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Toward a Tree-of-Life for the boas and pythons: Multilocus species-level phylogeny with unprecedented taxon sampling

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ABSTRACT

Snakes in the families Boidae and Pythonidae constitute some of the most spectacular reptiles and comprise an enormous diversity of morphology, behavior, and ecology. While many species of boas and pythons are familiar, taxonomy and evolutionary relationships within these families remain contentious and fluid. A major effort in evolutionary and conservation biology is to assemble a comprehensive Tree-of-Life, or a macro-scale phylogenetic hypothesis, for all known life on Earth. No previously published study has produced a species-level molecular phylogeny for more than 61% of boa species or 65% of python species. Using both novel and previously published sequence data, we have produced a species-level phylogeny for 84.5% of boid species and 82.5% of pythonid species, contextualized within a larger phylogeny of henophidian snakes. We obtained new sequence data for three boid, one pythonid, and two tropidophiid taxa which have never previously been included in a molecular study, in addition to generating novel sequences for seven genes across an additional 12 taxa. We compiled an 11-gene dataset for 127 taxa, consisting of the mitochondrial genes *CYTB*, 12S, and 16S, and the nuclear genes *bdnf*, *bmp2*, *c-mos*, *gpr35*, *rag1*, *ntf3*, *odc*, and *slc30a1*, totaling up to 7561 base pairs per taxon. We analyzed this dataset using both maximum likelihood and Bayesian inference and recovered a well-supported phylogeny for these species. We found significant evidence of discordance between taxonomy and evolutionary relationships in the genera *Tropidophis*, *Morelia*, *Liasis*, and *Leiopython*, and we found support for elevating two previously suggested boid species. We suggest a revised taxonomy for the boas (13 genera, 58 species) and pythons (8 genera, 40 species), review relationships between our study and the many other molecular phylogenetic studies of henophidian snakes, and present a taxonomic database and alignment which may be easily used and built upon by other researchers.

1. Introduction

Alethinophidian squamates include most extant snakes (~3030 of 3432 total sp.), though the majority of species (~2838 sp.) are included within the derived Caenophidia clade (i.e., Uetz and Hošek, 2013). The earliest diverging lineages within the alethonophidians are more frequently referred to as Henophidia (i.e., the boas, pythons, and kin), or Alethinophidia *sine* Caenophidia (e.g., Pyron et al., 2013a; Vidal et al., 2007). Henophidian snakes (including the basal "Amerophidia;" Vidal et al., 2007) are one of the most spectacular groups of reptiles and constitute a vast diversity of morphologies, behaviors, body sizes and ecologies. This group include both the smallest (*Tropidophis nigriventris*, <250 mm total length [TL]) and longest (*Malayopython reticulatus*, max. 10 m TL) extant constricting snakes, as well as the largest snake to have ever existed (†*Titanoboa cerrejonensis*, ~13 m TL) [Head et al., 2009; Uetz and Hošek, 2013]. They are also represented by enigmatic and hyper-diverse families Tropidophiidae (the dwarf boas) and Uropeltidae (the shield-tailed snakes); as well as by the nearly-extinct insular Mascarene family Bolyeriidae. In particular, the boas (Boidae) and pythons (Pythonidae) represent highly diverse families with near-global tropical and subtropical distributions. Molecular phylogenetic and biogeographic studies of the boas and pythons have yielded important insights into evolutionary processes (e.g., Colston et al., 2013; Noonan and Chippindale, 2006a,b; Noonan and Sites, 2010; Rawlings et al., 2008; Reynolds et al., 2013a), and an understanding of taxonomy, divergence, and diversification is becoming especially relevant given that many boa and python species are of significant conservation concern (Bohm et al., 2013; IUCN, 2012).

