FELIPE GOBBI GRAZZIOTIN

FILOGENIA MOLECULAR DA FAMÍLIA DIPSADIDAE (SERPENTES: COLUBROIDEA)

Tese apresentada ao Instituto de Biociências do Campus de Rio Claro, Universidade Estadual Paulista Júlio de Mesquita Filho, como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas (Zoologia).

Orientador: Dr. Hussam El Dine Zaher
Co-orientador: Dr. Sandro Luis Bonatto

Rio Claro
2011

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Comissão Examinadora

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Rio Claro, ____ de _____ de _____

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Resumo

A relação filogenética entre os caenofídeos (serpentes avançadas) tem sido matéria de debate durante décadas. As principais questões para a sistemática eram representadas pela condição monofilética da família Colubridae, e a composição de sua subfamílias. Mais recentemente, novos métodos para inferir filogenias baseadas em critérios objetivos, bem como a utilização da biologia molecular, lançaram alguma luz sobre estas questões tradicionais. Aqui, são apresentados os resultados de duas análises filogenéticas moleculares das serpentes cenofídeas, focando principalmente nas serpentes neotropicais (subfamílias Xenodontinae e Dipsadinae). Otimização direta com base na máxima parcimônia, e homologia estática (alinhamento múltiplo), utilizando máxima parcimônia e máxima verossimilhança foram aplicados em uma matriz expandida de dados molecular. Os principais resultados de ambas as análises são: posicionamento de *Acrochordus*, Xenodermatideos e Pareatideos como grupos irmãos sucessivos de todos os caenofídeos restantes; viperídeos e homalopsideos são clados irmãos sucessivos de todos as demias serpentes, foram recuperados os seguintes clados monofiléticos dentro do crown-group Caenophidia: psammofídeos Afro-Asiaticos (incluindo *Mimophis* de Madagascar), Elapidae, Pseudoxyrhophiinae, Colubrinae, Natricinae, Dipsadinae e Xenodontinae. *Homoroselaps* está associada com os atractaspidídeos. Dois grupos taxonômicos superiores dentro de Caenophidia e uma nova subfamília dentro Dipsadidae foram nomeados. As análises filogenéticas sugerem mudanças taxonômicas dentro dos xenodontíneos; cinco novas tribos, oito novos gêneros foram criados e dois gêneros foram ressuscitados. Os gêneros *Xenoxybelis* e *Pseudablabes* foram sinonimizados com *Philodryas*; *Liophis* e *Umbrivaga* com *Erythrolamprus* e *Lystrophis* e *Waglerophis* com *Xenodon*.

Palavras-Chave: Serpentes, Caenophidia, Dipsadidae, Xenodontinae, Filogenia Molecular, Sistemática, Taxônomia.

Abstract

The phylogenetic relationship among the caenophidian (advanced) snakes has been a matter of debate for decades. The principal issues for the systematic were represented by the monophyletic condition of the large family Colubridae, and the composition of its subfamilies. More recently, new methods for infering phylogenies based on objective criteria, and the use of molecular biology, shed some light on these traditional issues. Here, two molecular phylogenetic analyses of caenophidian snakes focusing principally in the Neotropical snakes (subfamilies Xenodontinae and Dipsadinae) are presented.
Direct optimization based on maximum parsimony, and static homology (multiple alignment) using maximum parsimony and maximum likelihood were applied on a expanded molecular data matrix. The major results of both analyses are: placement of Acrochordus, Xenodermatids, and Pareatids as successive outgroups to all remaining caenophidians; viperids and homalopsids are sucessive sister clades to all remaining snakes; the following monophyletic clades within crown group caenophidians: Afro-Asian psammophiids (including Mimophis from Madagascar), Elapidae, Pseudoxyrhophiinae, Colubrinae, Natricinae, Dipsadinae, and Xenodontinae. *Homoroselaps* is associated with atractaspidids. Two higher taxonomic clades within Caenophidia one new subfamily within Dipsadidae were nomed. The phylogenetic analyses suggest taxonomic changes within xenodontines, five new tribes, eight new genera were created and two genera were resurrected. The genera *Xenoxybelis* and *Pseudablabes* were synonymize with *Philodryas*; *Liophis* and *Umbrivaga* with *Erythrolamprus*; and *Lystrophis* and *Waglerophis* with *Xenodon*.

Keywords: Serpentes, Caenophidia, Dipsadidae, Xenodontinae, Molecular Phylogeny, Systematics, Taxonomy.

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Apresentação

Esta tese encontra-se estruturada em uma introdução, uma seção de artigos produzidos, uma conclusão geral e perspectivas.

Este formato visa, em sua introdução, ilustrar o conhecimento a cerca das relações filogenéticas entre os dipsadídeos, desde os primeiros trabalhos com enfoque molecular até o início de meu projeto.

Na seção de artigos produzidos, os resultados obtidos durante o doutorado encontram-se descritos na forma de dois artigos, os quais figuram como corpo da tese.

Já na conclusão geral, destaco os principais resultados da tese, enquanto nas perspectivas, comento os desdobramentos futuros dos trabalhos realizados durante meu doutorado.

Introdução

Sistemática das Serpentes avançadas

Nas últimas três décadas, a compreensão das relações filogenéticas entre os Caenophidia, conhecidos classicamente como “serpentes avançadas”, vem sofrendo profundas alterações, as quais são diretamente relacionadas com o advento da sistemática molecular e da utilização de critérios objetivos na aplicação do método filogenético (Lawson et al., 2005; Zaher et al., 2009).

A composição dos Caenophidia abrange tradicionalmente a grande maioria das serpentes atuais, distribuídas em cinco famílias: Acrochordidae, Viperidae, Colubridae, Atractaspididae e Elapidae; sendo as quatro últimas frequentemente alocadas na superfamília Colubroidea (Pough et al., 2004).

Apesar do debate e dos sensíveis avanços acerca da composição destes táxons no período pré-molecular (Dowling & Duellman, 1978; McDowell, 1987; Underwood, 1967), a família Colubridae continuou representando um problema central na taxonomia dos Caenophidia, tendo constantemente questionado o seu caráter monofilético e as relações entre seus grupos. McDowell (1987), ao comentar os avanços acerca da morfologia comparada dos colubrídeos, ressaltou que os resultados moleculares pioneiros da época, tomados como parâmetro de avaliação independente, já apontavam para a inadequação dos esquemas taxonômicos vigentes. Da mesma forma, Ferrarezzi (1994) e Zaher (1999) comentam que nenhuma sinapomorfia morfológica putativa, sugerida até então, era capaz de diagnosticar de forma definitiva a família Colubridae, deixando claro seu provável parafiletismo.

Os colubrídeos, em sua composição clássica, com mais de 300 gêneros contendo aproximadamente 1500 espécies (Uetz et al., 2010), são amplamente distribuídos por todos os continentes não austrais, à exceção da Austrália, onde representam dispersões recentes. Doze subfamílias eram comumente reconhecidas, sendo apenas quatro as sustentadas por um ou mais caracteres derivados compartilhados (McDowell, 1987; Zaher, 1999). Segundo Zaher (1999), Colubridae era composta pelas seguintes subfamílias: Xenodermatinae, Pareatinae, Calamariinae, Homalopsinae, Boodontinae, Pseudoxyrhophiinae, Colubrinae, Psammophiinae, Pseudoxenodontinae, Natricinae, Dipsadinae, e Xenodontinae.

Este esquema taxonômico para os colubrídeos foi de certa forma corroborado pelos primeiros trabalhos moleculares, uma vez que o monofiletismo de muitas subfamílias foi frequentemente recuperado (Cadle, 1988, Dowling et al., 1996). Contudo, a natureza parafilética da família tornou-se evidente com os avanços moleculares recentes (Kraus & Brown, 1998; Slowinski & Lawson, 2002; Vidal & Hedges, 2002, Kelly et al., 2003). Consequentemente, uma nova classificação para os colubrídeos foi proposta por Lawson et al. (2005) e Vidal et al. (2007). Os resultados destes estudos sugeriam que para tornar a taxonomia dos Caenophidia um reflexo das relações filogenéticas de seus componentes, a família Colubridae deveria incluir todos os táxons pertencentes à superfamília Colubroidea. Em outras palavras, para tornar Colubridae monofilético, os representantes das famílias Viperidae, Elapidae e Atractaspididae deveriam ser consideradas subfamílias de Colubridae.

Entretanto, evitando esta drástica mudança taxonômica, Lawson et al. (2005) restringiram o conceito de Colubridae, elevando à condição de família as subfamílias Pareatinae e Homalopsinae. Desta forma, Lawson et al. limitaram Colubridae a cinco subfamílias (Calamariinae, Colubrinae, Natricinae, Pseudoxenodontinae, Xenodontinae [incluindo Dipsadinae]) e deslocaram as subfamílias Psammophiinae, Boodontinae, Pseudoxyrhophiinae e Xenodermatinae para dentro da família Elapidae. Por outro lado, Vidal et al. (2007) não apenas restringiram ainda mais o conceito de Colubridae, elevando à família as subfamílias Xenodermatinae, Natricinae, Pseudoxenodontinae, Dipsadinae (incluindo Xenodontinae) e Colubrinae (incluindo Calamariinae), mas também o conceito de Colubroidea, o qual passou a ser restrito a apenas quatro famílias (Natricidae, Pseudoxenodontidae, Dipsadidae e Colubridae).

Apesar destes avanços na sistemática dos Caenophidia, as relações entre as espécies dentro das famílias de colubróideos (*sensu* Vidal et al., 2007) continuaram amplamente indefinidas.

A irradiação dos dipsadídeos neotropicais

A maior diversidade dos colubróideos está concentrada nos trópicos. No Novo Mundo, a região Neotropical compartilha com a Neártica alguns gêneros de colubrídeos (p. ex., *Drymarchon*, *Drymobius*, *Masticophis*), que provavelmente chegaram ao hemisfério sul por dispersão (Vanzolini e Heyer, 1985). A maioria dos gêneros presentes na região Neotropical pertence à irradiação de colubróideos centro e sul-

americanos, os quais eram comumente reunidos nas subfamílias Xenodontinae e Dipsadinae (Cadle, 1984a,b,c, 1985). Juntas, estas duas subfamílias constituem o grupo mais diversificado de colubróideos do mundo. Com 90 gêneros contendo mais de 600 espécies descritas, este conjunto abrange um pouco mais de 20% de toda a diversidade atual de Serpentes.

A maioria dos representantes destas duas subfamílias está distribuída por toda a extensão dos continentes sul-americano e centro-americano, do México ao extremo sul da América do Sul, da costa do Oceano Pacífico à costa do Atlântico. Algumas espécies, porém, alcançam o norte dos Estados Unidos (Dunn, 1928; Cadle, 1985).

As subfamílias Xenodontinae e Dipsadinae foram sempre consideradas como formando um grupo monofilético de "colubrídeos do Novo Mundo", informalmente denominados de "xenodontíneos" (*sensu lato*; McDowell, 1987). Denominação que deriva da definição dada por Dunn em 1928 (Ophiinae = Xenodontinae; Dunn, 1928). Entretanto, Cadle (1984a,b, 1988) questionou este esquema, apresentando os resultados de um estudo imunológico abrangente que apontava para um possível parafiletismo do grupo em relação aos colubrinae do novo mundo. Baseado nestes resultados imunológicos, Cadle (1984a,b,c, 1988) subdividiu os xenodontíneos em três grupos distintos, dos quais os táxons centro e sul-americanos representam, de um modo geral, as subfamílias Dipsadinae e Xenodontinae. O terceiro grupo abrange cinco gêneros de xenodontíneos norte-americanos, considerados por Cadle como colubrídeos *incertae sedis*. Apesar das limitações apresentadas pelos seus resultados (distâncias imunológicas apenas), o autor sugeriu que as duas subfamílias poderiam não ser proximamente relacionadas. O argumento usado por Cadle para rejeitar a possível condição de grupo-irmão entre os Xenodontinae e Dipsadinae foi a grande taxa de divergência imunológica, levando-o a sugerir uma provável origem africana para as duas subfamílias (Cadle, 1985). Zaher (1994), utilizando caracteres morfológicos, forneceu evidências que corroboram o monofiletismo dos Dipsadinae e dos Xenodontinae. Entretanto, estas também não confirmaram a suposta relação de grupo-irmão entre os táxons sul e centro-americano. Não havia tampouco uma definição satisfatória dos subgrupos pertencentes às duas subfamílias, embora os resultados obtidos por Dowling (1975), Dowling e Duellman (1978), Jenner (1981), Ferrarezzi (1994) e Zaher (1994) para os táxons da subfamília Xenodontinae apontavam para vários agrupamentos tribais provavelmente monofiléticos. Até o início desta tese, somente seis tribos de xenodontíneos estavam bem corroboradas por uma série de

caracteres morfológicos derivados e compartilhados: os Xenodontini (Dowling, 1975; Dixon, 1980; Zaher, 1999), Pseudoboini (Bailey, 1967; Zaher, 1994, 1999), Dipsadini (Peters, 1960; Zaher, 1999), Hydropsini (Roze, 1957; Zaher, 1999), Philodryadini (Zaher, 1999) e Elapomorphini (Savitsky, 1979; Ferrarezzi, 1993).

A partir dos anos 90, as análises moleculares utilizando sequencias de DNA passaram a fornecer evidencias que levavam a uma revisão das hipóteses para o grupo. Heise *et al.* (1995) apresentaram uma das primeiras análises filogenéticas de sequências de DNA dos grandes grupos de serpentes, que incluiu alguns representantes dos colubróideos neotropicais. A análise de fragmentos dos genes 12S e 16S rRNA feita por Heise *et al.* (1995) indicou o parafiletismo dos xenodontíneos (*sensu lato*), corroborando assim uma das hipóteses sugeridas por Cadle (1985, 1988). Entretanto, Kraus e Brown. (1998), encontraram resultados contrastantes com os de Cadle (1985, 1988) e Heise *et al.* (1995), ao analisarem um gene mitocondrial codificante (ND4), obtendo um clado monofilético para os xenodontíneos e uma baixa divergência genética entre os táxons. Kraus e Brown (1998) concluíram que os resultados imunológicos obtidos por Cadle derivavam de um viés da metodologia utilizada e não representavam o tempo de divergência entre os grupos.

Contudo, estes trabalhos moleculares pioneiros ainda sofriam com uma amostragem de táxons muito limitada (poucos colubróideos e apenas três xenodontíneos no trabalho de Heise *et al.* e seis no de Kraus e Brown) e com a escassez de sítios informativos. Foi somente a partir do trabalho realizado por Vidal *et al.* (2000) que se vislumbrou pela primeira vez um sinal filogenético molecular mais claro para os xenodontíneos. Sequenciando 85 táxons para os mesmos genes ribossomais empregados por Heise *et al.* (1995), os resultados encontrados por Vidal *et al*. (2000) apontam para o monofiletismo dos xenodontíneos *sensu lato*, e para o posicionamento do clado norte-americano como grupo-irmão dos clados centro (Dipsadinae) e sul-americanos (Xenodontinae). Entretanto, todos os agrupamentos basais da filogenia, referentes às relações dentro dos xenodontíneos, obtiveram baixos valores de *bootstrap* (menores que 50%), indicando claramente a falta de evidência para este nível filogenético. Esta falta de suporte desestabilizava a confiança na maioria dos agrupamentos propostos por Vidal *et al.* (2000), mas reforçava a ideia sugerida por Kraus de que os subgrupos de xenodontíneos não representam linhagens muito divergentes filogeneticamente (*contra* Cadle, 1984a, 1985). Vidal *et al.* ainda afirmaram que os xenodontíneos tiveram possivelmente uma origem na Ásia ou na América do Norte e que a colonização das

Américas Central e do Sul deu-se por dispersão, assim como a colonização das Galápagos e das Antilhas (*contra* Crother, 1999). Algumas tribos definidas por sinapomorfias morfológicas também foram sustentadas de forma significativa na análise molecular de Vidal *et al.* (2000), estas são: Xenodontini, Hydropsini, Pseudoboini e Alsophiini. Os dados moleculares também confirmaram o parafiletismo do gênero *Philodryas*, sugerido originalmente por Zaher (1999) que incluiu dentro deste primeiro o gênero *Xenoxybelis*.

Os resultados moleculares de Vidal *et al.* (2000) foram corroborados por alguns estudos moleculares posteriores (Kelly *et al.*, 2003; Slowisky e Lawson, 2002), mas foram curiosamente rejeitados pelos resultados apresentados por Pinou *et al.* (2004) que empregaram as mesmas sequências dos genes ribossomais 12S e 16S geradas por Vidal e seus colaboradores. Pinou *et al.* (2004) também acrescentaram novas sequências para os táxons "relictuais norte-americanos", encontrando uma topologia na qual os xenodontíneos não formavam um grupo monofilético, já que os natricíneos (representados pelo gênero *Natrix*) se enraizavam dentro desta irradiação. Com o estudo de Vidal et al., (2007), as subfamílias Xenodontinae e Dipsadinae passaram a ser designadas como pertencentes a família Dipsadidae. Entretanto, essa decisão taxonômica não foi acompanhada por nenhuma discussão sobre os caracteres classicamente utilizados para diagnosticar os grupos.

Os trabalhos acima mencionados demonstram que, no momento em que esta tese foi iniciada, existia pouco consenso entre as filogenias moleculares e a evidência morfológica conhecida para os grupos de xenodontíneos. Paralelamente, a sistemática dos Caenophidia encontrava-se em processo de intensa redefinição. Estes fatos não representavam apenas um problema de ordem taxonômica, uma vez que a falta de hipóteses filogenéticas para as duas subfamílias e a precariedade dos arranjos taxonômicos para os Caenophidia dificultavam a realização de estudos de cunho evolutivo voltados para a grande variação comportamental e ecológica existente nestes grupos.

Desta forma, meu doutorado teve como objetivo estabelecer as relações filogenéticas entre os componentes da irradiação de Dipsadidae (*sensu* Vidal et al., (2007)) neotropicais utilizando evidências moleculares (sequencias de DNA), com enfoque especial na definição dos agrupamentos tribais dentro de Xenodontinae. Contudo, os resultados obtidos possibilitaram uma revisão taxonômica mais ampla, emglobando a sistemática de todos Caenophidia.

Histórico dos artigos produzidos

O primeiro artigo aqui apresentado (Zaher, et al., 2009), se origina dos dados gerados no início do projeto de doutorado. Estes dados, em conjunto com as sequencias disponíveis no GenBank, possibilitaram uma análise filogenética dos Caenophidia, focando principalmente nos dipsadídeos da subfamília Xenodontinae. Os resultados desta análise em conjunto com aqueles obtidos por Zaher (1999), serviram como base para a definição de um novo esquema taxonômico para os Dipsadidae, ao mesmo tempo que possibilitaram propor um novo arranjo taxonômico coerente para todos os Caenophidia. Este artigo já conta com 49 citações (fonte: www.scopus.com), tendo suas mudanças taxonômicas repercutido fortemente na comunidade herpetológica (ver Mulcahy et al., 2011 e Myers, 2011 entre outros).

Apesar dos diversos avanços alcançados pelo primeiro artigo publicado, muitas questões permaneceram em aberto sugerindo a necessidade de mais estudos tanto sobre as relações filogenéticas entre os Caenophidia, quanto a sistemática dos Dipsadidae. Logo após a publicação deste artigo (Zaher et al., 2009), dois estudos questionaram os resultados filogenéticos e a taxonomia proposta. Hedges et al., (2009) questionou os resultados apresentados para os dipsadídeos das “West Indians”, enquanto que Vidal et al., (2010) questionou as decisões taxonômicas tomadas dentro das tribos Xenodontini e Philodryadini, bem como, questionou a validade das novas tribos propostas. Mais recentemente, Pyron et al., (2011) publicaram um abrangente estudo sobre as relações filogenéticas dos Caenophidia, onde defendem a taxonomia proposta por Lawson et al., (2005), questionando tanto o esquema taxonômico proposto por Vidal et al., (2007) quanto o proposto por nós em 2009.

Desta forma, realizamos um segundo estudo (Grazziotin, et al., *submetido*), onde foi abordada a questão da filogenia dos Dipsadidae tendo como pano de fundo o nosso primeiro trabalho (Zaher et al., 2009) e os trabalhos subsequentes, que de alguma forma questionaram a taxonomia proposta em 2009. Diversas sequencias novas foram incluídas nesta análise, bem como, todas as sequencias produzidas subsequentemente por outros autores. Esta reanálise possibilitou a revisão de alguns pontos importantes da sistemática da família, permitindo demostrar que a maioria das discordâncias entre os

autores não se sustentam nos resultados filogenéticos, representando apenas a preferencia taxonômica do autor. Este artigo encontra-se em revisão na revista *Cladistics*, tendo sido aceito pendendo revisões. A versão aqui apresentada consta do texto original ao qual foram incluídas todas as revisões sugeridas pelos avaliadores e pelo editor associado.

Capítulo 1: Artigo publicado na revista *Papéis Avulsos de Zoologia*

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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PALAVRAS-CHAVE: Serpentes, Colubridae, Caenophidia, phylogeny, classification, systematics, Xenodontinae, Dipsadinae, new genus, Elapoidea, Colubroidea, South America, West Indies.

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 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), 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 and Duellman, "1974-1978" [1978]; Ferrarezzi, 1994a,b; Meirte, 1992; Underwood and 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, 1999; Glaw et al., 2007a,b; Gravlund, 2001; Heise et al., 1995; Kelly et al., 2003, 2008, 2009; Keogh, 1998; Kraus and Brown, 1998;; Lawson et al., 2005; Mulcahy, 2007; Nagy et al., 2003, 2005; Pinou et al., 2004; Vidal et al., 2000, 2007, 2008; Vidal and Hedges, 2002). 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 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 and Brown, 1999). 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 and Duellman (1978), McDowell (1987), Williams and 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 and 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 and Whiting 1999) in small molecular data matrices, problems that were acknowledged by Kraus and Brown (1999) and Kelly et al. (2008), and supported by simulation and other studies (e.g., Goertzen and Theriot, 2003; Salisbury and 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 and 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).

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., 2005). 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., 2005). Parsimony analysis under direct optimization is distinct from most molecular phylogenetic analyses of snakes done so far, which have used model-based analyses (e.g., maximum-likelihood and Bayesian inferences).

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

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

series matrix. These were subsequently retro-translated to DNA in order to be analyzed in the POY search as static homology matrix.

