found nested within *Philodryas* and are thus synonymized here with the latter in order to retrieve a monophyletic group. Zaher (1999) provided hemipenial putative synapomorphies that supports the nesting of *Xenoxybelis* within *Philodryas,* as a possible member of his *Philodryas olfersii* group. Vidal *et al.* (2000) also found *Xenoxybelis* nested within *Philodryas. Pseudablabes* is, on the other hand, deeply nested in our analysis, forming a strongly supported clade with *Philodryas patagoniensis* (bootstrap 95%, Bremer support 5). However, a more detailed phylogenetic analysis of the newly extended genus *Philodryas* may show the necessity of a partition of the latter with some of the generic names synonymized here being applicable to the recovered monophyletic subunits. Although *Ditaxodon* is not part of the present molecular analysis, it has all putative morphological synapomorphies listed above for the Philodryadini (Zaher, 1999), and is thus included as a member of this tribe.

TRIBE CONOPHIINI new tribe
(Terminal taxon: *Conophis lineatus*)

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

Content: Conophis Peters, 1860 (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).

TRIBE HYDRODYNASTINI new tribe
(Clade 52)

Diagnosis: (100%, 26). Neck-flattening defensive behavior (Myers, 1986).

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

Comments: A similar defensive behavior has appeared in other Xenodontinae (*e.g.,* Xenodontini; see Myers, 1986).

TRIBE HYDROPSINI 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. elegantissimus, 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 even to the tribe Xenodontini (see the new tribe Caaeteboiini 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 elegantissimus* (Koslowsky, 1896) and *L. meridionalis* (Schenkel, 1902) while the second clade (58) includes *L. jaegeri* (Günther, 1858), *L. typhlus* (Linnaeus, 1758), and *Erythrolamprus aesculapii* (Linnaeus, 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. elegantissimus* (Koslowsky, 1896) belongs to the *Liophis anomalus* group that also includes *L. anomalus* (Günther, 1858) and *L. vanzolinii* 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 *anomalus* 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 vanzolinii* (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; *Hypsirhynchus* 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; asulcate 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 & Lütken, 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 sanctaecrucis* Cope, 1863.

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.**

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 hempenial body;

Content: Arrhyton dolichurum Werner, 1909; *Arrhyton landoi* Schwartz, 1965, *Arrhyton procerum* Hedges & Garrido, 1992; *Arrhyton supernum* Hedges & Garrido, 1992; *Arrhyton taeniatum* Günter, 1858; *Arrhyton tanyplectum* Schwartz & Garrido, 1981; *Arrhyton vittatum* Gundlach in Peters, 1861.

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.**

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.

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 seqüências de dois genes mitocondriais (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 pareatídeos como grupos externos sucessivos de todos os demais cenofídios (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 cenofidia, dos seguintes sub-grupos: psamophiídeos afro-asiáticos (incluindo o gênero* Mimophis, *de Madagascar), Elapidae (incluindo os hidrophiíneos, mas excluindo* Homoroselaps, *associado aos atractaspidídeos), Pseudoxyrhophiinae, 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 a 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* Pseudablabes *são considerados sinônimos de* Philodryas; Erythrolamprus, *sinônimo de* Liophis; Lystrophis *e* Waglerophis, *sinônimos de* Xenodon.

Palavras-Chave: Serpentes; Colubridae; Caenophidia; Filogenia; Classificação; Sistemática; Xenodontinae; Dipsadinae, Novos gêneros; Elapoidea; Colubroidea; América do Sul; Antilhas.

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