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A number of studies have investigated higher-level relationships among the henophidian snakes, largely recovering concordant topologies among families and subfamilies (Gower et al., 2005; Heise et al., 1995; Lawson et al., 2004; Pyron and Burbrink, 2012; Pyron et al., 2013a,b; Slowinski and Lawson, 2002; Vidal and Hedges, 2002, 2004; Vidal et al., 2007, 2009; Wiens et al., 2008, 2012). However, the placement of some families, such as Bolyeriidae and Calabariidae, remains contentious (Greene, 1997; Lawson et al., 2004, 2005; Lynch and Wagner, 2009; Noonan and Chippindale, 2006b; Vidal and Hedges, 2002, 2004; Wiens et al., 2008; Zaher, 1994; but see Pyron and Burbrink, 2012; Pyron et al., 2013a). A recent study (Pyron et al., 2013b), produced the most comprehensive species-level phylogeny for the squamate reptiles heretofore published. This project included the henophidian snakes, though these authors only achieved 56% and 65% species sampling for the boas and pythons, respectively, with significant missing data (Pyron et al., 2013b).

Other studies have attempted to infer interspecific relationships specifically within the boas and the pythons. For the Boidae, initial molecular phylogenies used a single mitochondrial (mtDNA) marker (*CYTB*) and excellent taxon representation to infer relationships among extant boids (Burbrink, 2004; Campbell, 1997). For Pythonidae, mtDNA studies built upon the morphological phylogeny inferred by Kluge (1993) and assisted greatly in clarifying relationships and taxonomy among these species, though often with limited taxon sampling (e.g., Rawlings et al., 2008). Multilocus approaches to higher level relationships among boas and pythons have generally included limited taxon sampling (e.g., Lee, 2005; Noonan and Chippindale, 2006a; Noonan and Sites, 2010; Pyron and Burbrink, 2012; Pyron et al., 2013a; Vidal and Hedges, 2004; Vidal et al., 2007), though Lynch and Wagner (2009) provided a robust phylogenetic hypothesis for 39 boid taxa (33 species and 6 subspecies), representing ~61% of boid species. While most relationships have remained remarkably stable even with increased taxon and marker sampling, some relationships, such as the placement of the boid genus *Eryx*, continue to be problematic (Lawson et al., 2004, 2005; Lee, 2005; Lynch and Wagner, 2009; Noonan and Chippindale, 2006a; Noonan and Sites, 2010; Pyron and Burbrink, 2012; Pyron et al., 2013a,b; Vidal and Hedges, 2002, 2004; Wiens et al., 2008; Wilcox et al., 2002).

In addition to this work, a number of intrageneric phylogenetic studies have been conducted within the boas and pythons. West Indian and South American boids have been well characterized, with cryptic species or unique lineages having been found using molecular data among the *Boa*, *Corallus*, *Epicrates*, and *Chilabothrus* genera (Colston et al., 2013; Henderson and Hedges, 1995; Hynková et al., 2009; Reynolds et al., 2013a; Rivera et al., 2011). Sand boas (*Eryx*) have been phylogenetically characterized, though with only 66.7% taxon coverage (10 of 15 taxa; Lynch and Wagner, 2009), and the genus *Gongylophis* Boulenger (resurrected by Tokar (1995)) continues to be used by some authors (e.g., O'Shea, 2007; Segniagbeto et al., 2011) but not others (e.g., Lynch and Wagner, 2009). The oceanic boas of Madagascar (*Acrantophis* and *Sanzinia*) and the Melanesian and Micronesian (Palauan) archipelagos (*Candoia*) have proven useful for understanding the processes of island diversification in snakes. Austin (2000) resolved a species-level phylogeny for *Candoia* in the Pacific using mitochondrial *CYTB*, a radiation that was further contextualized among the larger boid phylogeny by Noonan and Sites (2010). In Madagascar, Vences et al. (2001) found support for the distinction of *Sanzinia* and *Acrantophis*, and additional studies resolved the relationships of the two endemic genera using mtDNA (Vences and Glaw, 2003) and a multilocus dataset (Orozco-Terwengel et al., 2008). Importantly, Orozco-Terwengel et al. (2008) found evidence for a cryptic species in *S. madagascariensis* (*S. m. volontany*) and *A. dumerili* (*A.* cf. *dumerili*), but they did not explicitly describe these species.