Search strategy and support indexes

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

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

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

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

Finally, we conducted a round of TBR using an interactive pass algorithm (Wheeler, 2003), which applies the information of the three adjacent nodes to perform a three dimensional alignment optimization for the target node. The resultant dynamic homologies were transformed into static homologies and the implied alignment was exported in Hennig86 format. The phylogenetic results were then checked using the

TNT (Tree analysis using New Technology, version 1.1) software (Goloboff et al., 2008). For TNT Maximum Parsimony search we used the "new technology" algorithms, mixing rounds of TBR, SPR (Sub-tree Pruning and Regrafting), Drift, Ratchet, Sectorial search, and tree fusing. Searches were stopped after the consensus was stabilized for five rounds. To access the corroboration values and support values (sensu Grant and 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 analyses 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 argininae, rendering difficult to define whether *Acrochordus* and *Bitis* show a deletion at the same site that 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-argininae 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 as post-transcriptional modifications and RNA editing (Bennicke 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 and 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 Colubrine, 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 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 and 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 and Scanlon, 2002; Apesteguía and 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 and Brown (1998) found *Acrochordus* to cluster with *Xenodermus-Achalinus* (Xenodermatinae); in addition, Kraus and 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 and 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 and 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 phyletically 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 and 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 all molecular studies (Cadle, 1992; Knight and 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 all major lineates 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 and 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 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, Pinou et al. (2004) did not attempt 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 and Greene, 2000; Cundall and Irish, 2008; Dowling and Duellman, 1978; Ferrarezzi, 1994a, b; Greene, 1997; Kelly et al., 2003; Kraus and Brown, 1997; 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 and 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* + *Oxyrhabdion*) 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 of snakes, 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 and 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 and 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 and 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 and Irish, 2008; see also Cundall and 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 and 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 and 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 Pseudoxhyrhophiidae 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, 1963, 1978; Zaher, 1994); 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 and 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 and Campbell, 2001; *Bothrops* Wagler (*in* Spix), 1824; *Calloselasma* Cope, 1860; *Causus* Wagler, 1830; *Cerastes* Laurenti, 1768; *Cerrophidion* Campbell and Lamar, 1992; *Crotalus* Linnaeus, 1758; *Cryptelytrops* Cope, 1860; *Daboia* Gray, 1842; *Deinagkistrodon* Gloyd, 1979; *Echis* Merrem, 1820; *Eristicophis* Alcock (*in* Alcock and Finn), 1896; *Garthius* Malhotra and 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 and Thorpe 2004; *Porthidium* Cope, 1871; *Proatheris* Broadley 1996; *Protobothrops* Hoge and Romano-Hoge, 1983; *Pseudocerastes* Boulenger, 1896; *Sistrurus* Garman, 1884; *Triceratolepidophis* Ziegler, Herrmann, David, Orlov and Plauvels 2000; *Trimeresurus* Lacépède, 1804; *Tropidolaemus* Wagler, 1830; *Vipera* Laurenti, 1768; *Viridovipera* Malhotra and Thorpe, 2004; *Zhaoermia* Gumprecht and 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 and 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 and 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 and Latreille), 1801; *Erpeton* Lacépède, 1800; *Fordonia* Gray, 1842; *Gerarda* Gray, 1849; *Heurnia* de Jong, 1926; *Homalopsis* Kuhl and 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 (19787) 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 and 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; *Dromophis* Peters, 1869; *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 and Wollberg, 1970; McCarthy, 1985; Underwood and Kochva, 1993; Zaher, 1994, 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 and 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 and 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 and 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 and 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 and 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 and 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 and 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. (2007). *Bibilava* Glaw, Nagy, Franzen and Vences, 2007 was synonymized with *Thamnosophis* (Cadle and 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 and 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 and 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 and Smith 1991; *Liopeltis* Fitzinger, 1843; *Lycodon* Boie (in Fitzinger), 1826; *Lytorhynchus* Peters, 1862; *Macroprotodon* Duméril and Bibron (in Guichenot), 1850; *Maculophis* Burbrink and Lawson, 1997; *Masticophis* Baird (in Baird and Girard), 1853; *Mastigodryas* Amaral, 1934; *Meizodon* Fischer, 1856; *Oligodon* H.Boie (*in* Fitzinger), 1826; *Oocatochus* Helfenberger, 2001; *Opheodrys* Fitzinger, 1843; *Oreocryptophis* Utiger, Schätti and Helfenberger, 2005; *Oreophis* Utiger, Helfenberger, Schaetti, Schmidt, Ruf & Ziswiler, 2002; *Orthriophis* Utiger, Helfenberger, Schaetti, Schmidt, Ruf and 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; *Rhinobothrium* Wagler, 1830; *Rhinocheilus* Girard (in Baird and Girard), 1853; *Rhynchocalamus* Günther, 1864; *Rhynchophis* Mocquard, 1897; *Salvadora* Baird (in Baird and Girard), 1853; *Scaphiodontophis* Taylor and Smith, 1943; *Scaphiophis* Peters, 1870; *Scolecophis* Fitzinger, 1843; *Senticolis* Dowling and Fries, 1987; *Sibynophis* Fitzinger, 1843; *Simophis* Peters, 1860; *Sonora* Girard (in Baird and Girard), 1853; *Spalerosophis* Jan (*in* De Filippi), 1865; *Spilotes* Wagler, 1830; *Stegonotus* Duméril, Bibron and Duméril, 1854; *Stenorrhina* Duméril, 1853; *Stilosoma* Brown, 1890; *Symphimus* Cope, 1870; *Sympholis* Cope, 1862; *Tantilla* Girard (in Baird and 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 and 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 colubrines and natricines is considered to have derived from a centrifugally divided sulcus, but in different ways in the two groups (McDowell 1961). On unilobed organs of colubrines 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 natricines when the sulcus extends to only one of the lobes of a bilobed organ, it is

always to the left lobe (see also Rossman and Eberle, 1977; and Zaher, 1999: 25-26). Lawson et al. (2005) have shown that *Macroprotodon* lies within the subfamily Colubrinae, 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 subfamily Colubrinae.

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: 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 and Eberle, 1977; *Amphiesma* Duméril, Bibron and 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 and Girard), 1853; *Opisthotropis* Günther, 1872; *Parahelicops* Bourret, 1934; *Pararhabdophis* Bourret, 1934; *Regina* Baird (in Baird and Girard), 1853; *Rhabdophis* Fitzinger, 1843; *Seminatrix* Cope, 1895; *Sinonatrix* Rossman and Eberle, 1977; *Storeria* Girard (in Baird and Girard), 1853; *Thamnophis* Fitzinger, 1843; *Tropidoclonion* Cope, 1860; *Tropidonophis* Jan, 1863; *Virginia* Girard (in Baird and Girard), 1853; *Xenochrophis* Günther, 1864.

COMMENTS: Among natricids, the New World Natricines are a monophyletic tribe (Thamnophiini) supported by molecular and morphological evidence (Rossman and Eberle 1977; Alfaro and 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, Carphopiinae **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* Gray, 1842 and *Heterodon* Latreille (in Sonnini and Latreille), 1801 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 and 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* Villa, 1971, *Diaphorolepis* Jan, 1863, *Emmochliophis* Fritts and Smith, 1969, *Enuliophis* McCranie and Villa, 1993, *Enulius* Cope, 1871, *Hydromorphus* Peters, 1859, *Nothopsis* Cope, 1871, *Rhadinophanes* Myers and Campbell, 1981, *Synophis* Peracca, 1896, and *Tantalophis* Duellman, 1958, which have a dipsadid hemipenial morphology, belong within Dipsadidae, and we place them here incertae sedis.

Guo et al. (2008) 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* Fitzinger, 1843, *Lioheterophis* Amaral, 1934, *Sordellina* Procter, 1923, and *Uromacerina* Amaral, 1930 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: *Crisantophis* Villa, 1971; *Diaphorolepis* Jan, 1863; *Emmochliophis* Fritts and Smith, 1969; *Enuliophis* McCranie and Villa, 1971; *Enulius* Cope, 1871; *Hydromorphus* Peters, 1859; *Nothopsis* Cope, 1871; *Rhadinophanes* Myers and Campbell, 1981; *Synophis* Peracca, 1896; *Tantalophis* Duellman, 1958; *Xenopholis* Peters, 1869; *Cercophis* Fitzinger, 1843, *Lioheterophis* Amaral, 1934, *Sordellina* Procter, 1923 and *Uromacerina* Amaral, 1930; *Farancia* Gray, 1842; *Heterodon* Latreille (in Sonnini and Latreille), 1801; *Thermophis* Malnate, 1953.

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 and Girard), 1853; *Diadophis* Girard (in Baird and 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 and 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 and Smith, 1998; *Chersodromus* Reinhardt, 1860; *Coniophanes* Hallowell (in Cope), 1860; *Cryophis* Bogert and Duellman, 1963; *Dipsas* Laurenti, 1768; *Eridiphas* Leviton and 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 and 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 Jenner and Dowling, 1985; Philodryadini Jenner, 1983; 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: 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 and Cadle, 1994).

CONTENT: *Psomophis* Myers and 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, 1993a, 1994b; Savitzky, 1979; Zaher, 1994).

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

TRIBE TROPIDODRYADINI **new tribe**

(Terminal taxon: *Tropidodryas stiaticeps*)

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

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

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 Dum., Bibr. & Dum.), 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 and 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, 1994, 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 and 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 and 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 and Dowling, but which are not closely related; see Myers and Cadle, 1994, and Zaher, 1999).

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

***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, 1994; 1999).

Content: *Mussurana bicolor* (Peracca, 1904) **new combination**; *Mussurana montana* (Franco, Marques and Puorto, 1997) **new combination**; *Mussurana quimi* (Franco, Marques and 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, if a more detailed phylogenetic analysis of the newly extended genus *Philodryas* shows 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 Phylodryadini (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 *Pseudoreyx* 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 and 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 paraphyletic 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 and 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 and 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 and 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 and 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 and 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 contribution 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 and Garrido, 1992; *Arrhyton supernum* Hedges and Garrido, 1992; *Arrhyton taeniatum* Günter, 1858; *Arrhyton tanyplectum* Schwartz and 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 and 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 and 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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FIGURE CAPTION

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.

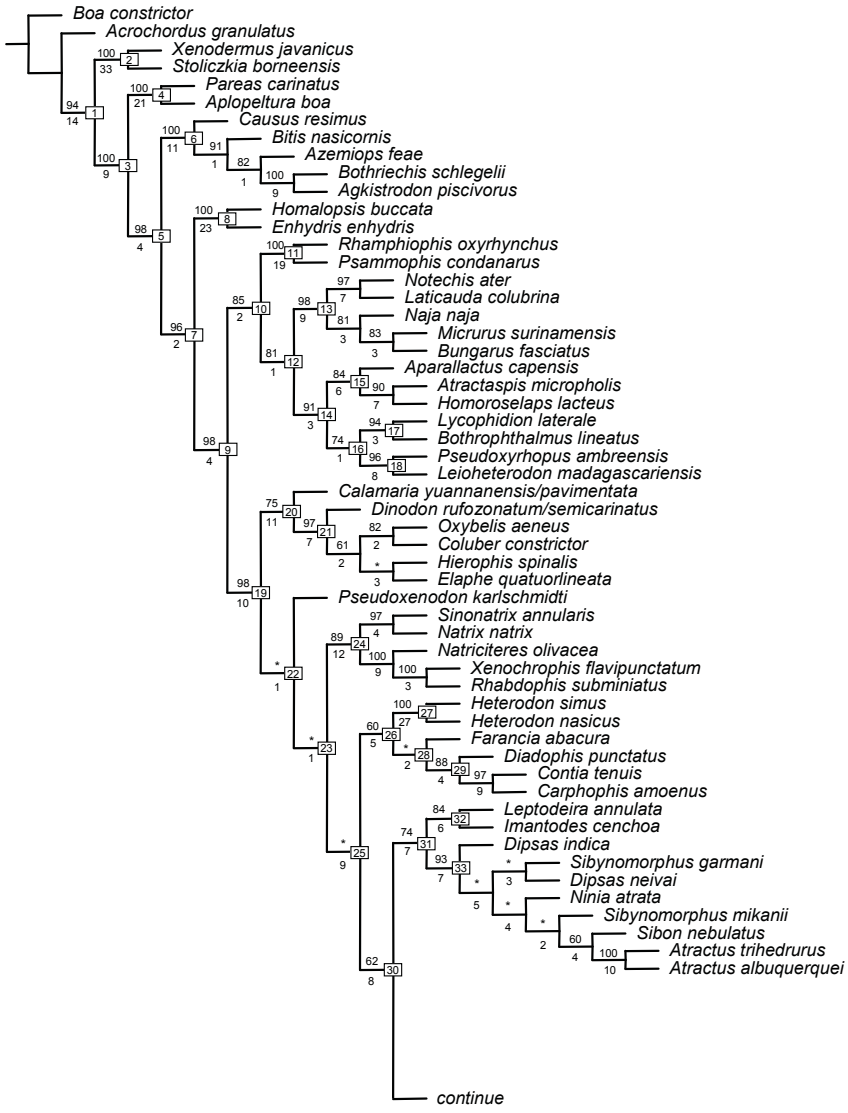
Boa constrictor
Acrochordus granulatus
Xenodermus javanicus
Stoliczkia borneensis
Pareas carinatus
Aplopeltura boa
Causus resimus
Bitis nasicornis
Azemiops feae
Bothriechis schlegelii
Agkistrodon piscivorus
Homalopsis buccata
Enhydris enhydris
Rhamphiophis oxyrhynchus
Psammophis condanarus
Notechis ater
Laticauda colubrina
Naja naja
Micrurus surinamensis
Bungarus fasciatus
Aparallactus capensis
Atractaspis microplolis
Homoroselaps lacteus
Lycophidion laterale
Bothrophthalmus lineatus
Pseudoxyrhopus ambreensis
Leioheterodon madagascariensis
Calamaria yuannanensis/pavimentata
Dinodon rufozonatum/semicarinatus
Oxybelis aeneus
Coluber constrictor
Hierophis spinalis
Elaphe quatuorlineata
Pseudoxenodon karlschmidti
Sinonatrix annularis
Natrix natrix
Natriciteres olivacea
Xenochrophis flavipunctatum
Rhabdophis subminiatus
Heterodon simus
Heterodon nasicus
Farancia abacura
Diadophis punctatus
Contia tenuis
Carphophis amoenus
Leptodeira annulata
Imantodes cenchoa
Dipsas indica
Sibynomorphus garmani
Dipsas neivai
Ninia atrata
Sibynomorphus mikanii
Sibon nebulatus
Atractus trihedrurus
Atractus albuquerquei
continue

Figure 1. *Continued*

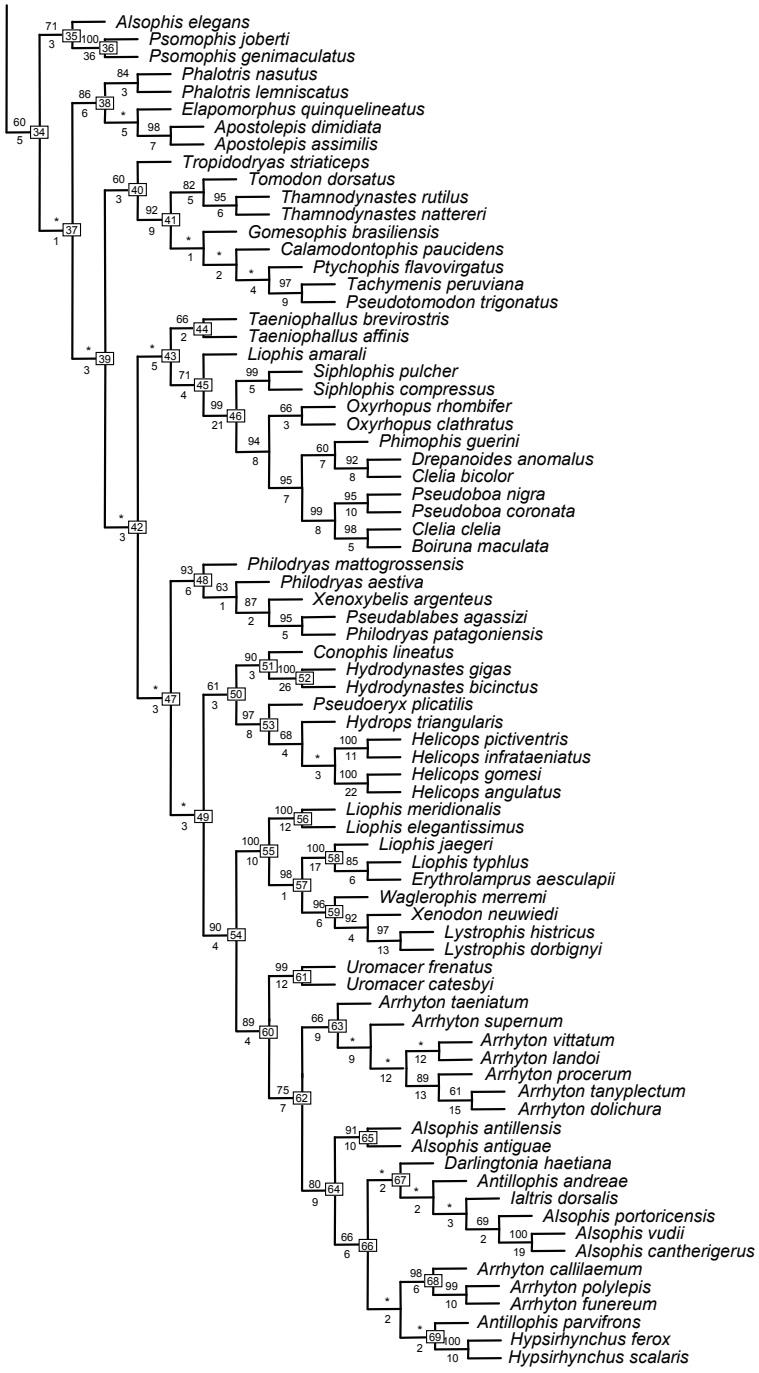

TABLE CAPTION

Table 1. Comparison among the principal molecular phylogenetic studies of Colubroidea .

Table 2. List of taxa and sequences analyzed in this study.

TABLE 1

References	Focused in	Number of taxa	Genes	base pairs
Kraus and Brown (1998)	Serpentes	37	ND4	694
Gravlund (2001)	Caenophidia	43	12S, 16S	722
Vidal and 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

TABLE 2

	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
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
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**

Capítulo 2: Artigo aceito para publicação na revista *Cladistics*

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

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Running title: Molecular phylogeny of New World Dipsadidae

Abstract

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

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Introduction

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

The Colubroides contains approximately 440 genera and 2150 species (Uetz, 2010) arranged into 13 families (Zaher et al., 2009): Atractaspididae Günther 1858; Calamariidae Bonaparte 1838; Colubridae Oppel 1811; Dipsadidae Bonaparte 1838; Elapidae Boie 1827; Homalopsidae Bonaparte 1845; Lamprophiidae Fitzinger 1843 (including the subfamilies Lamprophiinae and Pseudoxyrhophiinae Dowling 1975); Natricidae Bonaparte 1838; Pareatidae Romer 1956; Psammophiidae Bonaparte 1845; Viperidae Oppel 1811; Pseudoxenodontidae McDowell 1987; and Xenodermatidae Gray 1849.

The New World Dipsadidae represents one of the largest radiations of colubroidean snakes, with approximately 700 species distributed throughout the Americas and the West

Indies (Zaher et al., 2009; Hedges et al., 2009). Recent studies (Vidal et al., 2000, 2010; Pinou et al., 2004; He et al., 2009; Zaher et al., 2009) confirm evidence for three historically distinct lineages (Cadle, 1984a, b, 1985, 1988). These lineages usually are considered as distinct subfamilies, although there is no consensus concerning the monophyly of the lineage composed by the five, mainly North American, genera *Carphophis*, *Contia*, *Diadophis*, *Farancia*, and *Heterodon* (Zaher et al., 2009; Vidal et al., 2010).

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

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

Vidal et al. (2010) used most of the DNA sequences available in GenBank for the genes 12S and 16S rRNAs to provide a phylogenetic analysis of Dipsadidae, but they excluded most West Indian genera (i.e. *Uromacer*, *Hypsirhynchus*, *Schwartzophis*, *Antillophis*, *Caraiba*, *Darlingtonia*, *Magliophis*, and *Haitiophis*). They added data for seven genera not previously sequenced—*Crisantophis*, *Echinanthera*, *Manolepis*, *Nothopsis*,

Trimetopon, *Umbrivaga*, and *Xenopholis*. Vidal et al.'s (2010) results are highly consistent with those of Zaher et al. (2009) in recovering all tribes, save for their Conophiini, which is polyphyletic. Similarly, the intratribal relationships resolved by Vidal et al. (2010) are highly concordant with those of Zaher et al. (2009), differing substantially only within Dipsadinae, which is poorly sampled in both studies. Vidal et al. (2010) also recovered a paraphyletic lineage of North American dipsadids (their Heterodontinae; a name discussed in Appendix 1) with a monophyletic Carphophiinae (*sensu* Zaher et al., 2009). The analysis of Vidal et al. (2010) obtained low support for all deeper branches in the dipsadid tree (Bootstrap < 50%; Bayesian Posterior Probability [BPP] < 90%), rendering questionable any taxonomic conclusion regarding these deeper clades; Zaher et al. (2009) also acknowledged this trend. While obtaining a concordant phylogeny, Vidal et al. (2010) disagreed with several taxonomic changes made by Zaher et al. (2009).

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

To evaluate the conflicting taxonomies of Zaher et al. (2009), Hedges et al. (2009), and Vidal et al. (2010), we present a phylogenetic analysis of the New World dipsadids based on an expanded data matrix that combines all sequences from GenBank with 273 new sequences from 62 species. The matrix contains eight genes from 246 terminal taxa, of which 196 are dipsadids. Our sampling represents 115 genera of colubroideans and 70 genera of dipsadids, including two previously unsampled genera (*Rhachidelus* and *Sordellina*). We add 95 dipsadids to the data matrix published by Zaher et al. (2009), 75 to that of Vidal et al. (2010), and 126 to that of Pyron et al. (2011). All West Indian species in the Alsophiini used by Hedges et al. (2009) are included herein to test specifically the monophyly of the

Alsophiini and its constituent parts. We include all new sequences generated by Vidal et al. (2010) to reanalyze phylogenetic relationships within a broader context. Contrary to Vidal et al. (2010), our primary goal remains that of defining a stable taxonomic scheme that does not conflict with a recovered hypothesis of phylogenetic interrelationships (Zaher et al., 2009).

Material and methods

Taxon and gene sampling

Our data matrix comprises 246 terminal taxa, and sequences for five mitochondrial (12S, 16S, cytb, nd2, nd4) and three nuclear genes (bdnf, c-mos, rag2) (Appendix S1). We sequenced 273 DNA fragments for 62 species, including 63 sequences for 12S, 61 for 16S, 48 for cytb, two for nd4, 60 for bdnf, and 39 for c-mos. We added 13 genera absent from Zaher et al. (2009): *Rhachidelus*, *Xenopholis*, *Echinanthera*, *Sordellina, Geophis*, *Hypsiglena*, *Tretanorhinus*, *Thermophis*, *Nothopsis*, *Trimetopon*, *Crisantophis*, *Manolepis*, and *Umbrivaga*. Our sampling also was broadened by adding species in the following genera: *Apostolepis*, *Atractus*, *Oxyrhopus*, *Phalotris*, *Philodryas*, *Xenodon*, and *Erythrolamprus*. We incorporated 761 additional sequences from GenBank including 178 for 12S, 172 for 16S, 96 for cytb, 56 for nd2, 75 for nd4, 13 for bdnf, 112 for c-mos, and 59 for rag2. If multiple sequences were available in GenBank for a given taxon, we selected only one sequence and chose the most complete sequence for inclusion. The caenophidian tree was rooted using the boine *Boa constrictor* as the primary outgroup taxon.

Our analysis included representatives of the following families of caenophidians (number of representative species in parentheses, taxonomy following Zaher et al., 2009): Acrochordidae (1), Atractaspididae (3); Calamariidae (3); Colubridae (5); Dipsadidae (188,

including 146 Xenodontinae, 29 Dipsadinae, 3 Carphophinae, and 10 Dipsadidae *incertae sedis*); Elapidae (5); Elapoidea *incertae sedis* (1, *Oxyrhabdium leporinum*); Homalopsidae (2); Lamprophiidae (5, including 2 Pseudoxyrhophiinae and 3 Lamprophiinae); Natricidae (8); Pareatidae (2); Psammophiidae (2); Pseudoxenodontidae (4); Viperidae (5); Xenodermatidae (3). Inclusion of the non-dipsadid colubroideans facilitated an evaluation of the monophyly of the Dipsadidae.

DNA sequencing

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

PCRs were purified with shrimp alkaline phosphatase and exonuclease I (GE Healthcare) and the sequences for 12S, 16S, nd4 and c-mos were processed using the

DYEnamic ET Dye Terminator Cycle Sequencing Kit (GE Healthcare) in a MegaBACE 1000 automated sequencer (GE Healthcare) following the manufacturer's protocols. The cytb and bdnf sequences were processed using BigDye Terminator cycle sequencing kit in an ABI 3700 sequencer (Applied Biosystems). Both strands were checked and, when necessary, manually edited using FinchTV (Geopisa). The consensus of the two strands was constructed manually with Bioedit 7.0.9 (Hall, 1999).

Homology and search strategy

We used two distinct procedures to define molecular homologies: 1) dynamic homology (DH) using POY version 4.1.2 (Varón et al., 2008); and 2) static homology via multiple alignment using Clustal X (Thompson et al., 1997) and MAFFT (Katoh et al., 2002). The terms "Implied Alignment" (IA) and "Multiple Alignment" (MA) were used only to distinguish the two methodologically distinct static alignments that resulted from the dynamic homology and static homology procedures, respectively (Wheeler, 2003). DH was performed using Maximum Parsimony (MP) as the optimality criterion, whereas MA was analyzed by MP and Maximum Likelihood (ML). Thus, three sets of consensus trees were produced as follow: (1) a consensus tree derived from a Maximum Parsimony analysis using dynamic homology (MP/DH); (2) a consensus tree derived from a Maximum Parsimony analysis using Multiple Alignment (MP/MA); (3) a consensus tree derived from a Maximum Likelihood analysis using Multiple Alignment (ML/MA). The discussion and comparisons emphasize the MP/DH and ML/MA analyses, but when relevant, we also comment on results derived from the MP/MA analysis.

We used two optimality criteria (MP and ML) and two distinct methods of delimiting molecular homology (DH and MA) to allow comparisons with the results of Zaher et al.

(2009), Hedges et al. (2009) and Vidal et al. (2010), to avoid controversy regarding a specific approach, and to assess to what extent the different approaches affected the results.

Dynamic homology

This methodology followed that of Zaher et al. (2009), in which only non-coding rRNAs (12S and 16S) were submitted to the direct optimization procedure of POY. First, non-coding sequences (rRNAs) were prealigned using the E-INS-I algorithm implemented in MAFFT (Katoh et al., 2002). Regions with unambiguous homologies (likely stem regions) were used to split noncoding 12S and 16S rRNAs sequences into six fragments (Zaher et al., 2009), each comprising approximately 100 bp. The fragments were used as regions of homology constraint during searching. The remaining coding genes (cytb, nd4, nd2, rag2, bdnf, and c-mos) were translated to amino-acid sequences, aligned with Clustal X using the Gonnet series matrix, and subsequently retro-translated to nucleotides for analysis in POY. This approach was justified by codon frame evolution and the influence of acting hidden stop codons in coding genes (Seligmann and Pollock, 2004; Di Giulio, 2005; Baranov et al., 2009; Singh and Pardasani, 2009). It also increased the speed of the dynamic homology analysis (Faivovich et al., 2005) for gene fragments without indels (e.g. cytb, nd4, and rag2).

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

Search strategies for the dynamic homology analysis were performed using the command “Search” constrained by time, which implements tree buildings by random addition sequences (RAS), swapping by TBR, perturbations using ratchet, and tree fusing. This

command repeated the same strategy as many times as possible within the specified time. We conducted six rounds of 24-hr runs using the Cluster of the Museu de Zoologia da Universidade de São Paulo with 12 processors built in parallel.

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

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

Static homology

The effect of dynamic homology in our analysis was ascertained by comparing it with the MA as implemented above. The multiple sequence alignment process (Feng and Doolittle, 1987) of MAFFT was applied using the iterative refinement method implemented in the E-INS-I algorithm for the rRNAs sequences (Katoh et al. 2005). We concatenated the rRNAs with the retro aligned coding genes. The concatenated MA was analyzed in TNT using the command “xmult”, which implements rounds of SPR, TBR, tree drifting, ratchet and tree

fusing. Tree searches were stopped after the consensus stabilized for five rounds and a final step of TBR was conducted ("xmult = consense 5" and "bb" commands).

We also carried out a Maximum Likelihood analysis using RAxML 7.2.8 (Stamatakis, 2006). We divided our matrix in 20 partitions to allow different model parameters for each codon position for the coding genes, and for each rRNA sequence. The GTRGAMMA model was used for all partitions, as recommended in the program documentation. One hundred RAS were built and the rapid hill-climbing algorithm, knows as LSR (Lazy Subtree Rearrengment), was used to swap the trees. We opted for RAxML as it provided a fast and accurate ML algorithm that proved to be effective with large datasets (Stamatakis, 2006). One thousand pseudoreplications of non-parametric bootstrap were performed using the Cluster hosted at the Laboratório de Alto Desempenho – Pontifícia Universidade Católica do Rio Grande do Sul (LAD-PUCRS). This probabilistic approach enabled a direct comparison with results from two other studies that concentrated on dipsadid relationships (Hedges et al., 2009; Vidal et al., 2010) and with Pyron et al.'s (2011) broader analysis of colubroidean relationships.

Comparison of topologies using subtree pruning and regrafting

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

Results

Sequence characterization

The alignment derived from DH on POY produced a concatenated matrix comprised of 6030 characters. In comparison, MA produced a matrix of 5574 characters (complete alignments available on request). The difference in length between IA and MA (456 characters) was the result of homology determinations and the proportion of gaps inferred by the two methods. The DH analysis increased the sequence length of the unaligned files of 12S and 16S by approximately 61% and 70%, respectively. In contrast, the multiple alignment approach increased the sequence lengths by 16% for 12S and 6% for 16S (Table 1).

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

Comparison among methodologies

Four most parsimonious trees with 28911 steps were found in our MP/DH analysis using POY. These most parsimonious trees resulted in an almost fully resolved strict

consensus tree (Fig. 1). The MP analysis based on the MA found 8568 best trees with 28188 steps. The strict consensus tree (Appendix S2) had a greater number of polytomies than MP/DH. The MP/MA analysis obtained 87% (214) of the possible (244) clades. In contrast, the MP/DH analysis resolved 97% of all possible dichotomies (237/244). Apart from the larger number of polytomies, most of the main clades and higher taxa were recovered in the MP/MA analysis, with a significant number of differences occurring only among tribes and genera within the Dipsadidae (see below). All of these differences had low Bremer and bootstrap support values in MP/MA (Appendix S2). Additionally, MP/MA tended to produce lower support values (Bremer mean = 8.15; bootstrap mean = 64.02) than did MP/DH (Bremer mean = 11.14; bootstrap mean = 73.29).

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

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

Although tree topologies varied with methodology, the differences occurred on poorly supported nodes only. The basal relationships within Caenophidia were always recovered (Fig. 1), as were the relationships among genera within almost all tribes in the Xenodontinae. In contrast, relationships among xenodontine tribes and the position of some taxa (e.g. *Sordellina punctata*, *Crisantophis nevermanni*, *Caaeteboia amarali*, *Manolepis putnami*, and

Pseudalsophis) were unstable. Branch-lengths in the ML tree (Fig. 2) indicated that most of the conflicts occurred on very short branches. These short branches are connected to long terminal branches and this association might reflect long-branch attraction (Felsenstein, 1978), although this hypothesis is difficult to test (Bergsten, 2005).

Phylogenetic relationships and branch support among different tree topologies

Our analyses recovered the same broad pattern of relationships as Zaher et al. (2009) for caenophidian snakes (Fig. 1). The following higher-level clades were obtained by all methodologies with strong support (bootstrap for POY analysis, Bremer for POY analysis, and bootstrap for ML analysis, respectively): Colubroides (93/19/100), Colubriformes (99/25/100), Endoglyptodonta (88/12/<70), and Colubroidea (90/9/99). Compared to the tree of Zaher et al. (2009), our expanded sampling weakened bootstrap support for the Elapoidea (81%) yet increased Bremer support (14), and produced a bootstrap value of 97% for ML. The changes were probably related to the inclusion of *Oxyrhabdium leporinum*, the sister group to the Elapidae in our analysis (but see Pyron et al., 2011). The elapoid families Elapidae (90/11/100), Atractaspididae (90/18/95), and Psammophiidae (96/15/90) were all robustly supported. Within Elapoidea, the bootstrap and Bremer values for Lamprophiidae were low (<70/6/<70). Homalopsidae was retrieved in the MP/DH analysis as the sister group of Colubroidea, although with very low support values (<70/3), while falling as the sister group of the clade formed by Elapoidea and Colubroidea in the ML/MA analysis with high bootstrap value (84).

Within Colubroidea, Natricidae (94/21/99) and Colubridae (100/27/99) retained very high support, which corroborated the long-standing view of their monophyly. Calamariidae (93/15/90) and Pseudoxenodontidae (100/27/100), represented in Zaher et al.'s (2009)

analysis by only one terminal each, were well supported herein after the inclusion of *Pseudorabdion* and *Plagiopholis*, respectively, and after adding one additional species of *Calamaria* and two *Pseudoxenodon*. The clade formed by Calamariidae and Pseudoxenodontidae was robustly supported (80/16) in the MP/DH and this represented a novel hypothesis, although it was not recovered in the ML approach. Using ML, Calamariidae appeared as the sister group of Colubridae with a moderate bootstrap value (77), and Pseudoxenodontidae rooted more basally on the tree as the sister group of the remaining Colubroidea, but with a low bootstrap (<70). In Zaher et al. (2009), Calamariidae was resolved as the sister group of Colubridae while Pseudoxenodontidae formed the sister group of a clade comprised of Natricidae and Dipsadidae. Also differing from Zaher et al. (2009), Colubridae was the sister group of Dipsadidae in the MP/DH, while the ML/MA recovered Natricidae as the sister group of Dipsadidae (Fig. 2). However, the MP/DH's sister-group relationship was poorly supported (<70/8), revealing a highly unstable topology in both herein and in Zaher et al. (2009). Pyron et al. (2011), using a much larger sampling of non-dipsadid colubroideans, also obtained weak support for a sister-group relationship between Disadidae and Pseudoxenodontidae.

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

As for Zaher et al. (2009), we frequently recovered the following three main clades within Dipsadidae: the subfamilies Dipsadinae (77/3/<70) and Xenodontinae (74/10/82), and a clade composed by the subfamily Carphophiinae, and the *incertae sedis* genera *Heterodon*, *Farancia*, and *Thermophis*. *Thermophis* nested within Carphophiinae as the sister group of

Diadophis in the MP trees, receiving moderate bootstrap (70) but high Bremer (9) support values in the MP/DH analysis. It clustered as the sister group of Dipsadidae in the ML/MA with high bootstrap (0.98) support. *Farancia* also nested inside Carphophiinae in MP/DH tree, as the sister group of a clade composed by *Carphophis* and *Contia*. However, such hypotheses received low support values (<70/4). In contrast, the clade formed by *Carphophis* and *Contia* was recovered in both analyses, with high bootstrap and Bremer support values (91/14/72).

Within Dipsadinae, the following two clades were retrieved in all analyses with moderate to high support values: 1) a highly supported clade formed by the genera *Geophis* and *Atractus* (80/8/<70); and 2) a clade composed of the genera *Dipsas, Ninia*, *Sibon*, and *Sibynomorphus* (69/7/<70). The tribe Imantodini (*sensu* Myers, 2011), represented by *Imantodes* and *Leptodeira* (Mulcahy et al., 2011), was not monophyletic in both analyses, with *Nothopsis* falling as the sister group of *Leptodeira* in both MP and ML analyses, and *Trimetopon* as the sister group of *Imantodes* in the ML analysis. However, these clades were all very poorly supported (<70/<3). Our analyses also corroborated the paraphyletic nature of the genera *Dipsas* and *Sibynomorphus* and suggested that *Ninia* belonged to the traditional tribe Dipsadini of snail-eating snakes. The genera *Tretanorhinus* and *Hypsiglena* always nested inside Dipsadinae and as sister groups in the MP analyses, albeit with low support values (<70/3). In the ML analysis, the former “leptodeirine” *Hypsiglena* appeared as the sister group of *Trimetopon*, with a low bootstrap (<70), while *Tetranorhinus* positioned at the base of a weakly supported clade (-/6/0.85) containing *Trimetopon*, *Hypsiglena*, *Geophis*, *Atractus*, and Dipsadini (including *Ninia*). In turn, *Trimetopon* showed a highly unstable position. It nested within Dipsadinae in both MP/DH (as sister group of *Imantodes*) and ML/MA (as sister group of *Hypsiglena*) trees, but appeared within Xenodontinae as the sister group of Psomophiini in the MP/MA tree.

Within Xenodontinae, the following clades were retrieved with high support values in all analyses: Xenodontini (100/17/100), Psomophiini (100/26/100), Saphenophiini (100/32/100), Tropidrodryadini (100/39/100), Tachymenini (99/10/95), Pseudoboini (100/22/100), Hydropsini (98/12/97), Hydrodynastini (100/40/100), and Philodryadini (98/10/97). Elapomorphini was retrived with moderate support (83/10/<70) . A clade formed by the genera *Echinanthera* and *Taeniophallus*, and that corresponded to the tribe Echinantherini of Zaher et al. (2009), was retrieved with low support (<70) in the ML analysis. In both MP analyses, *Sordellina* nested inside Echinantherini, as the sister group of *Taeniophallus*, rendering the tribe paraphyletic. However, support values were also very low for this hypothesis; bootstrap and Bremer values dropped from <70/10 in the MP/DH to <70/1 in MP/MA. The strongly supported monophyletic genus *Arrhyton* (99/15/92) clustered within Alsophiini as the sister group to the remaining members of the tribe in the MP/DH tree, but it fell outside the alsophiines in the ML/MA tree. However, both hypotheses received very low support values.

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

Pseudalsophis, *Crisantophis*, *Hydrodynastes*, *Caaeteboia*, and *Sordellina*; they showed differing phylogenetic affinities in all three analyses.

Discussion

Higher level phylogeny of Colubroides and the sister group of Dipsadidae

Unless indicated otherwise, herein we follow Zaher et al.'s (2009) taxonomic scheme. Below we discuss only the revisions required by our expanded analysis.

Lawson et al. (2005), Vidal et al. (2007), and Pyron et al. (2011) investigated the higher level phylogeny of Colubroides based on the analysis of two, seven, and five genes, respectively. The three analyses use different suites of taxa. Lawson et al. (2005) sampled extensively in Colubridae but poorly in Dipsadidae (11), Natricidae (9), Calamariidae (1), and Pseudoxenodontidae (1). Alternately, Vidal et al. (2007) meagerly sampled Dipsadidae (3), Colubridae (4), Natricidae (1) and Pseudoxenodontidae (1). Pyron et al. (2011) analyzed an impressive suite of 761 colubroideans, including 99 dipsadids.

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

Homalopsidae has an unstable position among these studies, clustering as the sister group of the clade formed by the Elapoidea and Colubroidea (Vidal et al., 2007; Zaher et al., 2009; Lawson et al., 2005) or as the sister group of the Elapoidea (Pyron et al., 2011; their Lamprophiidae). In the ML/MA, our analysis recovers a sister-group relationship of the

homalopsids with the clade formed by elapoids and colubroids with high support values (84); however, in the MP/DH, the homalopsids are the sister group of Colubroidea, with low support values (<70/3).

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

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

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

Dipsadidae and Pseudoxenodontidae. These conflicting hypotheses indicate that higher-level relationships among colubroid families remain largely unresolved.

Despite our comprehensive sampling of Dipsadidae, the MP and ML analyses recover three disparate and poorly supported hypotheses of sister-group relationship among the families of Colubroidea (Figs. 1, 2). ML/MA recovers Zaher et al.'s (2009) result, with Natricidae being the sister group of Dipsadidae (<70), whereas MP/DH analysis recovers Colubridae as the sister group of Dipsadidae (<70/8). MP/MA retrieves a clade formed by Pseudoxenodontidae and Calamariidae as the sister group of Dipsadidae (<70/4). Thus, the relationships of the family Dipsadidae within the colubroid radiation remain uncertain.

Basal relationships in Dipsadidae

Zaher et al. (2009) defined Carphophiinae as containing only *Carphophis*, *Contia*, and *Diadophis*, with the positioning of *Heterodon* and *Farancia* as needing further investigation. In contrast, Vidal et al. (2007) defined the subfamily Heterodontinae (Appendix 1) to include all of the North American relictual dipsadids (*Carphophis*, *Contia*, *Diadophis*, *Farancia*, and *Heterodon*). The inclusion of *Thermophis zhaoermii* renders both arrangements non-monophyletic in the MP/DH tree by clustering it as the sister group of *Diadophis* (70/9) within a poorly supported clade (<70/2) that also includes *Farancia* but not *Heterodon*. Conversely, in the MP/MA analysis, *Thermophis* and *Diadophis* cluster together whereas *Farancia* forms a clade with *Heterodon* (<70/4). Thus, the positioning of *T. zhaoermii* in the North American Dipsadidae probably is not driven by the dynamic homology approach, but by the MP criterion. The ML/MA analysis resolves *T. zhaoermii* as the sister group of all other dipsadids and recovers Carphophiinae as a monophyletic group, although with low support (<70). *Heterodon* and *Farancia* form a clade that appears in the ML/MA as the sister

group to all other dipsadines, with low bootstrap support (<70). Pyron et al. (2011) reported an alternate set of relationships, with both *Heterodon* and *Farancia* nested inside Carphophiinae, and *Thermophis* resolved as the sister group of Pseudoxenodontidae instead of related to Dipsadidae. None of the hypotheses above can be excluded because of poorly supported relationships.

As noted above, the phylogenetic placements of *Diadophis*, *Farancia*, *Heterodon*, and *Thermophis* are unstable and controversial (Figs. 1, 2; Appendix S2). More specifically, both *D. punctatus* and *T. zhaoermii* have exceedingly long branches and this suggests that either long-branch attraction or repulsion may be biasing the MP analyses. Probabilistic models of molecular evolution might better handle such cases (Swofford et al., 1996; Phillippe et al., 2005), but this conclusion is highly controversial (Bergsten, 2005). The only consensus—if there is one—is that clades with long branches linked by small branches represent a problem for phylogenetic inference (Felsenstein, 2004; Kolaczkowski and Thornton, 2004) and no methodology can unequivocally detect it *a priori* (Huelsenbeck et al., 1996; Siddall and Whiting, 1999; Clements et al., 2003; Bergsten, 2005).

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

the Americas. Certainly, more work is needed to define the relationship between these basal dipsadids. Until then, we maintain *Thermophis*, *Farancia*, and *Heterodon* as Dipsadidae *incertae sedis*.

The subfamily Dipsadinae

Our inclusion of more terminals than Zaher et al. (2009) still leaves dipsadine relationships broadly unresolved. Few clades enjoy high support and each approach obtains a unique topology (Figs. 1, 2; Appendix S2). Similarly, independent studies often obtain different phylogenetic arrangements for dipsadine species (Mulcahy, 2007, 2008; Daza et al., 2009; Mulcahy and Macey, 2009, Zaher et al., 2009; Mulcahy et al., 2011; Pyron et al., 2011). Nevertheless, two clades are recovered in each of our three analyses with low to moderate support: (1) a clade comprised of *Atractus* and *Geophis* (80/8/<70); and (2) a clade formed by *Dipsas*, *Sibynomorphus*, *Sibon*, and *Ninia* (<70/7/<70).

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

Despite its unstable position, *Hypsiglena* never clusters with the other two sampled representatives of Cadle's (1984b) leptodeirine assemblage of Central American snakes *Imantodes* and *Leptodeira*, thereby supporting Mulcahy's (2007) hypothesis that this assemblage is a paraphyletic or even polyphyletic group. Recently, Myers (2011) erected the tribe Imantodini to include only *Leptodeira* and *Imantodes*, a decision previously suggested by Mulcahy (2007) and endorsed by Mulcahy et al. (2011). Here, Imantodini forms a weakly supported paraphyletic assemblage (<70/2/<70) that also includes *Nothopsis* in all three

analyses (MP/DH, MP/MA, ML/MA) and *Trimetopon* in the MP/DH analysis. Our analyses corroborate Vidal et al.'s (2010) results in which *Nothopsis* appears for the first time as the sister group of *Leptodeira*. Vidal et al. (2010) decided to add *Nothopsis* to Imantodini (their Leptodeirini), despite poor support values provided by their phylogenetic analyses. Although the clade composed by *Nothopsis* and *Leptodeira* is retrieved consistently in our analyses, support values for the hypothesis are always low (<70/1/<70), suggesting that Vidal et al.'s (2010) nomenclatural decision might have been premature. The lack of other "nothopsines" (e.g. *Synophis*, *Diaphorolepis*, and *Emmochliophis*) in the analysis, and the low support values for the clade formed by *Nothopsis*, *Leptodeira*, *Trimetopon*, and *Imantodes*, preclude an unequivocal allocation for *Nothopsis*. Therefore, we prefer to follow Zaher (1999) and Mulcahy et al. (2011), and consider this genus as a Dipsadinae *incertae sedis*.