There have been fewer molecular phylogenetic studies among the pythons, though several genera are well-characterized. Keogh et al. (2008) examined relationships among the Southeast Asian blood pythons (*Python curtus*, *P. brongersmai*, *P. breitensteini*), finding support for the specific distinction of these lineages. Rawlings et al. (2004) examined molecular divergence in the mitochondrial control region among the *Liasis* pythons of the Lesser Sundan archipelago, Australia, and New Guinea, finding support for the elevation of three species (*L. fuscus*, *L. mackloti*, and *L. olivaceus*) and a sister relationship to *Apodora* (but see Rawlings et al., 2008; this study). Using partial coding sequence (cds) from the mitochondrial cytochrome B (*CYTB*) gene paired with morphological data, Harvey et al. (2000) resolved a phylogeny for the scrub pythons (*Morelia amethistina* complex) of eastern Indonesia, PNG, and Australia, recognizing five species (*M. amethistina*, *M. clastolepis*, *M. kinghorni*, *M. nauta*, and *M. tracyae*). Though only two species were included in the molecular dataset, Schleip (2008) identified at least six new species within the white-lipped python complex (*Leiopython albertisii*) using a combined molecular and morphometric approach.

Finally, a number of explicitly intraspecific molecular (single locus and multilocus) studies of the boas (Hynková et al., 2009; McCartney-Melstad et al., 2012; Puente-Rolón et al., 2013; Reynolds et al., 2011, 2013b; Rodríguez-Robles et al., 2001; Tzika et al., 2008; Wood et al., 2008) and pythons (Auliya et al., 2002; Austin et al., 2010; Carmichael, 2007; Rawlings and Donnellan, 2003) have been conducted, with some discovery of cryptic species. North American rubber boas (*Charina*) were found to comprise two species (Rodríguez-Robles et al., 2001). Hynková et al. (2009) suggested that Central American *Boa constrictor* might constitute a separate species (*B. imperator*), a finding that is supported (though not explicitly tested) by the *CYTB* gene tree in Reynolds et al. (2013a). This taxonomic arrangement has not been widely accepted due to the ambiguous origins of many *Boa constrictor* sequences on GenBank and limited marker sampling (*CYTB* only). Increased marker sampling and a thorough range-wide phylogeographic analysis would greatly improve our understanding of this widespread species. Rawlings and Donnellan (2003) discovered cryptic diversity across the Australo-Papuan green python (*M. viridis*), though they did not elevate the reciprocally monophyletic clades. These species have been subsequently recognized as *M. azurea* (synonym of *M. azureus* Meyer 1874) and *M. viridis* by Schleip and O'Shea (2010), although *M. azurea* is not specifically recognized by Rawlings et al. (2008) nor Reptile Database (Uetz and Hošek, 2013; v24 July 2013) pending further investigation.

The online repository GenBank represents an ever-increasing wealth of information that can be mined for large-scale phylogenetic studies. By combining datasets across higher-order taxonomic groups, the supermatrix approach (de Quieroz and Gatesy, 2007; Sanderson, 2007) can be a powerful method for phylogenetic inference (Driskell et al., 2004; McMahon and Sanderson, 2006; Pyron and Wiens, 2011; Thomson and Shaffer, 2010; Wiens et al., 2005) and has been widely used in systematic studies of snakes (e.g., Pyron et al., 2011, 2013a,b; Siler et al., 2013). Though some studies have suggested that missing sequence data might lead to biases in phylogenetic inference (Lemmon et al., 2009; Zhang et al., 2013), the supermatrix approach has been repeatedly shown to lead to well supported phylogenetic trees which are consistent with studies including complete sequence data for smaller clades (Pyron and Wiens, 2011; Pyron et al., 2013a,b; Wiens and Morrill, 2011).