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

Surprisingly, the tribe Dipsadini, as defined by Zaher (1999) and Harvey et al. (2008) (i.e. including the genera *Dipsas*, *Sibynomorphus*, *Sibon*, *Tropidodipsas*, and *Plesiodipsas*), is paraphyletic in respect to *Ninia* in the MP trees. However, the tribe is retrieved as monophyletic in the ML tree, although with low support (<70). In the MP trees, *Ninia* consistently nests inside a larger clade formed by *Sibon*, *Sibynomorphus*, and *Dipsas* in one of two positions—either as the sister group of (1) *Sibynomorphus turgidus* and *S. mikanii* in MP/DH, or (2) *S. mikanii* in MP/MA. Similarly, *Sibon* also shows three distinct sister-group relationships, as follow: (1) sister to all the other Dipsadini in ML/MA; (2) sister to a clade

formed by the other Dipsadini and *Ninia*, with the exclusion of *Dipsas articulata* and *D. indica*, in MP/DH; and (3) sister to *Sibynomorphus turgidus* in MP/MA. Each association is weakly supported. Further, all three analyses point to paraphyly in the genera *Sibynomorphus* and *Dipsas* with respect to each other. Several species of both genera are more closely related to each other than to their congeners, a result that finds support in morphology (Fernandes, 1995). To render both genera monophyletic, *Sibynomorphus* Fitzinger, 1843, would have to be synonymized with *Dipsas* Laurenti, 1768. However, the poor taxonomic sampling for Dipsadini (only 3 of the 5 genera and 16% of their species) and the unstable positions of *Sibon* and *Ninia* suggest that such a decision would be premature. No taxonomic consensus can emerge without a broader sampling of the remaining snail-eating snakes and further clarification of the phylogenetic affinities of the genus *Ninia*, represented here by only one species.

Xenopholis*, and polyphyly of the "Nothopsini"*

Upon adding the second known species of *Xenopholis*, *X. undulatus*, the genus appears to be monophyletic (Figs. 1, 2) and with high support values (100/12/99). Our analyses support the allocation of *Xenopholis* to Dipsadidae (Zaher, 1999), although as a member of Xenodontinae, rather than a Dipsadinae *incertae sedis*. Further, the relationships of *Xenopholis* suggest that the unilobed hemipenis of *X. scalaris* represents a secondary loss of one of the lobes as opposed to the retention of the dipsadine condition.

Xenopholis never clusters inside any suprageneric taxon within Xenodontinae, confirming its uniqueness. Further, the placements of *Nothopsis* and *Xenopholis* in Dipsadinae and Xenodontinae (Vidal et al., 2010), respectively, preclude recognition of the tribe Nothopsini as defined by either Savitzky (1974) or Dowling (1975). This result also

rejects allocation of these genera to Xenodermatidae, as suggested by Dowling and Pinou (2003). Therefore, we consider *Xenopholis* as Xenodontinae *incertae sedis*, pending a better sampling in Dipsadinae and inclusion of other "nothopsines".

The subfamily Xenodontinae

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

Our analyses support the generic arrangement of Zaher et al. (2009) in Philodryadini. The new arrangements for *Philodryas argentea* and *Ph. agassizii* (formerly *Xenoxybelis argenteus* and *Pseudablabes agassizii*, respectively) are maintained after a broader sampling of *Philodryas*. *Philodryas agassizii* clusters with *Ph. patagoniensis* with high support values (99/6/88) and *Ph. argentea* clusters either with a clade formed by *Ph. viridissima* and *Ph. nattereri* (70/5) in MP/DH, or with *Ph. viridissima* (<70) in ML/MA. Similarly, Pyron et al. (2011) placed *X. boulengeri* in *Philodryas* as the sister taxon of *Ph. baroni*. Therefore, we maintain Zaher et al.'s (2009) synonymy of *Xenoxybelis* with *Philodryas*. The genus *Philodryas* now contains 20, instead of 18, species (Zaher et al., 2008; Appendix 1).

The tribe Saphenophiini

Our study unequivocally supports Zaher's (1999) hypothesis based on morphology that continental *Pseudalsophis elegans* is closely related to the Galapagos Island species of Xenodontinae (herein represented by *Pseudalsophis dorsalis*), rather than to West Indian *Alsophis* and *Antillophis*, and mainland *Philodryas* (Thomas, 1997). Following Zaher (1999), Zaher et al. (2009) assigned all Galapagos species to a new genus, *Pseudalsophis* (along with *Alsophis elegans*), and created the tribe Saphenophiini for the genera *Pseudalsophis* and *Saphenophis*. Sampling only *P. elegans* as a representative of Saphenophiini, Vidal et al. (2010) stated that their resolution of *Manolepis putnami* (a dipsadid *incertae sedis*) as the sister group of *P. elegans* rendered the Saphenophiini paraphyletic. However, paraphyly in the Saphenophiini requires *Manolepis* to cluster inside the Saphenophiini, a test not performed by Vidal et al. (2010) because they only sampled one species of Saphenophiini. Although our sampling of Saphenophiini does not include *Saphenophis*, the phylogenetic analyses never recover *M. putnami* as the sister group of *P. elegans* (Figs. 1, 2; Appendix S2). A monophyletic *Pseudalsophis* is always recovered with high support values (100/32/100). Therefore, we resurrect the tribe Saphenophiini, as originally stated by Zaher et al. (2009), and pending further testing with the inclusion of *Saphenophis*.

The tribe Conophiini and the genera Manolepis *and* Crisantophis

Zaher et al. (2009) erected the tribe Conophiini on the basis of the peculiar hemipenial morphology shared by *Conophis* and *Manolepis* (Zaher, 1999) and the phylogenetic position of the former within xenodontines. Although our results for MP agree with Vidal et al.'s

(2010) conclusion that this tribe is not monophyletic, our ML/MA analysis retrieves a monophyletic Conophiini with a low bootstrap support (<70). However, the position of *Manolepis* is highly unstable within Xenodontinae, and three distinct hypotheses of sister-group relationship are obtained from our analyses, all with low support values: (1) as the sister group of Hydropsini in the MP/DH (<70/9); (2) as the sister group of *Conophis* in the ML/MA (<70); and (3) as the sister group of Pseudoboini in the MP/MA (<70/1). Therefore, we consider *Manolepis* as Xenodontinae *incertae sedis* and redefine the tribe Conophiini to contain *Conophis* only, pending future analysis.

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

The tribe Xenodontini

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

Our results support the synonymization of *Waglerophis* and *Lystrophis* with *Xenodon* (Zaher et al., 2009). The inclusion of seven additional species (total of 11 species) obtains a congruent topology (Figs 1, 2), with former genera *Lystrophis* and *Waglerophis* nested within the traditional *Xenodon* in a sequence of well supported clades. This taxonomic change is also supported by morphological evidence (Zaher, 1999; Moura-Leite, 2001; Masiero, 2006). As previously suggested by Zaher (1999), *X. werneri* clusters inside *Xenodon* as the sister group of *X. merremi*. Hence, the absence of the apical disk in their hemipenis is a reversal within the Xenodontini (*contra* Yuki, 1993). The loss of the disk and the elongated hemipenial lobes are two morphological synapomorphies that support the clade formed by *X. merremi* and *X. werneri* (Zaher, 1999).

Our phylogenetic results and those of Vidal et al. (2010) support the taxonomic changes in the tribe Xenodontini made by Zaher et al. (2009). However, controversy remains with respect to the recognition of *Liophis* and *Erythrolamprus*. Our results recover a monophyletic *Erythrolamprus* (priority of the name *Erythrolamprus* over *Liophis* in Appendix 1) with high support values in all approaches (100/15/100), except for the inclusion

of *Umbrivaga pygmaea*, as first reported by Vidal et al. (2010). Both MP and ML approaches place *E. aesculapii, E. mimus,* and *U. pygmaea* in this clade with strong support (Figs. 1, 2). This is not surprising because a close phylogenetic affinity between species traditionally included in *Liophis* and *Erythrolamprus* are recovered persistently in recent literature; Vidal et al. (2000) were first to report a paraphyletic *Liophis* in relation to *Erythrolamprus* and Zaher et al. (2009), and Vidal et al. (2010) do the same.

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

The tribe Pseudoboini

The tribe Pseudoboini contains *Boiruna, Clelia, Drepanoides, Mussurana, Oxyrhopus, Phimophis, Pseudoboa, Rhachidelus,* and *Siphlophis* (Zaher et al., 2009). Monophyly of the tribe is highly supported molecularly (100/22/100) and morphologically (Zaher, 1994; Zaher, 1999; Zaher et al., 2009). Both *Siphlophis* and *Oxyrhopus* are retrieved with high support values (98/8/98 and 89/6/87, respectively). A third clade, comprising *Phimophis guerini, Clelia rustica, C. clelia, Boiruna maculata, Pseudoboa coronata, Ps. neuwiedii, Ps. nigra, Rhachidelus brazili, Mussurana bicolor,* and *Drepanoides anomalus,* also receives high

support values in all analyses (88/7/74). The genus *Rhachidelus* is sampled for the first time in a molecular analysis and, although it firmly nests in Pseudoboini, its phylogenetic position differs in the MP/DH and ML/MA analyses. It is the sister group of *Boiruna* in the MP/DH analysis, but clusters as the sister group of *Pseudoboa* in the ML/MA tree, showing strong support in MP/DH (96/20) but low support in ML/MA (<70). The MP/MA tree recovers the same affinities as in ML/MA.

Although Zaher et al. (2009) corrected several problems with respect to the monophyly of Pseudoboini, further adjustments are needed. Our results render the genera *Clelia* Fitzinger, 1826, and *Phimophis* Cope, 1860, polyphyletic. Surprinsigly, *Ph. iglesiasi* is positioned as the sister group of *Oxyrhopus*, with low support (<70/7/<70). Further, *Ph. guerini*, the other sampled species of *Phimophis*, clusters with *Clelia rustica* with strong support in all three analyses (96/5/93). Zaher (1994) provided morphological evidence for this affinity; *C. rustica* appears as the sister group of the genus *Phimophis* with which it shares the presence of an antero-dorsally enlarged and ossified premaxilla and "Y-shaped" divergent anterior extremities of the nasals. We create a new genus for *C. rustica* (Cope, 1878) to maintain a monophyletic *Clelia* (Appendix 1). We also transfer *C. hussami* Morato, Franco and Sanches, 2003 to this new genus owing to its obvious affinities with the latter; unfortunately, no tissues or sequence data are available for this species. Further, we create a new genus for *Ph. iglesiasi* to maintain the monophyly of *Phimophis* (Appendix 1). The small, psammophilous species *Ph. chui* and *Ph. scriptorcibatus*, from the sand-dunes of the Rio São Franciso, Brazil, are allocated into this new genus due to their morphological similarities with *Ph. iglesiasi*. This new genus is characterized by the absence of loreal scales. The genus *Phimophis* Cope, 1860, now includes *Ph. guerini* (Duméril, Bibron, and Duméril, 1854), *Ph. guianensis* (Troschel, 1848), and *Ph. vittatus* (Boulenger, 1896), and is

characterized by the presence of a slightly to strongly upcurved spatulate, rostral scale and an enlarged and distally rounded terminal caudal scale.

Phylogenetic affinities of Sordellina *and the tribe Echinantherini*

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

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

Zaher et al. (2009) did not address the long-standing taxonomic issue of whether or not *Echinanthera* and *Taeniophallus* are monophyletic (Di-Bernardo, 1992, 1996; Myers and Cadle, 1994; Schargel et al., 2005). Following Schargel et al. (2005) and Santos-Jr et al. (2008), *Taeniophallus* contains nine species—*T. affinis*, *T. bilineatus*, *T. brevirostris*, *T. nebularis*, *T. nicagus*, *T. occipitalis*, *T. persimilis*, *T. poecilopogon*, and recently described *T. quadricellatus*. *Echinanthera* comprises six species—*E. amoena*, *E. cephalomaculata*, *E. cephalostriata*, *E. cyanopleura*, *E. melanostigma*, and *E. undulata*. Our sampling of five of the 15 recognized species in Echinantherini shows that the current generic delimitation is natural and concordant with all phylogenetic analyses. Recently, Myers (2011) questioned the definition of Echinantherini given by Zaher et al. (2009), based on the distinct hemipenial

morphology of *T. nebularis*. However, assignment of *T. nebularis* to the genus *Taeniophallus* is problematic, as noted by Schargel et al. (2005), and we consider it as tentative because there is no compelling evidence (morphological or molecular) supporting such allocation.

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

Monophyly of Alsophiini

Vidal et al. (2010) argued that Hedges et al. (2009) extensively resolved the relationships, classification, and biogeography of the West Indian Xenodontinae (WIX). However, our results reveal that some aspects of the phylogenetic relationships and the taxonomy of the WIX remain controversial. Hedges et al. (2009), like Zaher et al. (2009), considered the tribe Alsophiiini to be a monophyletic unit. However, our data matrix with a larger sampling of WIX and mainland xenodontines resulted in a polyphyletic Alsophiini in all three analyses (Figs. 1, 2; Appendix S2). *Uromacer* always clusters outside of the other WIX, either as the sister group of Saphenophiini (MP/DH; <70/4) or as the sister group of Xenodontini (MP/MA and ML/MA; <70/1/<70), although with low bootstrap and Bremer support values. *Arrython* (*sensu* Zaher et al., 2009) also clusters outside the WIX in the ML/MA analysis, forming the sister group to the clade composed by *Uromacer* and Xenodontini (<70). However, the MP/DH analysis places *Arrhyton* in the West Indian radiation, clustering it as the sister group to the other alsophiines (excluding *Uromacer*) in a clade with low support values (<70/5). In the MP/MA tree, *Arrhyton* falls in a polytomy with

a clade formed by *Uromacer* and Xenodontini and another clade containing the remaining Alsophiini. No morphological synapomorphies support the monophyly of any of the clades formed by *Uromacer*, *Arrhyton*, and Xenodontini in the MP/DH and ML/MA analyses.

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

Monophyletic components within Alsophiini

According to Zaher et al. (2009), the tribe Alsophiini contains 11 genera—*Caraiba*, *Schwartzophis*, *Magliophis*, *Ialtris*, *Darlingtonia*, *Hypsirhynchus*, *Arrhyton*, *Antillophis*, *Alsophis*, *Uromacer*, and *Ocyophis*; the first three genera represent new taxa and the last one is resurrected (Fig. 3). Hedges et al. (2009) rejected most of Zaher et al.'s (2009) taxonomic scheme (Fig. 3). They synonymized *Schwartzophis* and *Antillophis* with *Hypsirhynchus*, and *Darlingtonia* with *Ialtris*; they also described the new genera *Borikenophis*, *Haitiophis*, and *Cubophis* to accommodate the species previously arranged in *Ocyophis* by Zaher et al. (2009). Further, Hedges et al. (2009) placed *Oc. ater* and *Oc. melanichnus*, two probably extinct species, in their expanded *Hypsirhynchus*.

Our three analyses unambiguously support the recognition of the genera *Antillophis*, *Hypsirhynchus*, *Darlingtonia*, and *Schwartzophis*, as originally suggested by Zaher et al. (2009). They also corroborate Hedges et al.'s (2009) genera *Haitiophis*, *Cubophis* and *Borikenophis* by recovering a paraphyletic *Ocyophis* (*sensu* Zaher et al., 2009; Fig. 3). Additionally, we believe that *Ocyophis* should be retained for *O. ater* (Gosse, 1863) and *O. melanichnus* (Cope, 1863), for reasons detailed in Appendix 1. Given this new arrangement, the tribe Alsophiini contains 13 genera (Figs. 1, 2; Appendix 1; Appendix S2).

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

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

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

Relationships within the genera *Alsophis*, *Schwartzophis*, *Borikenophis*, and *Cubophis* are well established and identical to the ones found by Hedges et al. (2009).

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Table caption

Table 1

Sequence size for the gene fragments used in this study. Fragment length in base pairs for the larger sequence before alignment. IA, implied alignment generated by POY 4; MA, multiple alignment.

Table 1

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

Figure caption

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

Fig. 2. Tree estimated from the maximum-likelihood analysis. Numbers above and below branches show support values for Bremer and bootstrap. Abbreviations: b.POY = bootstrap support values from POY; B.POY = Bremer support values from POY; b.ML = bootstrap values from the ML analysis in RAxML; b.MP = bootstrap support values from MP analysis in TNT; B.MP = Bremer support values from MP analysis in TNT. Asterisks indicate bootstrap values lower than 70%. Dashes indicate clades not recovered by specific analysis. Names of the higher taxa are shown near their respective clades. Terminal names followed by an asterisk are from from Vidal et al. (2010).

Fig. 3. Comparison of the taxonomies (central box) and phylogenies for the West Indian xenodontines based on the results of Zaher et al. (2009), Hedges et al. (2009) and the current analysis. A) Phylogenetic relationship derived from Fig. 1. Thick branches represent relationships also recovered in Zaher et al. (2009); dotted branches represent taxa not sampled

by Zaher et al. (2009). B) Phylogenetic relationships extracted from Hedges et al. (2009). Thick branches represent relationships also recovered herein. Terminal names followed by an asterisk are from Hedges et al. (2009).

Fig. 4. Variation in the hemipenial morphology and the phylogenetic relationships used to construct the taxonomy of the West Indian xenodontids. Illustrations of the sulcated (right) and asulcated (left) hemipenial faces, based on Zaher (1999). 01, *Ocyophis ater*; 02, *Schwartzophis callilaemum*; 03, *Schwartzophis polylepis*; 04, *Hypsirhynchus ferox*; 05, *Antillophis parvifrons*; 06, *Cubophis cantherigerus*; 07, *Cubophis vudii*; 08, *Caraiba andreae*; 09, *Haitiophis anomalus*; 10, *Ialtris dorsalis*; 11, *Darlingtonia haetiana*; 12, *Borikenophis portoricensis*; 13, *Magliophis exiguum*; 14, *Alsophis rijgersmaei*; 15, *Alsophis sibonius*; 16, *Arrhyton taeniatum*; 17, *Uromacer catesbyi*. Black and open circles on the nodes represent highly and lowly supported clades, respectively, for MP/DH. Dotted branches do not necessarily represent the phylogenetic relationships recovered herein.

Figure 1.

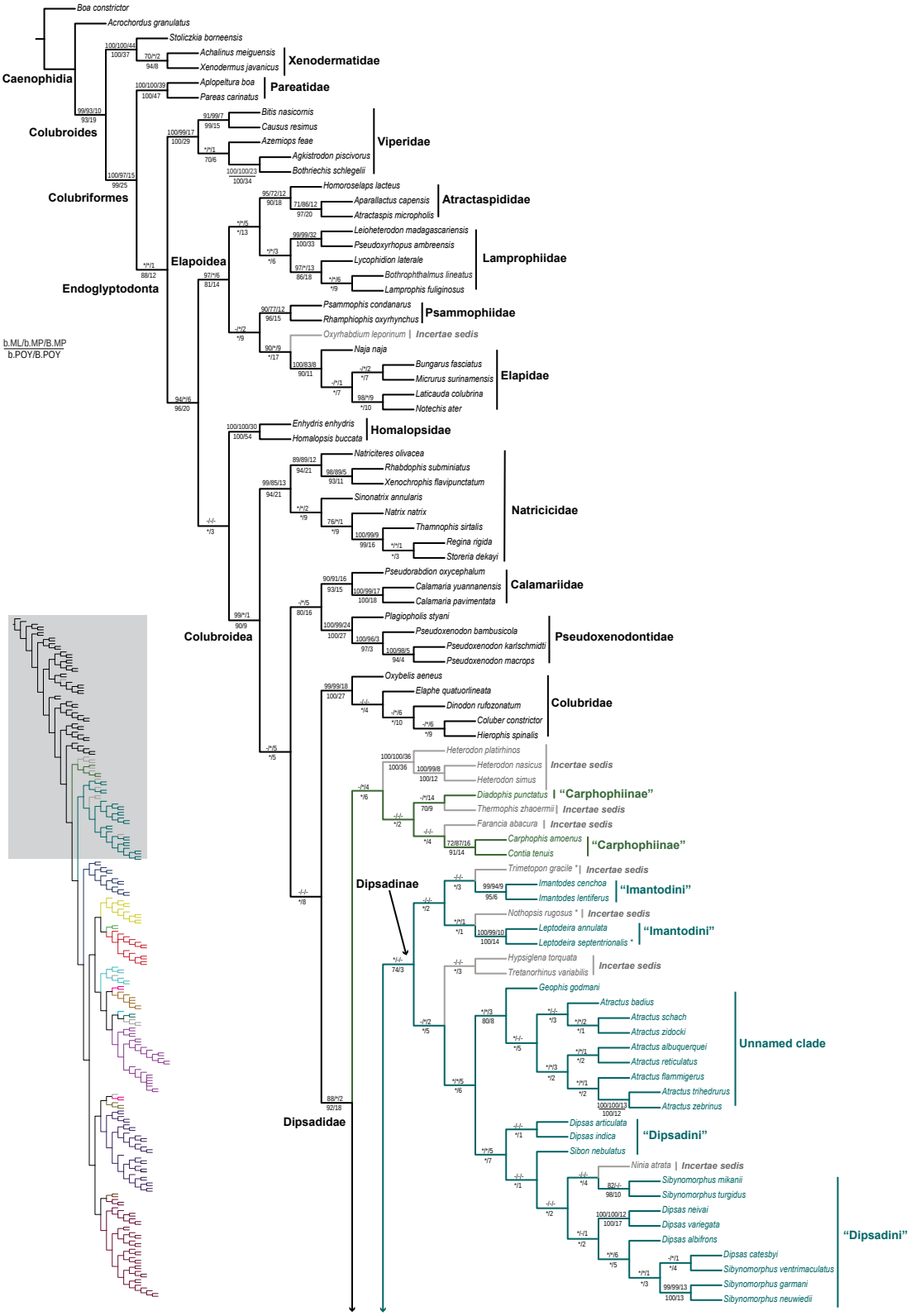

Boa constrictor
Acrochordus granulatus
Stoliczkia borneensis
Achalinus meiguensis
Xenodermus javanicus
Xenodermatidae
Caenophidia
Aplopeltura boa
Pareas carinatus
Pareatidae
Colubroides
Bitis nasicornis
Causus resimus
Azemiops feae
Agkistrodon piscivorus
Bothriechis schlegelii
Viperidae
Colubriformes
Homoroselaps lacteus
Aparallactus capensis
Atractaspis micropholis
Atractaspididae
Leioheterodon madagascariensis
Pseudoxyrhopus ambreensis
Lycophidion laterale
Bothrophthalmus lineatus
Lamprophis fuliginosus
Lamprophiidae
Elapoidea
Endoglyptodonta
Psammophis condanarus
Rhamphiophis oxyrhynchus
Psammophiidae
b.ML/b.MP/B.MP
b.POY/B.POY
Oxyrhabdium leporinum | Incertae sedis
Naja naja
Bungarus fasciatus
Micrurus surinamensis
Laticauda colubrina
Notechis ater
Elapidae
Enhydris enhydris
Homalopsis buccata
Homalopsidae
Natriciteres olivacea
Rhabdophis subminiatus
Xenochrophis flavipunctatus
Sinonatrix annularis
Natrix natrix
Thamnophis sirtalis
Regina rigida
Storeria dekayi
Natricicidae
Pseudorabdion oxycephalum
Calamaria yuannanensis
Calamaria pavimentata
Calamariidae
Colubroidea
Plagiopholis styani
Pseudoxenodon bambusicola
Pseudoxenodon karlschmidti
Pseudoxenodon macrops
Pseudoxenodontidae
Oxybelis aeneus
Elaphe quatuorlineata
Dinodon rufozonatum
Coluber constrictor
Hierophis spinalis
Colubridae
Heterodon platirhinos
Heterodon nasicus
Heterodon simus
Incertae sedis
Diadophis punctatus | "Carphophiinae"
Thermophis zhaoermii | Incertae sedis
Farancia abacura | Incertae sedis
Carphophis amoenus
Contia tenuis
"Carphophiinae"
Trimetopon gracile * | Incertae sedis
Dipsadinae
Imantodes cenchoa
Imantodes lentiferus
"Imantodini"
Nothopsis rugosus * | Incertae sedis
Leptodeira annulata
Leptodeira septentrionalis *
"Imantodini"
Hypsiglena torquata
Tretanorhinus variabilis
Incertae sedis
Geophis godmani
Atractus badius
Atractus schach
Atractus zidocki
Atractus albuquerquei
Atractus reticulatus
Atractus flammigerus
Atractus trihedrurus
Atractus zebrinus
Unnamed clade
Dipsas articulata
Dipsas indica
"Dipsadini"
Sibon nebulatus
Ninia atrata | Incertae sedis
Sibynomorphus mikanii
Sibynomorphus turgidus
Dipsas neivai
Dipsas variegata
Dipsas albifrons
Dipsas catesbyi
Sibynomorphus ventrimaculatus
Sibynomorphus garmani
Sibynomorphus neuwiedii
"Dipsadini"
Dipsadidae

Figure 1. *Continued*

Figure 1. *Continued*

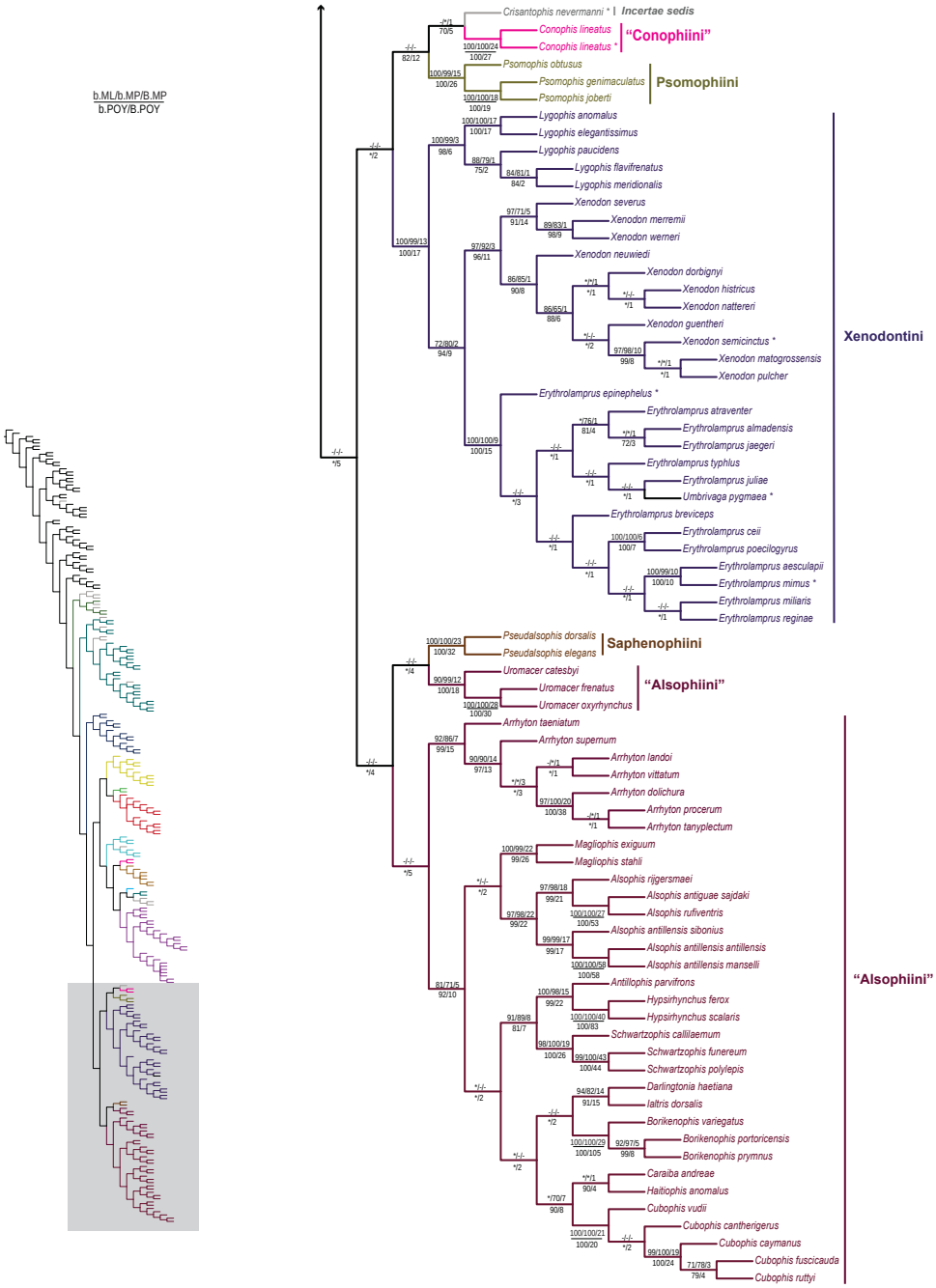


Figure 2.

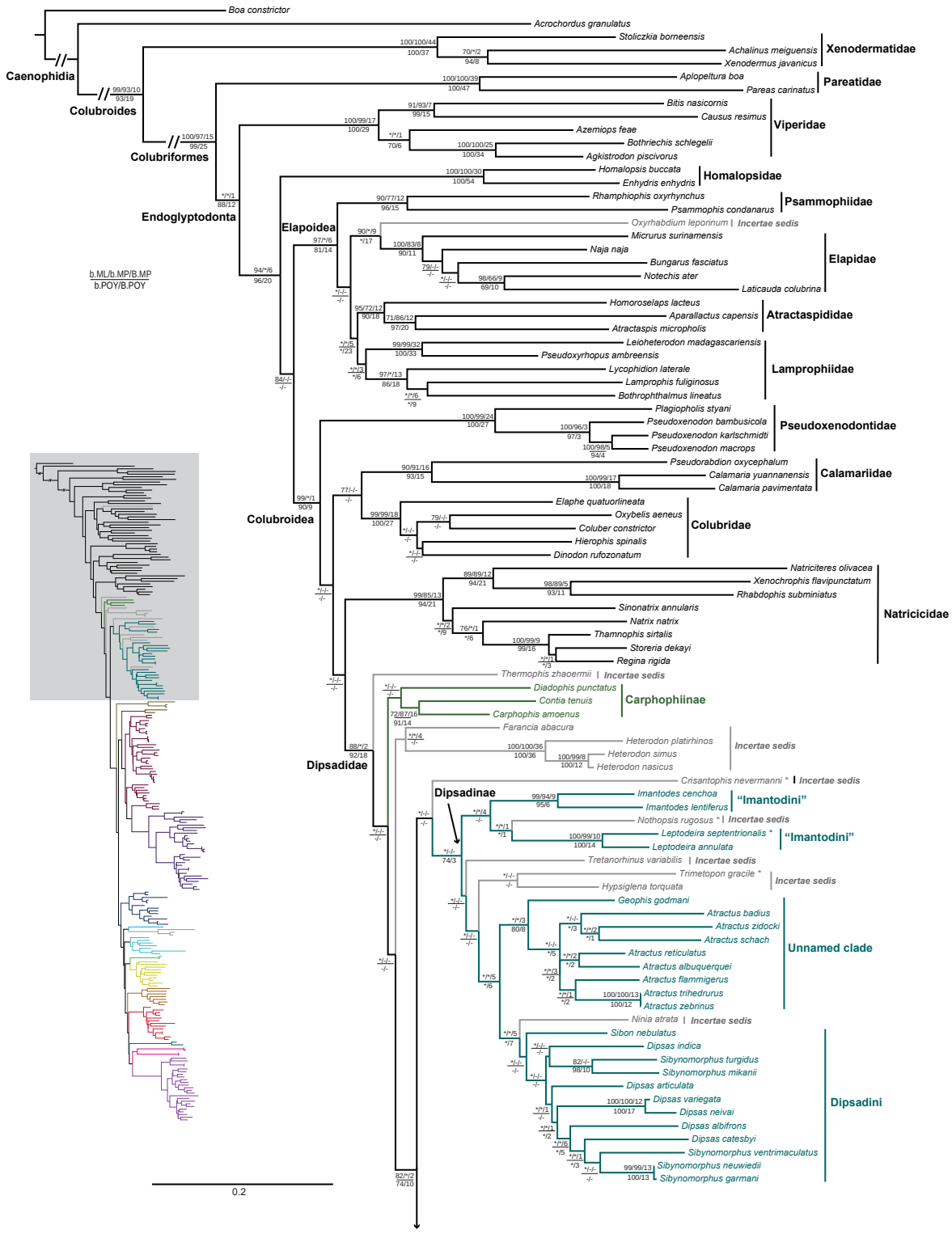

Boa constrictor
Acrochordus granulatus
Stoliczkia borneensis
Achalinus meiguensis
Xenodermus javanicus
Xenodermatidae
Caenophidia
Aplopeltura boa
Pareas carinatus
Pareatidae
Colubroides
Bitis nasicornis
Causus resimus
Viperidae
Azemiops feae
Bothriechis schlegelii
Agkistrodon piscivorus
Colubriformes
Homalopsis buccata
Enhydris enhydris
Homalopsidae
Endoglyptodonta
Rhamphiophis oxyrhynchus
Psammophis condanarus
Psammophiidae
Elapoidea
Oxyrhabdium leporinum
Incertae sedis
Micrurus surinamensis
Naja naja
Bungarus fasciatus
Notechis ater
Laticauda colubrina
Elapidae
b.ML/b.MP/B.MP
b.POY/B.POY
Homoroselaps lacteus
Aparallactus capensis
Atractaspis micropholis
Atractaspididae
Leioheterodon madagascariensis
Pseudoxyrhopus ambreensis
Lycophidion laterale
Lamprophis fuliginosus
Bothrophthalmus lineatus
Lamprophiidae
Plagiopholis styani
Pseudoxenodon bambusicola
Pseudoxenodon karlschmidti
Pseudoxenodon macrops
Pseudoxenodontidae
Pseudorabdion oxycephalum
Calamaria yuannanensis
Calamaria pavimentata
Calamariidae
Colubroidea
Elaphe quatuorlineata
Oxybelis aeneus
Coluber constrictor
Hierophis spinalis
Dinodon rufozonatum
Colubridae
Natriciteres olivacea
Xenochrophis flavipunctatum
Rhabdophis subminiatus
Sinonatrix annularis
Natrix natrix
Thamnophis sirtalis
Storeria dekayi
Regina rigida
Natricicidae
Thermophis zhaoermii
Incertae sedis
Diadophis punctatus
Contia tenuis
Carphophis amoenus
Carphophiinae
Farancia abacura
Heterodon platirhinos
Heterodon simus
Heterodon nasicus
Incertae sedis
Dipsadidae
Crisantophis nevermanni *
Incertae sedis
Dipsadinae
Imantodes cenchoa
Imantodes lentiferus
"Imantodini"
Nothopsis rugosus *
Incertae sedis
Leptodeira septentrionalis *
Leptodeira annulata
"Imantodini"
Tretanorhinus variabilis
Incertae sedis
Trimetopon gracile *
Hypsiglena torquata
Incertae sedis
Geophis godmani
Atractus badius
Atractus zidocki
Atractus schach
Atractus reticulatus
Atractus albuquerquei
Atractus flammigerus
Atractus trihedrurus
Atractus zebrinus
Unnamed clade
Ninia atrata
Incertae sedis
Sibon nebulatus
Dipsas indica
Sibynomorphus turgidus
Sibynomorphus mikanii
Dipsas articulata
Dipsas variegata
Dipsas neivai
Dipsas albifrons
Dipsas catesbyi
Sibynomorphus ventrimaculatus
Sibynomorphus neuwiedii
Sibynomorphus garmani
Dipsadini
0.2

Figure 2. *Continued*

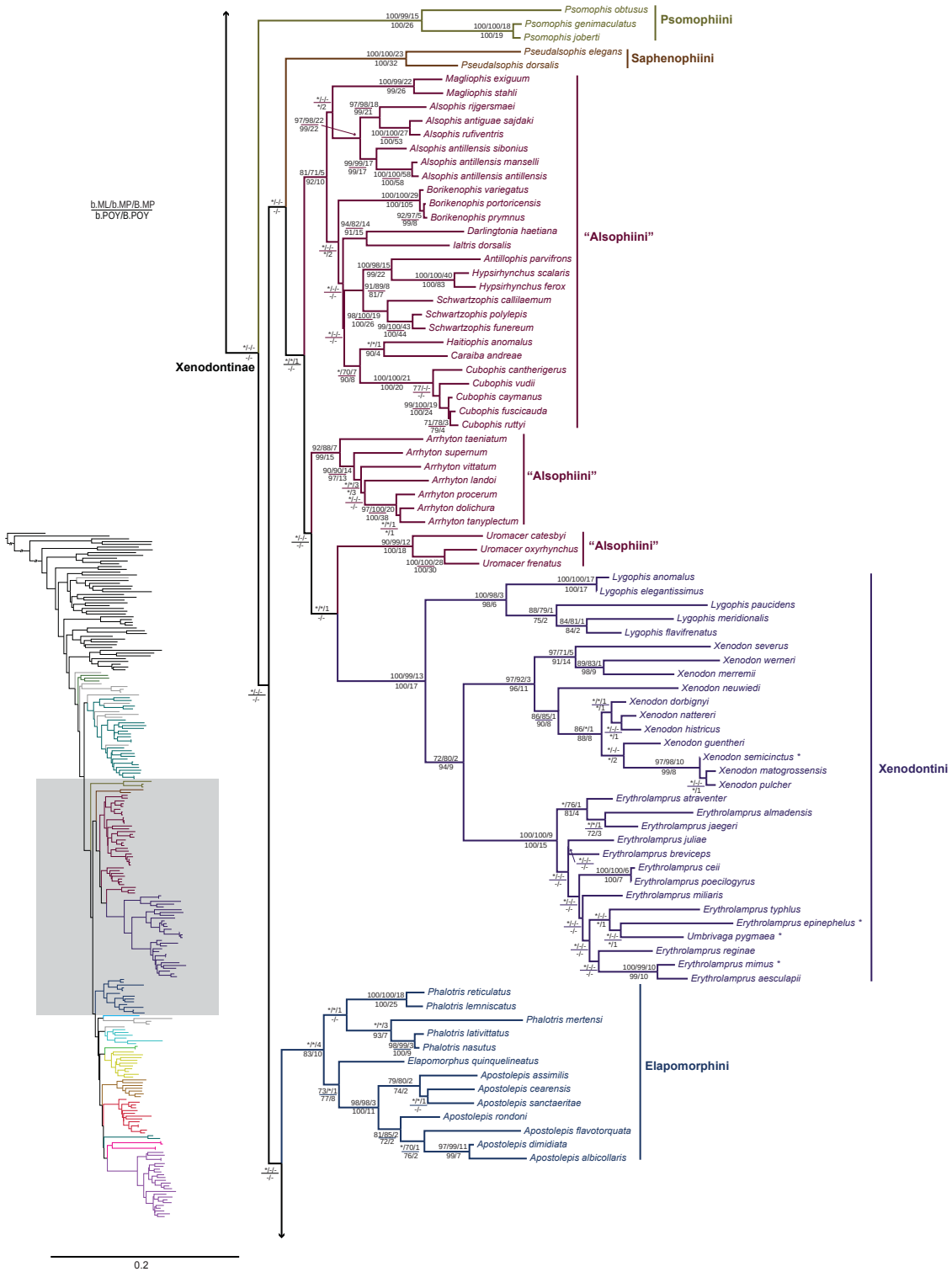


Figure 2. *Continued*

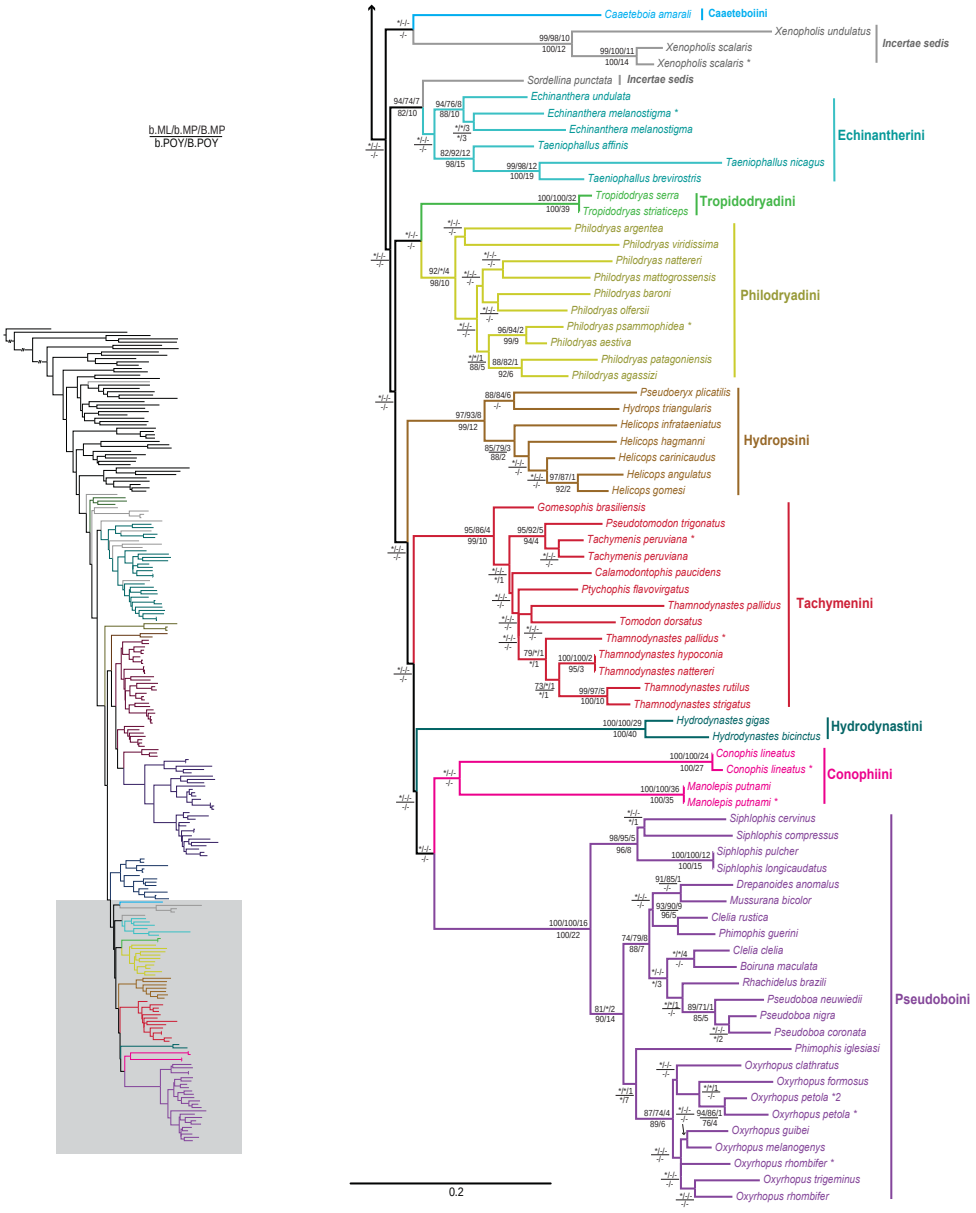


Figura 3.

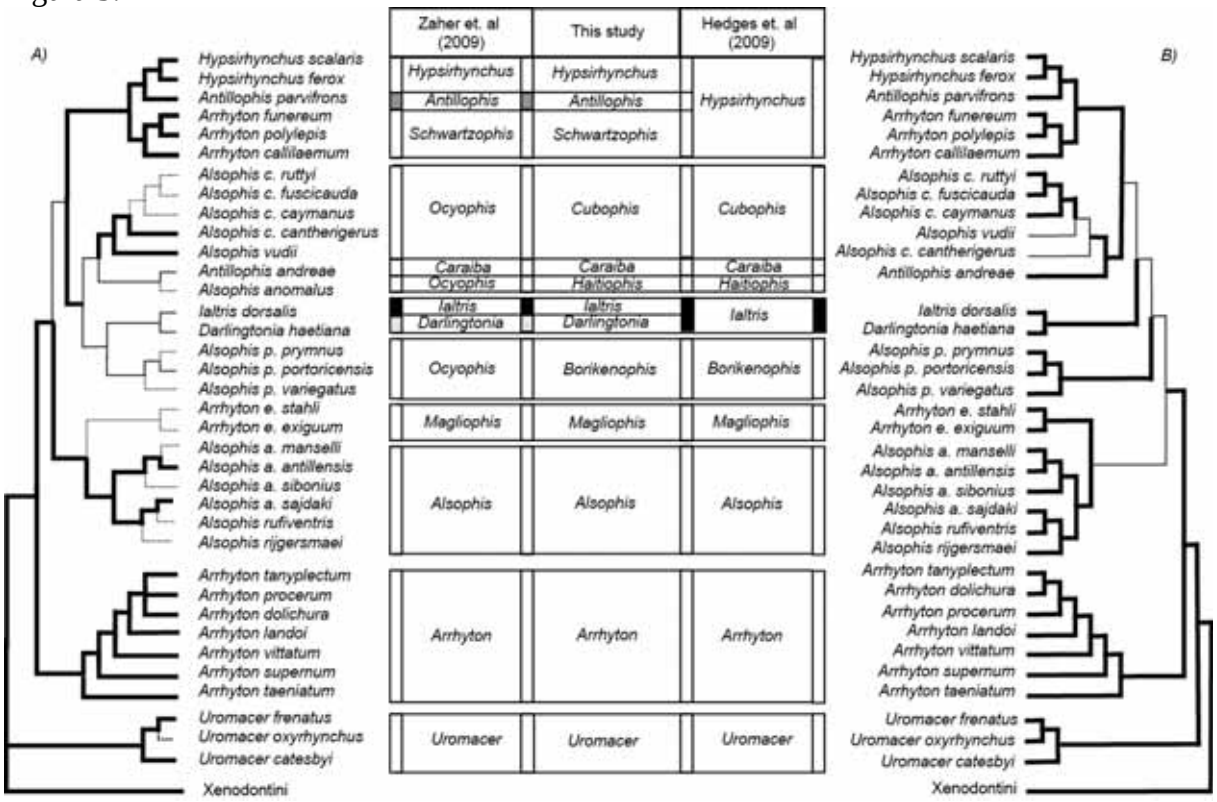
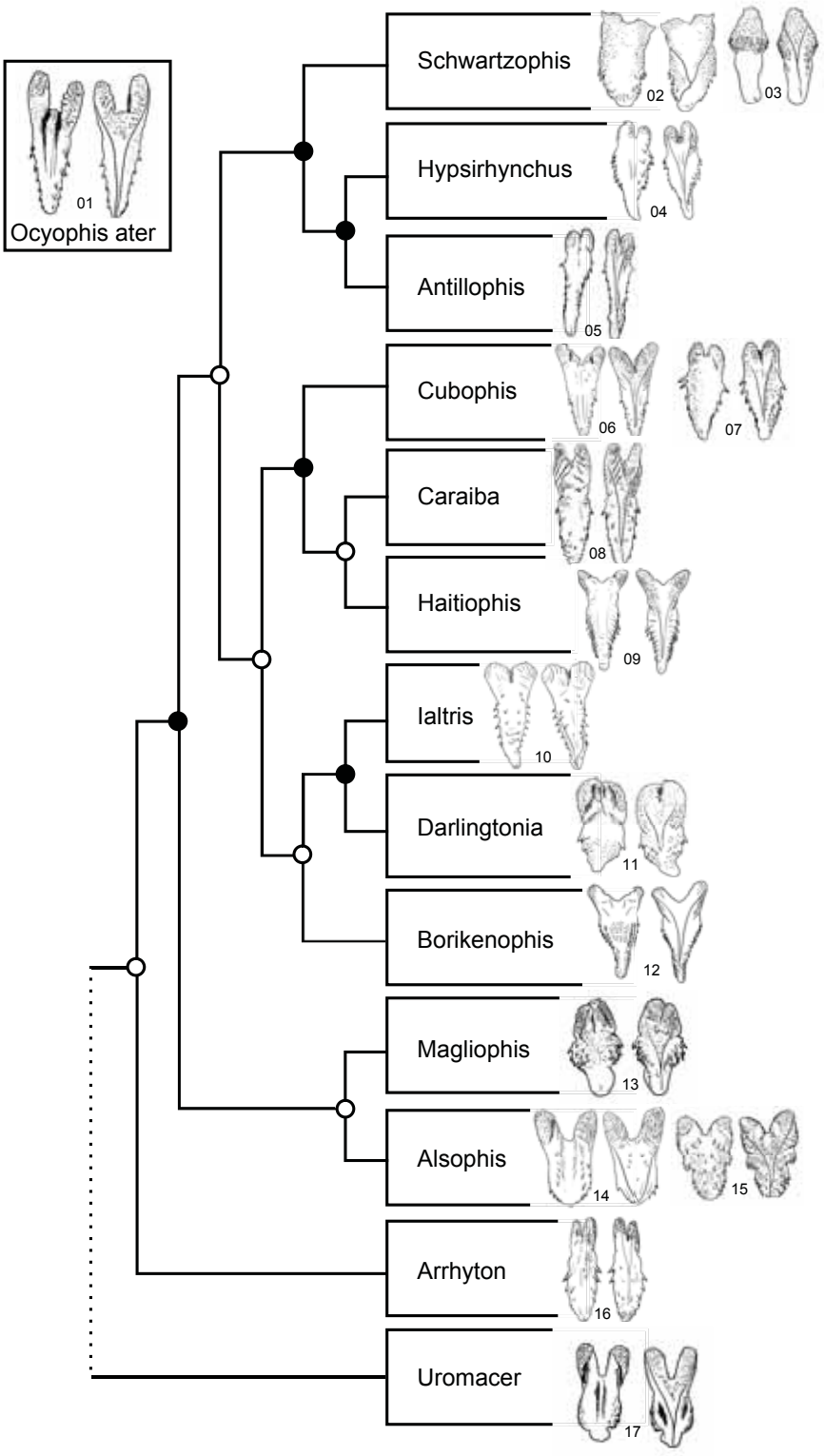

A)
B)
Zaher et. al (2009)
This study
Hedges et. al (2009)
Hypsirhynchus scalaris
Hypsirhynchus ferox
Antillophis parvifrons
Arrhyton funereum
Arrhyton polylepis
Arrhyton callilaemum
Alsophis c. ruttyi
Alsophis c. fuscicauda
Alsophis c. caymanus
Alsophis c. cantherigerus
Alsophis vudii
Antillophis andreae
Alsophis anomalus
Ialtris dorsalis
Darlingtonia haetiana
Alsophis p. prymnus
Alsophis p. portoricensis
Alsophis p. variegatus
Arrhyton e. stahli
Arrhyton e. exiguum
Alsophis a. manselli
Alsophis a. antillensis
Alsophis a. sibonius
Alsophis a. sajdaki
Alsophis rufiventris
Alsophis rijgersmaei
Arrhyton tanyplectum
Arrhyton procerum
Arrhyton dolichura
Arrhyton landoi
Arrhyton vittatum
Arrhyton supernum
Arrhyton taeniatum
Uromacer frenatus
Uromacer oxyrhynchus
Uromacer catesbyi
Xenodontini
Hypsirhynchus
Antillophis
Schwartzophis
Ocyophis
Caraiba
Ocyophis
Ialtris
Darlingtonia
Ocyophis
Magliophis
Alsophis
Arrhyton
Uromacer
Hypsirhynchus
Antillophis
Schwartzophis
Cubophis
Caraiba
Haitiophis
Ialtris
Darlingtonia
Borikenophis
Magliophis
Alsophis
Arrhyton
Uromacer
Hypsirhynchus
Cubophis
Caraiba
Haitiophis
Ialtris
Borikenophis
Magliophis
Alsophis
Arrhyton
Uromacer

Figura 4.


01
Ocyophis ater
Schwartzophis
02
03
Hypsirhynchus
04
Antillophis
05
Cubophis
06
07
Caraiba
08
Haitiophis
09
Ialtris
10
Darlingtonia
11
Borikenophis
12
Magliophis
13
Alsophis
14
15
Arrhyton
16
Uromacer
17

Supporting Information

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

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

Appendix S2. Strict consensus of 8568 most parsimonious trees found using TNT based on the multiple alignment. Numbers below branches show bootstrap and Bremer support values, respectively. Terminal names followed by an asterisk are from Vidal et al. (2010).

Appendix

On the use of the name Heterodontinae Bonaparte, 1845.

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

Pinou, 1993; Pinou et al., 2004) should not be referred to as the subfamily Heterodontinae until a well-defined nomenclatural resolution is obtained.

New taxa and taxonomic arrangements derived from the analysis

Philodryas Wagler, 1830.

Type-species: *Coluber Olfersii* Lichtenstein, 1823.

Diagnosis: No unambiguous morphological synapomorphy known so far.

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

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

potentially valid junior synonyms, its specific epithet must be replaced by a new substitution name (Articles 57.3.1. and 59.1). Therefore, we propose *georgeboulengeri* as a replacement name for the species. The replacement name intends to keep the hommage originally made by Procter to George A. Boulenger.

Erythrolamprus Boie, 1926.

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

Diagnosis: No unambiguous morphological synapomorphy known so far.

Contents: *Erythrolamprus aesculapii* (Linnaeus, 1766); *Erythrolamprus albertguentheri* **new replacement name** for *Liophis guentheri* Peracca, 1897; *Erythrolamprus almadensis* (Wagler, 1824) **new combination**; *Erythrolamprus andinus* (Dixon, 1983) **new combination**; *Erythrolamprus atraventer* (Dixon & Thomas, 1985) Forlani, Bernardo, Haddad & Zaher, 2010; *Erythrolamprus bizona* (Jan, 1863); *Erythrolamprus breviceps* (Cope, 1860) **new combination**; *Erythrolamprus carajasensis* (Cunha, Nascimento & Ávila-Pires, 1985) **new combination**; *Erythrolamprus ceii* (Dixon, 1991) **new combination**; *Erythrolamprus cobella* (Linnaeus, 1758) **new combination**; *Erythrolamprus cursor* (Lacépède, 1789) **new combination**; *Erythrolamprus dorsocorallinus* (Esqueda, Natera, La Marca & Ilija-Fistar, 2007) **new combination**; *Erythrolamprus epinephelus* (Cope, 1862) **new combination**; *Erythrolamprus festae* (Peracca, 1897) **new combination**; *Erythrolamprus frenatus* (Werner, 1909) **new combination**; *Erythrolamprus guentheri* (Garman, 1883); *Erythrolamprus ingeri* (Roze, 1958) **new combination**; *Erythrolamprus jaegeri* (Gunther, 1958) Forlani, Bernardo, Haddad & Zaher, 2010; *Erythrolamprus janaleeae* (Dixon, 2000) **new combination**; *Erythrolamprus juliae* (Cope, 1879) **new combination**; *Erythrolamprus leucogaster* (Jan, 1863) **new combination**; *Erythrolamprus longiventris* (Amaral, 1925) **new combination**; *Erythrolamprus maryellenae*

(Dixon, 1985) **new combination**; *Erythrolamprus melanotus* (Shaw, 1802) **new combination**; *Erythrolamprus mertensi* (Roze, 1964) **new combination**; *Erythrolamprus miliaris* (Linnaeus, 1758) Forlani, Bernardo, Haddad & Zaher, 2010; *Erythrolamprus mimus* (Cope, 1868); *Erythrolamprus ocellatus* Peters, 1869; *Erythrolamprus oligolepis* (Boulenger, 1905) **new combination**; *Erythrolamprus ornatus* (Garman, 1887) **new combination**; *Erythrolamprus perfuscus* (Cope, 1862) **new combination**; *Erythrolamprus poecilogyrus* (Wied, 1825) Forlani, Bernardo, Haddad & Zaher, 2010; *Erythrolamprus problematicus* (Myers, 1986) **new combination**; *Erythrolamprus pseudocorallus* (Roze, 1959); *Erythrolamprus pyburni* (Markezich & Dixon, 1979) **new combination**; *Erythrolamprus pygmaeus* (Cope, 1868) **new combination**; *Erythrolamprus reginae* (Linnaeus, 1758) **new combination**; *Erythrolamprus sagittifer* (Jan, 1863) Scrocchi, Abdala, Nori & Zaher, 2010; *Erythrolamprus semiaureus* (Cope, 1862); *Erythrolamprus steinbachi* (Boulenger, 1905) **new combination**; *Erythrolamprus subocularis* (Boulenger, 1902) **new combination**; *Erythrolamprus taeniogaster* (Jan, 1863) **new combination**; *Erythrolamprus taeniurus* (Tschudi, 1845) **new combination**; *Erythrolamprus torrenicola* (Donnelly & Myers, 1991) **new combination**; *Erythrolamprus trebbaui* (Roze, 1958) **new combination**; *Erythrolamprus triscalis* (Linnaeus, 1758) **new combination**; *Erythrolamprus typhlus* (Linnaeus, 1758) Forlani, Bernardo, Haddad & Zaher, 2010; *Erythrolamprus viridis* (Günther, 1862) **new combination**; *Erythrolamprus vitti* (Dixon, 2000) **new combination**; *Erythrolamprus williamsi* (Roze, 1958) **new combination**.

Comments: Zaher et al. (2009) erroneously synonymized *Erythrolamprus* into *Liophis* and they did so while showing the correct dates for the generic epithets: "*Liophis* Wagler, 1830 (includes *Erythrolamprus* Boie, 1826)..." (Zaher et al., 2009: 146). Following the rule of priority (article 23.1 of the International Code of Zoological Nomenclature, 1999), *Erythrolamprus* should be recognized (Curcio et al., 2009). We follow Article 51G of the

Code when citing new combinations made by previous authors (Forlani et al., 2010; Scrocchi et al., 2010). *Erythrolamprus guentheri* (Garman, 1883) and *Erythrolamprus guentheri* (Peracca, 1897) are secondary homonyms. According to Articles 57.3 and 60.3 of the Code, *Erythrolamprus guentheri* (Peracca, 1897) is the junior homonym and, having no known available and potentially valid junior synonym, its specific epithet must be replaced by a new substitution name. We propose *albertguentheri* as a replacement name for the species that intends to keep the hommage originally made by Peracca to Günther. We follow Frota et al. (2005) and Giraudo et al. (2006), and recognize *Liophis oligolepis* and *L. semiaureus* as valid species, respectively.

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

Type-species: *Oxyrrhopus rusticus* Cope, 1878.

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

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

Content: *Paraphimophis hussami* Morato, Franco & Sanches, 2003 **new combination**; *Paraphimophis rusticus* (Cope, 1878) **new combination**.

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

Type-species: *Rhinostoma iglesiasi* Gomes, 1915.

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

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

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

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

Tribe Alsophiini Fitzinger, 1843

Type-genus: *Alsophes* Fitzinger, 1843: 25.

Diagnosis: No morphological synapomorphies known.

Content: *Alsophis* Fitzinger, 1843; *Antillophis* Maglio, 1970 **resurrected**; *Arrhyton* Günther, 1858; *Borikenophis* Hedges & Vidal, 2009; *Caraiba* Zaher, Grazziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009; *Cubophis* Hedges & Vidal, 2009; *Darlingtonia* Cochran, 1935 **resurrected**; *Haitiophis* Hedges & Vidal, 2009; *Hypsirhynchus* Günther, 1858; *Ialtris* Cope, 1862; *Magliophis* Zaher, Grazziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009; *Ocyophis* Cope, 1886 **resurrected**; *Schwartzophis* Zaher, Grazziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009 **resurrected**.

Hypsirhynchus Günther, 1858

Type species: *Hypsirhynchus ferox* Günther, 1858.

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

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

Antillophis Maglio, 1970, **resurrected**

Type species: *Dromicus parvifrons* Cope, 1862.

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

Content: *A. parvifrons* (Cope, 1862).

Comments: *Antillophis* was synonymized with *Hypsirhynchus* by Hedges et al. (2009). However, these two genera have remarkably different hemipenial morphologies (Fig. 4). *Hypsirhynchus* has a moderately bilobed, slightly bicaliculate, and semicapitate hemipenis with enlarged lateral spines arranged in several parallel rows. In contrast, *Antillophis* has a long, slender, semicaliculate hemipenis with relatively small and almost completely nude lobes, with basal pockets in the proximal region of the hemipenial body, and relatively larger and calcified papillae that ornament the edge of the capitulum.

Darlingtonia Cochran, 1935, **resurrected**

Type species: *Darlingtonia haetiana* Cochran, 1935.

Diagnosis: Scales smooth, without pits, in 19 rows; anal single, loreal absent; strongly bilobed, semicalyculated and semicapitated hemipenis with the capitulum restricted to the sulcate and lateral surface of the lobes, formed by papillate calyces; relatively long lobes, representing almost half the total length of the organ.

Content: *D. haetiana* Cochran, 1935.

Comments: The synonymization of *Darlingtonia* with *Ialtris* (Hedges et al., 2009) is not justified given the significantly distinct, external and hemipenial morphologies of these genera (Fig. 4). Synonymization is based on the genera being sister taxa and in having seven supralabials. The organ of *Darligtonia* is semicalyculated and the capitulum is restricted to the sulcate and lateral surfaces of the lobes and formed by papillate calyces. In contrast, *Ialtris* completely lacks calyces and the lobes that are ornamented with flounces in a typical "bicalyculate" position (Zaher, 1999). Further, *Darlingtonia* differs from *Ialtris* in having eight infralabials (9 in *Ialtris*), 132–144 ventrals (vs. 160–192) and 40–54 subcaudals (vs. 57–115), an entire anal scale (vs. divided), no loreal scale (vs. present), and ungrooved teeth (vs. grooved) (data from Cochran, 1941; Schwartz and Rossman, 1976; and Schwartz and Henderson, 1991).

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

Type species: *Arrhyton callilaemum* Gosse, 1851.

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

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

Comments: Hedges et al. (2009) ignored the striking uniqueness in the hemipenial morphology of *Schwartzophis*, an omission that disserves morphological evidence (Fig. 4). Zaher (1999) noted hemipenial particularities in all three species of *Schwartzophis* (as the *Arrhyton callilaemum* Group); the almost unilobed hemipenis is unique among WIXs. Among mainland components, it only occurs in Elapomorphini and *Xenopholis*. In contrast, all other

xenodontines have bilobed hemipenes. *Schwartzophis* also differs from *Hypsirhynchus* and *Antillophis* in lacking calyces on the capitulum. The recognition of *Schwartophis* allows the hemipenes to serve as a valuable diagnostic character.

Ocyophis Cope, 1886, **resurrected**

Type species: *Natrix ater* Gosse, 1863

Diagnosis: Number of dorsal scales rows at midbody 17; hemipenis (only known for *O. ater*) semicalyculate, semicapitate and deeply bilobed, with few well-developed enlarged lateral spines arranged in two parallel rows; large papillate calyces forming the capitula, which are positioned laterally; row of large papilla ornamenting the lobular crotch.

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

Comments: Hedges et al. (2009) placed *Ocyophis ater* and *O. melanichnus* (*sensu* Zaher et al., 2009) in *Hypsirhynchus*. These two species are rare and probably extinct; thus, neither Zaher et al. (2009) nor Hedges et al. (2009) had tissues or sequence data. However, their allocation of *O. ater* and *O. melanichnus* to *Hysirhynchus* is unjustified. The assignment of *O. ater* to *Hypsirhynchus* is based on the absence of a loreal scale and on skull similarities taken from Maglio (1970). Whereas Maglio (1970) noted strong similarity between *O. ater* and *Hypsirhynchus*, his hypothesis of phyletic relationships (Maglio, 1970: Fig. 18) places *O. ater* as the sister group of a lineage formed by *Hypsirhynchus* and *Uromacer*. Zaher (1999) remarked on the puzzling hemipenial morphology of *O. ater* (Fig. 4) and he avoided allocation for this species.

The long-standing composition of *Hypsirhynchus* (as in Zaher et al., 2009) reflects its morphological distinction from *O. ater*, from which it differs in several meristic and anatomical features. Both taxa have distinct, non-overlapping counts in the following suite of characters (*Hypsirhynchus* : *O. ater*): number of subcaudals (71–93 : 144–162), dorsal scale

rows (19 : 17), maxillary teeth (13–14 : 18), pterygoid teeth (17–19 : 26–27), palatine teeth (7 : 13–16), and dentary teeth (18–19 : 22–25), apical pits (1 : 2) (data from Cochran, 1941; Maglio, 1970; and Schwartz and Henderson, 1991). Therefore, we resurrect the genus *Ocyophis* Cope, 1886 to include *O. ater*, its type species (*Natrix ater* Gosse, 1863).

Hedges et al. (2009) placed *Ocyophis melanichnus* into *Hypsirhynchus* because of the presence of relatively large posterior supralabial scales and its occurence in Hispaniola. This species is one of the poorest known WIX, and we must base its taxonomy on morphological data provided by a few specimens. Cochran (1941) observed that this rare species lacks a groove behind the eye between the last upper labials and the temporals. This separates it from *Al. antillensis* and *B. portoricensis*. Maglio (1970) analyzed scalation and skull morphology. The antithesis of Cochran (1941), he positioned *O. melanichnus* as the sister group of a clade formed by the *Al. antillensis* Group and the *B. portoricensis* Group. In assigning *O. melanichnus* to *Hypsirhynchus*, Hedges et al. (2009) ignored the conclusion of Maglio (1970) and based their taxonomy only on the shape pattern of the supralabials and the snake's distribution. The following suite of non-overlapping characters distinguish *Hypsirhynchus* (*sensu* Zaher et al., 2009) from *O. melanichnus* (*Hypsirhynchus* : *O. melanichnus*): number of ventrals (156–182 : 189); number of subcaudals (71–93 : 108); midbody dorsal scale rows (19 : 17); temporal scale formulae (1+2/1+2 : 2+2/2+2); maxillary teeth (13–14 : 20); pterygoid teeth (17–19 : 28); palatine teeth (7 : 16); dentary teeth (18–19 : 24); and number of apical pits (1 : 2) (data from Cochran, 1941; Maglio, 1970 and Schwartz and Henderson, 1991). Because no morphological or molecular evidence supports the transfer of *O. melanichnus* into *Hypsirhynchus*, we opt to maintain it in *Ocyophis* (Zaher et al., 2009). This genus may still be paraphyletic with respect to the other well-established assemblages of WIX and further studies are necessary in order to clarify its phylogenetic affinities.

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

Terminal	12S	16S	cytb	nd2	nd4	bdnf	c-mos	rag2
Achalinus meiguensis	FJ424614	FJ424614	FJ424614	FJ424614	FJ424614	-	-	-
Acrochordus granulatus	AB177879	AB177879	AF217841	AB177879	U49296	-	AF471124	EF144093
Agkistrodon piscivorus	AF259225	AF057278	EU483451	DQ523161	AF156579	**YPX802**	AF471096	-
Alsophis anomalus	FJ666091	FJ666092	-	-	-	-	-	-
Alsophis antiguae sajdaki	AF158455	AF158524	FJ416731	FJ416769	FJ416805	-	-	FJ416842
Alsophis antillensis	FJ41669	FJ416702	FJ416726	FJ416764	FJ416800	**CTMZ04929**	-	FJ416837
Alsophis biserialis dorsalis	**CTMZ-4647**	**CTMZ4647**	**CTMZ04647**	-	-	-	**CTMZ4647**	-
Alsophis cantherigerus	AF158405	AF158475	AF544669	FJ416782	FJ416818	FJ433999	AF544694	EF144109
Alsophis caymanus	FJ416693	FJ416704	FJ416745	FJ416784	FJ416820	-	-	FJ416856
Alsophis elegans	AF158401	AF158470	**CTMZ07428**	-	-	**CTMZ07428**	**CTMZ07428**	-
Alsophis fuscicauda	FJ416695	FJ416706	FJ416747	FJ416786	FJ416822	-	-	-
Alsophis manselli	AF158459	AF158528	FJ416727	FJ416765	FJ416801	-	-	FJ416838
Alsophis p. portoricensis	FJ416696	FJ416707	FJ416732	FJ416770	FJ416806	**CTMZ04118**	AF471126	FJ416843
Alsophis p. prymnus	AF158448	-	FJ416733	FJ416771	FJ416807	-	-	FJ416844
Alsophis rijgersmaei	FJ416697	FJ416708	FJ416729	FJ416767	FJ416803	-	-	FJ416840
Alsophis rufiventris	FJ416698	FJ416709	FJ416730	FJ416768	FJ416804	-	-	FJ416841
Alsophis ruttyi	FJ416699	FJ416710	FJ416746	FJ416785	FJ416821	-	-	-
Alsophis sibonius	FJ416692	FJ416703	FJ416728	FJ416766	FJ416802	-	-	FJ416839
Alsophis variegatus	FJ416700	FJ416711	FJ416734	FJ416772	FJ416808	-	-	FJ416845
Alsophis vudii	AF158443	AF158512	FJ416744	FJ416783	FJ416819	-	**CTMZ04066**	FJ416855
Antillophis andreae	AF158442	AF158511	FJ416743	FJ416781	FJ416817	-	-	FJ416854
Antillophis parvifrons	AF158441	AF158510	FJ416740	FJ416778	FJ416814	**YPX108**	-	FJ416851
Aparallactus capensis	FJ404129	AY188045	AY188006	-	FJ404331	-	AY187967	FJ404404
Aplopeltura boa	AF544761	AF544787	-	-	U49312	FJ433984	AF544715	-

Apostolepis dimidiata	GQ457782	GQ457725	**CBGM0042**	-	-	**CBGM0042**	GQ457844	-
Apostolepis flavotorquata	**APFL001**	**APFL001**	-	-	-	-	**APFL001**	-
Apostolepis rondoni	**APRO001**	-	-	-	-	-	**APRO001**	-
Apostolepis sanctaeritae	**APAM003**	**APBI001**	-	-	-	-	**APBI001**	-
Arrhyton callilaemum	AF158440	AF158509	FJ416737	FJ416775	FJ416811	-	-	FJ416848
Arrhyton dolichura	AF158438	AF158507	FJ416721	FJ416759	FJ416795	-	-	FJ416832
Arrhyton exiguum	FJ416694	FJ416705	FJ416724	FJ416762	FJ416798	-	AF471117	FJ416835
Arrhyton funereum	AF158451	AF158520	FJ416739	FJ416777	FJ416813	-	-	FJ416850
Arrhyton landoi	AF158439	AF158508	FJ416720	FJ416758	FJ416794	-	-	FJ416831
Arrhyton polylepis	AF158450	AF158519	FJ416738	FJ416776	FJ416812	-	-	FJ416849
Arrhyton procerum	AF158452	AF158521	FJ416723	FJ416761	FJ416797	-	-	FJ416834
Arrhyton stahli	-	-	FJ416725	FJ416763	FJ416799	-	-	FJ416836
Arrhyton supernum	AF158436	AF158505	FJ416718	FJ416756	FJ416792	-	-	FJ416829
Arrhyton taeniatum	AF158453	AF158522	FJ416717	FJ416755	FJ416791	-	-	FJ416828
Arrhyton tanyplectum	AF158446	AF158516	FJ416722	FJ416760	FJ416796	-	-	FJ416833
Arrhyton vittatum	AF158437	AF158506	FJ416719	FJ416757	FJ416793	-	-	FJ416830
Atractaspis micropholis	AF544740	AF544789	AY612006	-	FJ404336	FJ433994	AF544677	EF144105
Atractus albuquerquei	GQ457783	GQ457726	**YPx110**	-	-	**YPX110**	GQ457845	-
Atractus badius	AF158425	AF158485	-	-	-	-	-	-
Atractus flammigerus	AF158402	AF158471	-	-	-	-	-	-
Atractus reticulatus	**ATRE001**	-	-	-	-	-	**ATRE001**	-
Atractus schach	**ATSC001**	**ATSC001**	-	-	-	-	**ATSH001**	-
Atractus trihedrurus	GQ457784	GQ457727	**YPx112**	-	-	**YPX112**	GQ457846	-
Atractus zebrinus	**ATZE001**	**ATZE001**	-	-	-	-	**ATZE002**	-
Atractus zidocki	AF158426	AF158487	-	-	-	-	-	-
Azemiops feae	AF512748	AY352713	AY352747	-	U41870	EU402628	AF544695	-
Bitis nasicornis	DQ305411	DQ305434	AY188009	-	DQ305475	-	AF471130	-
Boa constrictor	AB177354	AB177354	AY575035	AB177354	AB177354	AY988030	AF544676	-
Boiruna maculata	GQ457785	**BOMA002V**	**YPx113**	-	-	**YPX113**	GQ457847	-
Bothriechis schlegelii	AF057213	AF057260	AF039270	-	U41874	FJ433983	AF544680	EF144095

Bothrophthalmus lineatus	FJ404146	FJ404198	AF471090	-	FJ404349	-	AF471129	FJ404421
Bungarus fasciatus	U96793	Z46501	AJ749349	EU579523	EU547037	**YPX591**	AY058924	EF144100
Calamaria pavimentata	-	-	AF471081	-	-	**YPX548**	AF471103	EF144116
Calamaria yuannanensis	**YPx503**	**YPx503**	**YPx503**	-	-	-	AF471103	-
Calamodontophis paucidens	GQ457786	GQ457728	-	-	-	-	GQ457848	-
Carphophis amoenus	AY577013	AY577022	AF471067	-	-	-	DQ112082	-
Causus resimus	AY223649	AY223662	AY223555	-	-	-	AF544696	-
Clelia bicolor	GQ457787	GQ457729	-	-	-	-	GQ457849	-
Clelia clelia	AF158403	AF158472	-	-	-	-	**CTMZ00711**	-
Clelia rustica	**CLRU001**	**YPx114**	**YPx114**	-	-	-	**CLRU001**	-
Coluber constrictor	AY122819	**L01770**	EU180347	AY487002	U49300	**YPX528**	AY486938	-
Conophis lineatus	GQ457788	**COLI001**	**YPx116**	-	-	**YPX116**	**CTMZ04125**	-
*Conophis lineatus **	GU018143	GU018161	-	-	-	-	-	-
Contia tenuis	AY577021	AY577030	AF471095	-	DQ364664	GU112361	AF471134	-
*Crisantophis nevermanni **	GU018152	GU018169	-	-	-	-	-	-
Darlingtonia haetiana	AF158458	AF158527	FJ416736	FJ416774	FJ416810	-	-	FJ416847
Diadophis punctatus	AY577015	AF544793	EU193670	-	DQ364667	**EU402637/YPX089**	AF471122	EF144110
Dinodon rufozonatum	AF233939	AB008539	AF471063	-	-	**YPX540**	AF471163	-
Dipsas albifrons	**DIAL001**	**YPx117**	**YPx117**	-	-	**YPX117**	-	-
Dipsas articulata	**YPx118**	**YPx118**	-	-	-	**YPX118**	-	-
Dipsas catesbyi	**DICA001**	**DICA001**	**YPx119**	-	-	**YPX119**	**DICA001**	-
Dipsas indica	GQ457789	GQ457730	-	-	-	-	GQ457850	-
Dipsas neivai	GQ457790	GQ457731	-	-	-	-	GQ457851	-
Dipsas variegata	AF158406	AF158476	-	-	-	-	-	-
Drepanoides anomalus	GQ457791	GQ457732	**CBGM0038**	-	-	-	GQ457852	-
Echinanthera affinis	**CBGM0427**	**CBGM0427**	**CBGM00427**	-	**EAF003**	**CBGM0427**	GQ457853	-
Echinanthera brevirostris	GQ457793	GQ457734	**CBGM0037**	-	-	**CBGM0037**	GQ457854	-
Echinanthera melanostigma	**ypx120**	**YPX120**	**YPx120**	-	-	-	-	-
*Echinanthera melanostigma **	GU018153	GU018174	-	-	-	-	-	-
Echinanthera undulata	**EUN001**	**EUN001**	**CBGM0292**	-	-	**CBGM0292**	**EUN002**	-

Elaphe quatuorlineata	AY122798	AF215267	AY486931	AY487028	AY487067	-	AY486955	-
Elapomorphus quinquelineatus	GQ457794	GQ457735	**CBGM0070**	-	-	**CBGM0070**	GQ457855	-
Enhydris enhydris	AF499285	AF499299	EF395904	-	-	-	AF544699	-
Erythrolamprus aesculapii	GQ457795	GQ457736	-	-	-	**CBGM0030**	GQ457856	-
Erythrolamprus mimus *	GU018157	GU018175	-	-	-	-	-	-
Farancia abacura	Z46467	AY577025	U69832	DQ902239	DQ902307	-	AF471141	-
Geophis godmani	**YPx123**	**YPx123**	**YPx123**	-	-	**YPX123**	-	-
Gomesophis brasiliensis	GQ457796	GQ457737	-	-	-	-	-	-
Helicops angulatus	GQ457797	GQ457738	AF471037	FJ416751	-	**CBGM0081**	GQ457857	FJ416824
Helicops carinicaudus	**HECA001**	-	-	-	-	-	**HECA001**	-
Helicops gomesi	GQ457798	GQ457739	-	-	-	-	GQ457858	-
Helicops hagmanni	**HEHA001**	**HEHA001**	-	-	-	-	**HEHA001**	-
Helicops infrataeniatus	GQ457799	GQ457740	**YPx124**	-	U49310	-	GQ457859	-
Heterodon nasicus	GQ457801	AY577027	-	-	-	-	GQ457861	-
Heterodon platirhinos	AY577019	AY577028	**YPx568**	FJ416750	AF402659	**YPX568**	**YPx568**	FJ416823
Heterodon simus	AY577020	AY577029	AF217840	DQ902242	DQ902310	-	AF471142	-
Hierophis spinalis	AY541508	AY376773	AY486924	AY487017	AY487056	-	AY376802	-
Homalopsis buccata	AF499288	AF544796	EF395917	-	-	-	AF544701	EF144097
Homoroselaps lacteus	FJ404135	AY611843	AF217833	-	FJ404339	**YPX158**	AY611901	FJ404410
Hydrodynastes bicinctus	GQ457802	GQ457742	**YPx125**	-	-	**YPX125**	GQ457862	-
Hydrodynastes gigas	GQ457803	GQ457743	-	-	-	**CBGM0098**	GQ457863	-
Hydrops triangularis	GQ457804	GQ457744	AF471039	-	-	**YPX126**	GQ457864	-
Hypsiglena torquata	EU728591	EU728591	EU728591	EU728591	EU363050	-	AF471159	-
Hypsirhynchus ferox	AF158447	AF158515	FJ416742	FJ416780	FJ416816	-	-	FJ416853
Hypsirhynchus scalaris	AF158449	AF158518	FJ416741	FJ416779	FJ416815	-	-	FJ416852
Ialtris dorsalis	AF158456	AF158525	FJ416735	FJ416773	FJ416809	-	-	FJ416846
Imantodes cenchoa	GQ457805	GQ457745	EF078505	EU728586	EU728586	**YPX127**	GQ457865	-
Imantodes lentiferus	AF158463	AF158532	EF078513	-	-	-	-	-
Lamprophis fuliginosus	AY122681	FJ404204	DQ486339	-	FJ404364	-	FJ387204	FJ404438

Laticauda colubrina	U96799	EU547138	AF217834	-	EU546998	EU402647	AY058932	EF144101
Leioheterodon madagascariensis	AF544768	AY188061	AY188022	-	U49318	**YPX502**	AY187983	EF144103
Leptodeira annulata	GQ457806	GQ457746	FJ416713	FJ416749	FJ416787	FJ433998	GQ457866	EF144108
Leptodeira septentrionalis *	GU018148	GU018163	-	-	-	-	-	-
Liophis almadensis	**LIAL001**	**LIAL001**	-	-	-	-	**LIAL001**	-
Liophis amarali	GQ457807	GQ457747	**CBGM0239**	-	-	-	GQ457867	-
Liophis anomalus	**LIAN001**	**LIAN001**	-	-	-	-	-	-
Liophis atraventer	**LIAT001**	**LIAT001**	-	-	-	-	**LIAT001**	-
Liophis breviceps	AF158464	AF158533	-	-	-	-	-	-
Liophis ceii	**LICE001**	**LICE001**	-	-	-	-	**LICE001**	-
Liophis elegantissimus	GQ457808	GQ457748	-	-	-	-	GQ457868	-
Liophis epinephelus *	GU018158	GU018176	-	-	-	-	-	-
Liophis flavifrenatus	**LIFL001**	**LIFL001**	-	-	-	-	-	-
Liophis jaegeri	GQ457809	GQ457749	-	-	-	-	GQ457869	-
Liophis juliae	AF158464	AF158514	-	-	-	-	-	-
Liophis meridionalis	GQ457810	GQ457750	-	-	-	-	GQ457870	-
Liophis miliaris	**LIMI001**	**LIMI001**	**YPx129**	-	-	**YPX129**	**LIMI001**	-
Liophis paucidens	**LIPA001**	-	-	-	-	-	**LIPA001**	-
Liophis poecilogyrus	**LIPO002**	**LIPO002**	-	-	-	-	-	-
Liophis reginae	**LIRE003**	**LIRE001**	-	-	-	-	**LIRE003**	-
Liophis typhlus	GQ457811	GQ457751	-	-	-	-	GQ457871	-
Lycophidion laterale	FJ404179	FJ404197	FJ404297	-	FJ404377	-	FJ404280	FJ404451
Lystrophis dorbignyi	GQ457812	GQ457752	-	-	-	-	-	-
Lystrophis histricus	GQ457813	GQ457753	**YPx130**	-	-	**YPX130**	-	-
Lystrophis matogrossensis	**LYMA001**	**LYMA001**	-	-	-	-	-	-
Lystrophis nattereri	**LYNA001**	**LYNA001**	-	-	-	-	-	-
Lystrophis pulcher	**LYPU001**	**LYPU001**	-	-	-	-	-	-
Lystrophis semicinctus *	GU018156	GU018173	-	-	-	-	-	-
Manolepis putnami	**CTMZ-07419**	**CTMZ07419**	**CTMZ07419**	-	-	**CTMZ07419**	**CTMZ07419**	-

*Manolepis putnami **	GU018151	GU018171	-	-	-	-	-	-
Micrurus surinamensis	AF544770	AF544799	EF137415	-	AF228444	FJ433991	EF137422	EF144102
Naja naja	Z46453	Z46482	EU547039	DQ343648	EU546997	-	AF435020	-
Natriciteres olivacea	AF544772	AF544801	AF471058	-	-	-	AF471146	-
Natrix natrix	AY122682	AF158530	AY866540	-	AY873724	**EU402655/YPX538**	AF471121	-
Ninia atrata	GQ457814	**YPx131**	**YPx131**	-	-	**YPX131**	GQ457874	-
Notechis ater	EU547131	EU547180	AF217836	-	EU547034	-	EU546944	-
*Nothopsis rugosus **	GU018159	GU018177	-	-	-	-	-	-
Oxybelis aeneus	AF158416	AF158498	AF471056	-	-	-	AF471148	-
Oxyrhabdium leporinum	-	-	AF471029	-	-	-	DQ112081	FJ404466
Oxyrhopus clathratus	GQ457815	GQ457754	-	-	-	-	GQ457875	-
Oxyrhopus formosus	**OXFO001**	AF158482	-	-	-	-	-	-
Oxyrhopus guibei	**OXGU001**	**OXGU001**	**YPx132**	-	-	**YPX132**	**OXGU001**	-
Oxyrhopus melanogenys	**OXME001**	AF158489	-	-	-	-	**OXME001**	-
*Oxyrhopus petola **	GU018150	GU018162	-	-	-	-	-	-
*Oxyrhopus petola *2*	GU018144	GU018162	-	-	-	-	-	-
Oxyrhopus rhombifer	GQ457816	GQ457755	-	-	-	-	GQ457876	-
*Oxyrhopus rhombifer **	GU018146	GU018165	-	-	-	-	-	-
Oxyrhopus trigeminus	**OXTR001**	**OXTR001**	**CBGM0102**	-	-	-	-	-
Pareas carinatus	AF544773	AF544802	**YPx92(44)**	-	**YPx92(44)**	FJ433985	AF544692	EF144096
Phalotris lativittatus	**PHLA001**	**PHLA001**	-	-	-	-	**PHLA001**	-
Phalotris lemniscatus	GQ457817	GQ457756	**CBGM0241**	-	-	**YPX133**	GQ457877	-
Phalotris mertensi	**PHME001**	**CTMZ0630**	-	-	-	-	-	-
Phalotris nasutus	GQ457818	GQ457757	**CBGM0230**	-	-	-	GQ457878	-
Phalotris reticulatus	**PHRE001**	**CBGM0255**	**CBGM0255**	-	-	-	-	-
Philodryas aestiva	GQ457819	GQ457758	-	-	-	-	GQ457879	-
Philodryas baroni	**PHBA001**	**PHBA001**	AF236812	-	-	-	-	-
Philodryas mattogrossensis	GQ457820	GQ457759	-	-	-	-	GQ457880	-
Philodryas nattereri	**PHNAT006**	**PHNAT006**	AF236806	-	-	-	**PHNAT006**	-
Philodryas olfersii	**PHOL001**	**PHOL001**	**YPx134**	-	-	**YPX134**	**PHOL001**	-

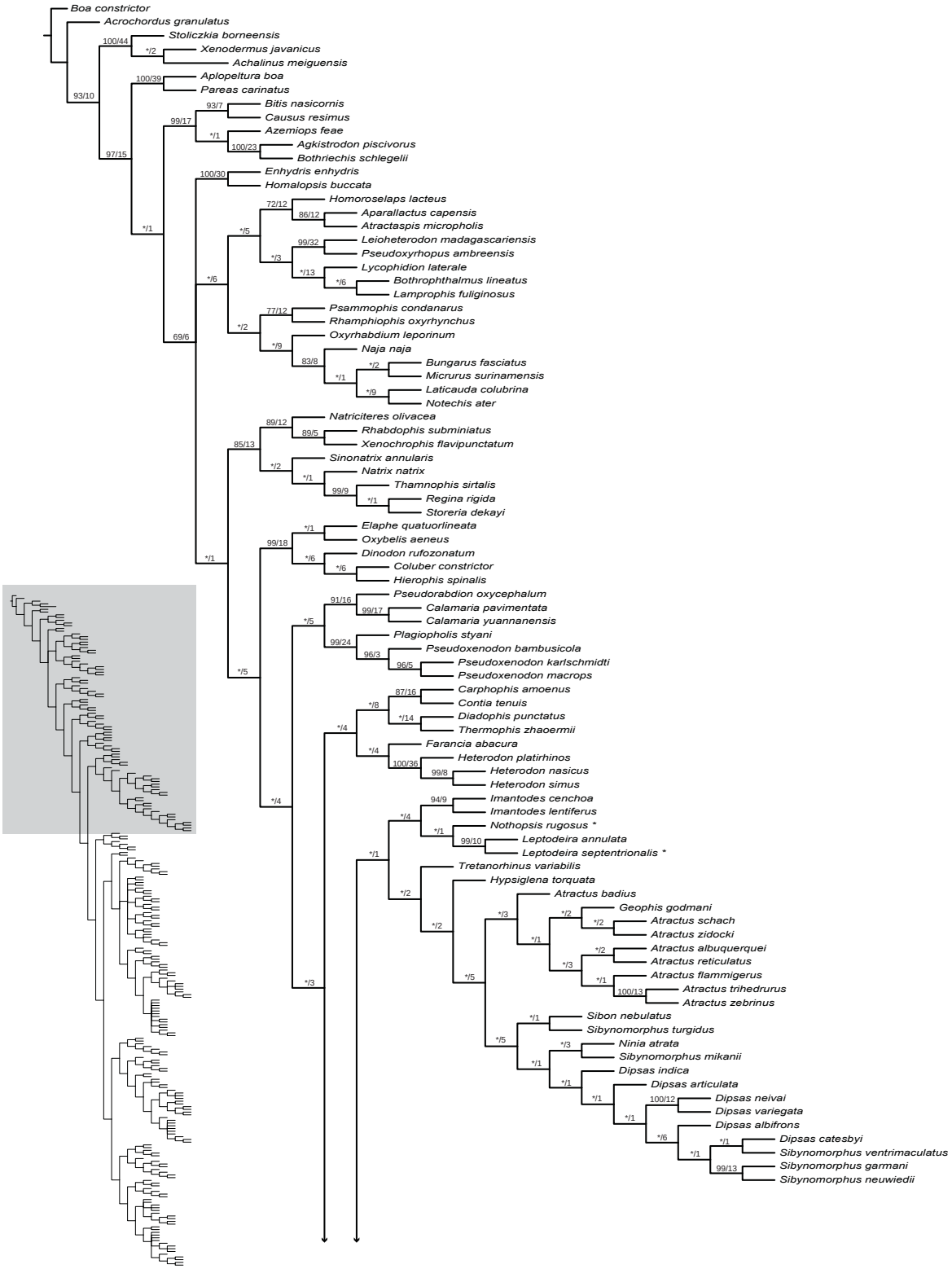
Philodryas patagoniensis	GQ457821	GQ457760	AF236808	-	-	-	GQ457881	-
Philodryas psammophidea *	GU018149	GU018168	-	-	-	-	-	-
Philodryas viridissima	AF158419	AF158474	AF236807	-	-	-	-	-
Phimophis guerini	GQ457822	GQ457761	-	-	-	-	GQ457882	-
Phimophis iglesiasi	**PHIG001**	**PHIG001**	GQ895881	-	-	-	GQ895823	-
Plagiopholis styani	-	-	EU496918	-	-	-	EU496916	-
Psammophis condanarus	Z46450	Z46479	AF471075	-	-	-	AF471104	FJ404426
Pseudablabes agassizi	GQ457823	GQ457762	-	-	-	-	GQ457883	-
Pseudoboa coronata	GQ457824	GQ457763	-	-	-	-	GQ457884	-
Pseudoboa neuwiedii	AF158423	AF158490	-	-	-	-	-	-
Pseudoboa nigra	GQ457825	GQ457764	**YPx136**	-	-	**YPX136**	GQ457885	-
Pseudoeryx plicatilis	GQ457826	GQ457765	-	-	-	-	GQ457886	-
Pseudorabdion oxycephalum	-	-	AF471073	-	-	-	DQ112083	-
Pseudotomodon trigonatus	GQ457827	GQ457766	-	-	-	-	GQ457887	-
Pseudoxenodon bambusicola	**YPx551**	**YPx551**	-	-	-	**YPX551**	**YPx551**	EF144111
Pseudoxenodon karlschmidti	**YPx564**	**YPx564**	AF471080	-	-	**YPX564**	AF471102	-
Pseudoxenodon macrops	**YPx536**	**YPx536**	**YPx536**	-	-	-	-	-
Pseudoxyrhopus ambreensis	FJ404188	AY188074	AY188035	-	FJ404385	-	AY187996	FJ404459
Psomophis genimaculatus	GQ457828	GQ457767	-	-	-	-	GQ457888	-
Psomophis joberti	GQ457829	GQ457768	**YPx137**	-	-	**YPX137**	GQ457889	-
Psomophis obtusus	**POB001**	**POB001**	-	-	-	-	-	-
Ptychophis flavovirgatus	GQ457830	GQ457769	-	-	-	-	GQ457890	-
Regina rigida	AF402636	-	AF471052	AF384838	-	-	AF471120	-
Rhabdophis subminiatus	AF544776	AF544805	**YPx566**	-	U49325	**YPX566**	AF544713	-
Rhachidelus brazili	**RHBRA001V**	**RHBRA001V**	**YPx139**	-	-	**YPX139**	-	-
Rhamphiophis oxyrhynchus	Z46443	Z46738	**YPx523**	-	-	**YPX523**	AF544710	FJ404400
Sibon nebulatus	AF544777	AF544806	EU728583	EU728583	EU728583	-	AF544736	-
Sibynomorphus garmani	GQ457831	GQ457770	-	-	-	-	GQ457891	-
Sibynomorphus mikanii	GQ457832	GQ457771	**YPx141**	-	-	**YPX141**	GQ457892	-
Sibynomorphus neuwiedii	**SINE001**	**SINE001**	-	-	-	-	-	-

Sibynomorphus turgidus	**SITU001**	**SITU001**	-	-	-	-	-	-
Sibynomorphus ventrimaculatus	**SIVE001**	**SIVE001**	-	-	-	-	**SIVE001**	-
Sinonatrix annularis	AF544778	AF544807	AF036024	-	-	-	AF544712	-
Siphlophis cervinus	**SICE001**	**SICE001**	-	-	-	-	**CBGM0033**	-
Siphlophis compressus	GQ457833	GQ457772	-	-	-	-	GQ457893	-
Siphlophis longicaudatus	**SILO003**	**SILO001**	-	-	-	-	**CTMZ0655**	-
Siphlophis pulcher	GQ457834	GQ457773	**YPx142**	-	-	**CBGM0052**	GQ457894	-
Sordellina punctata	**SOPU001**	**SOPU001**	**CTMZ04952**	-	-	**YPX143**	**CTMZ04952**	-
Stoliczkaia borneensis	AF544779	AF544808	-	-	-	FJ433982	AF544721	EF144094
Storeria dekayi	AF402639	**YPx567**	AF471050	AF384841	EF417365	**YPX567**	AF471154	-
Tachymenis peruviana	GQ457835	GQ457774	-	-	-	**YPX145**	GQ457895	-
*Tachymenis peruviana **	GU018147	GU018167	-	-	-	-	-	-
Taeniophallus nicagus	**YPx146**	**YPx146**	-	-	-	-	**CTMZ0483**	-
Thamnodynastes hypoconia	**THHY001**	-	-	-	-	-	-	-
Thamnodynastes nattereri	GQ457836	GQ457775	-	-	-	-	-	-
Thamnodynastes pallidus	AF158420	AF158492	-	-	-	-	-	-
*Thamnodynastes pallidus **	GU018155	GU018166	-	-	-	-	-	-
Thamnodynastes rutilus	GQ457837	GQ457776	-	-	-	-	GQ457896	-
Thamnodynastes strigatus	**THST001**	**YPx147**	**YPx147**	-	-	**YPX147**	-	-
Thamnophis sirtalis	AF402646	-	-	DQ995397	AY136269	**YPX539**	DQ902094	-
Thermophis zhaoermii	GQ166168	GQ166168	GQ166168	-	GQ166168	-	EU496917	-
Tomodon dorsatus	GQ457838	GQ457777	**YPx148**	-	-	**YPX148**	GQ457897	-
Tretanorhinus variabilis	AF158460	AF158529	-	-	-	-	-	-
*Trimetopon gracile **	GU018160	GU018178	-	-	-	-	-	-
Tropidodryas serra	**YPx149**	**YPx149**	**YPx149**	-	-	-	-	-
Tropidodryas striaticeps	GQ457839	GQ457778	AF236811	-	-	**YPX149**	-	-
*Umbrivaga pygmaea **	GU018154	GU018172	-	-	-	-	-	-
Uromacer catesbyi	AF158454	AF158523	FJ416714	FJ416752	FJ416788	-	-	FJ416825
Uromacer frenatus	AF158444	AF158513	FJ416715	FJ416753	FJ416789	-	-	FJ416826

Uromacer oxyrhynchus	FJ416701	FJ416702	FJ416716	FJ416754	FJ416790	-	-	FJ416827
Waglerophis merremi	GQ457840	**YPx150**	**YPx150**	-	-	**YPX150**	-	-
Xenochrophis flavipunctatum	AF544780	AF544809	-	FJ416748	-	-	AF544714	EF144112
Xenodermus javanicus	AF544781	AF544810	AY425810	-	U49320	EU402667	AF544711	-
Xenodon guentheri	**XEGU001**	**XEGU001**	-	-	-	-	-	-
Xenodon neuwiedi	GQ457841	GQ457779	AF236814	-	-	-	-	-
Xenodon severus	**XESE001**	**XESE001**	**YPx151**	-	-	**YPX151**	-	-
Xenodon werneri	AF158468	AF158538	-	-	-	-	-	-
Xenopholis scalaris	**XESC001**	**XESC002**	GQ895897	-	-	-	**XESC001**	-
Xenopholis scalaris *	GU018145	GU018164	-	-	-	-	-	-
Xenopholis undulatus	**XEUN001**	**XEUN001**	-	-	-	-	**XEUN001**	-
Xenoxybelis argenteus	GQ457842	GQ457780	**CBGM0039**	-	-	**CBGM0039**	GQ457899	-

* sequences from Vidal et al. (2010); codes in bold represent the sequences generated in this study.

Appendix S2.


Boa constrictor
Acrochordus granulatus
Stoliczkia borneensis
Xenodermus javanicus
Achalinus meiguensis
Aplopeltura boa
Pareas carinatus
Bitis nasicornis
Causus resimus
Azemiops feae
Agkistrodon piscivorus
Bothriechis schlegelii
Enhydris enhydris
Homalopsis buccata
Homoroselaps lacteus
Aparallactus capensis
Atractaspis micropholis
Leioheterodon madagascariensis
Pseudoxyrhopus ambreensis
Lycophidion laterale
Bothrophthalmus lineatus
Lamprophis fuliginosus
Psammophis condanarus
Rhamphiophis oxyrhynchus
Oxyrhabdium leporinum
Naja naja
Bungarus fasciatus
Micrurus surinamensis
Laticauda colubrina
Notechis ater
Natriciteres olivacea
Rhabdophis subminiatus
Xenochrophis flavipunctatum
Sinonatrix annularis
Natrix natrix
Thamnophis sirtalis
Regina rigida
Storeria dekayi
Elaphe quatuorlineata
Oxybelis aeneus
Dinodon rufozonatum
Coluber constrictor
Hierophis spinalis
Pseudorabdion oxycephalum
Calamaria pavimentata
Calamaria yuannanensis
Plagiopholis styani
Pseudoxenodon bambusicola
Pseudoxenodon karlschmidti
Pseudoxenodon macrops
Carphophis amoenus
Contia tenuis
Diadophis punctatus
Thermophis zhaoermii
Farancia abacura
Heterodon platirhinos
Heterodon nasicus
Heterodon simus
Imantodes cenchoa
Imantodes lentiferus
Nothopsis rugosus *
Leptodeira annulata
Leptodeira septentrionalis *
Tretanorhinus variabilis
Hypsiglena torquata
Atractus badius
Geophis godmani
Atractus schach
Atractus zidocki
Atractus albuquerquei
Atractus reticulatus
Atractus flammigerus
Atractus trihedrurus
Atractus zebrinus
Sibon nebulatus
Sibynomorphus turgidus
Ninia atrata
Sibynomorphus mikanii
Dipsas indica
Dipsas articulata
Dipsas neivai
Dipsas variegata
Dipsas albifrons
Dipsas catesbyi
Sibynomorphus ventrimaculatus
Sibynomorphus garmani
Sibynomorphus neuwiedii

Appendix S2. *Continued*

Appendix S2. *Continued*

Conclusões

Com base nos resultados conjuntos das análises filogenéticas dos dois artigos apresentados, podemos concluir que:

1. Os Caenophidia são compostos por dois clados, sendo um composto pela família Acrochordidae e o outro por um clado que inclui a família Xenodermatidae e os demais Caenophidia. Estes dois clados são recuperados em todas as análises, com altos valores de suporte, sendo que para o último grupo foi designado o nome de Colubroides (Caenophidia não Acrochordidae). A diagnose para Colubroides é dada por pelo menos oito sinapomorfias morfológicas putativas.

2. Dentre os Colubroides, dois grupos são altamente suportados por todos os métodos, a família Xenodermatidae e os demais Colubroides. Este último grupo foi denominado de Colubriformes (Colubroides não Xenodermatidae) e sua diagnose é dada por três sinapomorfias morfológicas putativas.

3. Os Colubriformes são compostos por dois clados, sendo um composto exclusivamente pela família Pareatidae, enquanto que o outro é formado por todos os demais Colubriformes. Ambos os clados apresentam valores de suporte alto em todos os métodos utilizados. O clado formado pelos Colubroides, com exceção dos Pareatidae, foi nomeado de Endoglyptodonta (Colubriformes não Pareatidae) e sua diagnose morfológica se baseia em um única sinapomorfia putativa.

4. Quatro clados principais compõem os Endoglyptodonta. Estes clados representam as famílias Viperidae e Homalopsidae e as superfamílias Colubroidea (*sensu* Vidal et al., 2007) e Elapoidea (*sensu* Kelly et al., 2009). Os quatro clados apresentam alto suporte e são recuperados por todas as metodologias utilizadas.

5. Dentre os quatro clados de Endoglyptodonta, os Viperidae posicionam-se, com alto suporte, como o grupo irmão de todos os demais representantes do grupo.

6. A relação entre as superfamílias Colubroidea, Elapoidea e a família Homalopsidae não pôde ser definida, pois as hipóteses filogenéticas encontradas são conflitantes e com baixo suporte.

7. Elapoidea é composto pelas famílias Psammophiidae, Elapidae, Atractaspididae e Lamprophiidae. Todas as famílias de Elapoidea, com exceção dos Lamprophiidae, foram recuperadas com alto suporte em todos os métodos.

8. Lamprophiidae é grupo irmão de Atractaspididae para todos os métodos utilizados. Contudo, esta relação apresenta baixo suporte em todas as análises.

9. Todas as análises filogenéticas corroboram os resultados de Kelly et al., (2009) que indicam que *Oxyrhabdium leporinum* não pertence à família Xenodermatidae, sendo grupo irmão do clado composto por todos os Elapidae.

10. A posição de Psammophiidae não pode ser definida, uma vez que ora agrupa-se com o clado composto por *Oxyrhabdium* e Elapidae, ora agrupa-se como o grupo irmão de todos os demais Elapoidea. Ambas hipóteses apresentando baixo suporte.

11. Colubroidea é composto pelas famílias Colubridae, Natricidae, Calamariidae, Pseudoxenodontidae e Dipsadidae. Em todas as análises, as famílias de Colubroidea foram recuperadas com alto suporte. Contudo, a relação entre as famílias não pode ser estabelecida, uma vez que os resultados foram conflitantes entre os métodos utilizados e os valores de suporte foram baixos.

12. Os Dipsadidae formam um grupo monofilético bem suportado, composto pelas subfamílias Carphophinae, Dipsadinae e Xenodontinae.

13. As subfamílias Dipsadinae e Xenodontinae são recuperadas em todas as análise com suportes que variam de moderado a alto, contudo a subfamília Carphophinae é recuperada apenas em algumas análises.

14. Foram sequenciados e posicionados filogeneticamente pela primeira vez os seguintes gêneros de dipsadídeos: *Apostolepis*, *Boiruna*, *Conophis*, *Elapomorphus*, *Gomesophis*,

Lystrophis, *Ninia*, *Phalotris*, *Pseudablabes*, *Pseudotomodon*, *Psomophis*, *Rachidelus*, *Sibynomorphus*, *Sordellina*, *Tachymenis*, *Taeniophallus*, *Tomodon*, *Tropidrodryas*, e *Waglerophis*.

15. O gênero *Thermophis* passa a ser considerado um Dipsadidae de posição incerta, sendo alocado ora como o grupo irmão de todos os demais dipsadídeos ora como grupo irmão do gênero norte americano *Diadophis*.

16. As espécies relictuais de dipsadídeos (gêneros *Carphophis*, *Diadophis*, *Contia*, *Heterodon* e *Farancia*), junto com *Thermophis*, formam um clado nas análises de máxima parcimônia. Por outro lado, nas análises de máxima verossimilhança, os dipsadídeos relictuais formam um grupo parafilético.

17. Na análise de máxima verossimilhança a subfamília Carphophiinae (*Carphophis*, *Diadophis* e *Contia*) é recuperada, posicionando-se como grupo irmão do clado formado pelas subfamílias Xenodontinae e Dipsadinae. Nesta mesma análise os gêneros *Farancia* e *Heterodon* formam um clado que que se posiciona como grupo irmão do clado formado pelas subfamílias Carphophiinae, Xenodontinae e Dipsadinae, sugerindo, desta forma, que a subfamília Heterodontinae proposta por Vidal et al., (2007) é parafilética.

18. Dentro de Dipsadinae, poucos agrupamentos obtiveram alto suporte nas análises filogenéticas. Contudo três clados foram recorrentemente recuperados por todos os métodos: um clado que representa a tribo Dipsadini (*Dipsas*, *Sibynomorphus* e *Sibon*); um clado composto pelas espécies de *Atractus* e *Geophis*; e um clado composto pelos Imantodini (*Imantodes* e *Leptodeira*). Este último clado apareceu associado, em todas as análises, ao gênero Nothopsis, porém com baixo suporte.

19. O gênero *Ninia* aparece como intimamente associado aos Dipsadini, sendo seu grupo irmão nas análises de máxima verossimilhança e posicionando dentro da tribo nas análises de máxima parcimônia.

20. Dentre os Xenodontinae, a grande maioria das tribos definidas por sinapomorfias morfológicas é recuperada na filogenia molecular. Contudo, a relação filogenética entre as

tribos é instável, variando consideravelmente entre as análises realizadas, bem como, apresentando valores de suporte baixos.

21. As tribos Xenodontini, Philodryadini, Hydropsini e Pseudoboini, primeiramente suportadas pela análise molecular de Vidal et al., (2000), foram corroboradas por todas as análises com alto valor de suporte.

22. A tribo Elapomorphini é composta dos gêneros *Elapomorphus*, *Phalotris* e *Apostolepis*, sendo que o presente trabalho representa a primeira confirmação, com caracteres moleculares, de seu monofiletismo (sugerido por Savitzki, 1979; Ferrarezzi 1993; Zaher, 1994).

23. A tribo Tachymenini é composta pelos gêneros *Calamodontophis*, *Gomesophis*, *Pseudotomodon*, *Ptycophis*, *Tachymenis*, *Thamnodynastes* e *Tomodon*, sendo que o presente trabalho representa a primeira confirmação, com caracteres moleculares, de seu monofiletismo (sugerido por Bailey, 1967; Ferrarezi, 1994; Franco, 1999).

24. Novas tribos se fizeram necessárias para alocar gêneros considerados previamente como Dipsadidae *incertae sedis*, uma vez que representam possíveis linhagens independentes. Entre elas: Echinatherini (gêneros *Echinanthera*, *Taeniophallus* e *Sordellina*), Tropidodryadini (*Tropidodryas*), Conophiini (*Conophis*), Caaeteboiini (*Caaeteboia*), Saphenophiini (*Saphenophis* e *Pseudoalsophis*), Hydrodnastini (*Hydrodynastes*), Psomophiini (*Psomophis*).

25. Nos Xenodontini, os gêneros *Waglerophis* e *Lystrophis* encontram-se alocados, com alto suporte em todas as análises, dentro de *Xenodon*, tornando o gênero parafilético. Desta forma, *Waglerophis* e *Lystrophis* foram sinonimizados com *Xenodon*.

26. As espécies dos grupos *Liophis lineatus* e *L. anomalus*, como definidas por Michaud e Dixon (1987) e Dixon (1985), não agrupam-se em nenhuma análise com os outros representantes de *Liophis*, sendo revalidado o gênero *Lygophis* para designar as espécies destes dois grupos.

27. Os gêneros *Erythrolamprus* e *Uromacerina* foram alocados por todas as análises filogenéticas dentro do gênero *Liophis*, tornando-o parafilético. Desta forma, *Uromacerina* e *Liophis* são sinonimizados a *Erythrolamprus*, o qual possui prioridade sobre *Liophis* (Cursio et al., 2009).

28. *Liophis amarali* não é posicionado em nenhuma análise junto com as espécies do gênero *Liophis*. Para essa espécie foi criado o gênero monotípico, *Caaeteboia*.

29. Nos Philodryadini, os gêneros *Pseudablabes* e *Xenoxybelis* encontram-se posicionados filogeneticamente dentro de *Philodryas* (como sugerido por Zaher, 1999). Sendo assim, *Pseudablabes* e *Xenoxybelis* foram sinonimizados a *Philodryas*, evitando a condição parafilética do gênero.

30. Dentre os Pseudoboini, os gêneros *Clelia* e *Phimophis* são polifiléticos em todas as análises realizadas. Para manter uma taxonomia que represente grupos monofiléticos dentro da tribo, três gêneros são criados: *Mussurana*, para *C. bicolor*, *C. montana* e *C. quimi*; *Paraphimophis*, para *C. rustica* e *C. hussami*; e *Rodriguesophis*, para *Phimophis iglesiasi*, *P. chui*, e *P. scriptorcibatus*.

31. O gênero *Rhachidelus* foi alocado nos Pseudoboini, agrupando-se ora com *Pseudoboa*, ora com *Boiruna*.

32. Nos Echinantherini, a validade dos gêneros *Echinanthera* e *Taeniophallus*, como definidos por Schargel et al. (2005), é corroborada por todas as análises filogenéticas, com alto suporte. Contudo, a relação entre estes gêneros é incerta, uma vez que, *Sordellina* ora agrupa-se como grupo irmão de *Taeniophallus*, ora como grupo irmão do clado formado por *Taeniophallus* mais *Echinanthera* (ambas resoluções com baixo suporte).

33. As serpentes do Arquipélago das Galápagos não estão associadas ao gênero continental *Philodryas*, e nem tampouco aos gêneros insulares *Antillophis* e *Alsophis*, como proposto Thomas (1997). As análises filogenéticas demostram que as serpentes das Galápagos estão associadas a *Alsophis elegans* em um clado com alto valor de suporte, o qual representa uma linhagem distinta das *Alsophis* da Antilhas. Estes resultados corroboram a hipótese de Zaher (1999) com caracteres hemipenianos e um novo gênero, *Pseudalsophis*, foi criado para

essas espécies. Baseando-se nos resultados de Zaher (1999), foi criada a tribo Saphenophiini para incluir os gêneros *Pseudalsophis* e *Saphenophis*.

34. A monofilia da tribo Alsophiini não é sustentada na maioria das análises. Apesar do baixo suporte encontrado para essas topologias, o gênero *Uromacer* não agrupou com os demais Alsophiini. Desta forma, o gênero passou a ser considerado Xenodontinae *incertae sedis*.

35. Dentre os Alsophiini os gêneros *Alsophis*, *Antillophis* e *Arrython* são parafiléticos. Para manter uma sistemática baseada em grupos monofiléticos foram criados três gêneros: *Schwartzophis*, para as espécies do grupo *Arrhyton callilaemum* (*sensu* Zaher, 1999); *Magliophis*, para as espécies do grupo *Arrhyton exiguum* (*sensu* Zaher, 1999); e *Caraiba*, para *Antillophis andreae*.

36. Os gêneros *Schwartzophis*, *Ialtris*, *Antillophis* (*sensu* Zaher et al., 2009) e *Darlingtonia*, foram sinonimizados por Hedges et al., (2009). Contudo, são concordantes com todas as hipóteses filogenéticas apresentadas. Estes gêneros apresentam características únicas tanto de hemipênis como de folidose e dentição. Desta forma, sua sinonimização com outros gêneros de Alsophiini, não é corroborada pela evidência conhecida e por isso foram revalidados.

37. O gênero *Ocyophis* (*sensu* Zaher et al., 2009) é parafilético em relação aos outros gêneros de Alsophiini. As análise filogenéticas corroboram os gêneros *Borikenophis*, *Cubophis* e *Haitiophis* criados por Hedges et al., (2009) para a maioria das espécies que compunham *Ocyophis* (*sensu* Zaher et al., 2009). Contudo, não existe evidência para a alocação das espécies aparentemente extintas, *O. ater* e *O. melaneuchus*, em *Hypsirhyncus* (como proposto por Hedges et al., 2009). Sendo assim, o esquema taxonômico que melhor representa o conhecimento atual é a manutenção de ambas espécies em *Ocyophis*.

38. As características hemipenianas são altamente distinguíveis entre os gêneros de Alsophiini, e representam caracteres diagnósticos importantes para a sistemática do grupo.

39. As relações entre a maioria dos gêneros de Alsophiini é fracamente suportanda, sendo questionável qualquer afirmação biogeográfica, baseada nos dados atuais, sobre dispersão ou cladogenese entre as espécies das Antilhas.

40. Apesar da inclusão de diversos dipsadídeos *incertae sedis* na análise, alguns terminais variaram consideravelmente suas afinidades, e desta forma, são sua posição filogenética continua sendo considerada instável. Para os Xenodontinae os gêneros *incertae sedis* são: *Manolepis* e *Xenopholis*; já para os Dipsadidae os gêneros *incertae sedis* são: *Crysantophis*, *Trimetopon*, *Thermophis*, *Farancia* e *Heterodon*.

41. Outros gêneros de Dipsadidae, não foram incluídos nestas análises, e por atualmente não apresentarem evidências que os posicionem em algum grupo de dipsadídeos, continuaram classificados como *incertae sedis*, sendo eles: *Cercophis*, *Diaphorolepis*, *Emmochliophis*, *Euliophis*, *Enulius*, *Hydromorphus*, *Lioheterophis*, *Rhadinophanes*, *Synophis* e *Tantalophis*.

Perspectivas

Apesar dos diversos avanços obtidos, muitas perguntas acerca da sistemática dos Dipsadidae continuam sem respostas. Além disso, pouco se sabe sobre os processos que moldaram a evolução do grupo.

As principais questões que ainda carecem de respostas, são:

1) a definição do grupo irmão de Dipsadidae;
2) a posição filogenética dos dipsadídeos relictuais;
3) a posição filogenética dos dipsadídeos *incertae sedis*;
4) a filogenia dos elementos da subfamília Dipsadinae;
5) a relação entre as tribos de Xenodontinae;
6) a filogenia dentro das tribos de Xenodontinae;
7) o tempo de divergência entre os clados;

Os principais avanços para sistemática dos colubroidea Neotropicais provavelmente virão da resolução de tais questões.

No âmbito deste doutorado foram produzidos três conjuntos de dados adicionais, os quais ainda não foram analisados. Estes dados foram gerados procurando resolver alguns dos pontos comentados acima e serão alvo de futuras análises.

1) Visando definir o grupo irmão dos Dipsadidae, foram sequenciados 10 genes (12S, 16S, cytb, cox1, cmos, bdnf, rag1, jun, ame, nt3) para uma grande diversidade de Colubroides. Em conjunto com os genes sequenciados, foram incluídas sequencias depositadas no GenBank para mais 18 genes. Atualmente esta matriz molecular conta com 28 genes para 1027 terminais, onde são amostrados todos os principais grupos de Caenophidia. Esta análise possibilitará não apenas a definição da posição dos Dipsadidae dentro dos Colubroides, mas a provável revisão taxonômica de todo o grupo.

2) Foram produzidas sequencias para os mesmos 10 genes para outros 153 táxons, porém focando exclusivamente a família Dipsadidae. Estas sequencias permitirão explorar as relações filogenéticas dentro e entre as tribos de Xenodontinae utilizando um conjunto maior de evidências e terminais. Por outro lado, também servirão de base para a datação das divergências entre os principais clados dentro da família.

3) Visando inferir as relações filogenéticas e tempos de divergência entre as espécies de serpentes do Arquipélago das Galápagos, foram geradas também sequencias para três genes mitocondriais (12S, 16S e cytb) e três nucleares (cmos, bdnf e nt3). Paralelamente, foram produzidas sequencias para três genes mitocondriais (cytb, cox1 e nd4) para 142 indivíduos de *Pseudalsophis* das Galápagos. Estes dados possibilitarão compreender os processos filogeográficos destas espécies, bem como inferir os processos de especiação para serpentes nas Galápagos.

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