Here we use novel sequence data combined with an 11-gene supermatrix approach to investigate phylogenetic relationships of the boas and pythons relative to the other henophidian snakes. Using both maximum likelihood (ML) and Bayesian inference, we resolve species-level evolutionary relationships across the boas

and pythons in the context of the henophidian snake phylogeny. We generated new sequence data for four boa and python taxa with no previously published sequences, yielding 84.5% species coverage for boas and 82.5% species coverage for pythons, as well as adding new sequence data for three taxa of henophidian relatives with no previously published sequences. Finally, we added sequence data from seven genes sequenced across a total of 12 additional taxa to supplement the data matrix. Importantly, we have generated a working taxonomic database and an associated alignment, which may be easily edited and used by other researchers in future studies as molecular data for additional taxa continue to become available.

2. Materials and methods

2.1. Taxa and molecular data

Though many species of boas and pythons are familiar, taxonomy in these groups remains contentious and fluid; and hence no complete consensus exists regarding taxonomic bi- and trinomials. In order to begin with the greatest consistency, we assembled a taxonomic list from the latest version (28 July 2013) of the online Reptile Database (Uetz and Hošek, 2013; http://www.reptile-database.org/) and from the working list used by the IUCN/SSC Boa and Python Specialist Group (www.iucn.org), which are highly similar and are frequently used by herpetologists for taxonomic reference (e.g., Pyron et al., 2013a,b). We constrained our list to include the following recognized alethinophidean families basal to Caenophidia: Aniliidae, Anomochilidae, Boidae, Bolyeriidae, Calabariidae, Cylindrophiidae, Loxocemidae, Pythonidae, Tropidophiidae, Uropeltidae, Xenopeltidae, and Xenophidiidae (Curcio et al., 2012; Noonan and Chippindale, 2006a; Pyron and Burbrink, 2012; Pyron et al., 2013a,b; Wiens et al., 2008, 2012). We included all recognized species and subspecies (including those from this study) for each family in our database (and hence search criteria). One recently extinct taxon was included (†*Bolyeria multocarinata*) though no sequence data exist for this species. Our final database consisted of 257 recognized taxa, including 205 species and an additional 52 subspecies. This complete list is also available as a Supplemental appendix (Appendix B1).

We collected accession numbers for all available genes (>55 loci) across all taxa in our database by searching the online repository GenBank for each currently recognized family and genus as well as recently recognized genera. From this database, we identified the 11 loci that were the most broadly sampled (20.5–85% of boa and python species represented at any locus) and which have been used previously in studies of both higher and lower-level taxonomy. These included three mitochondrial genes: cytochrome b (*CYTB*) and the large and small subunits of the mitochondrial ribosome genes (*12S* and *16S*; omitting adjacent tRNAs), as well as eight nuclear genes: recombination-activating protein 1 (*rag1*), oocyte maturation factor (*c-mos*), neutrophin-3 (*ntf3*), brain-derived neutrophic factor (*bdnf*), bone morphogenetic protein 2 (*bmp2*), ornithine decarboxylase intron (*odc*), solute-carrier family 30 member 1 (*slc30a1*), and 35 G protein-coupled receptor R35 (*gpr35*). We used a minimum threshold of 200 bp for inclusion of a sequence and excluded ambiguously named sequences (i.e., those labeled as isolates or as "sp"). In addition, mining a database like GenBank requires caution, as many taxa are mislabeled. For instance, a *CYTB* sequence for *Tropidophis haetianus* is accessioned as *T. haitianus* (*sic*; see: Henderson and Powell, 2009), and sequences for *Chilabothrus subflavus* are accessioned as *Epicrates* (*Chilabothrus*) *subflavens* (*sic*). Additionally, in some cases we included sequences from multiple individuals of the same species, which could mislead inference due to the inclusion of sequences from species for which the taxonomy is incongruent with present revisions. However, these issues are not expected to lead to incorrect inference among higher-level groups. All GenBank searches were concluded by 10 January, 2013 and accession numbers for each sequence used in this study are available as Supplemental material (Appendix B1).

Of the 257 taxa included in our initial database, 127 had one or more sequences of the 11 loci available on GenBank or among our newly generated sequence data and were included in the subsequent analyses. Most families are well-represented on GenBank or among our novel sequences except for the diverse and understudied Uropeltidae (74.5% of taxa with no sequence data; but see Pyron et al., 2013a,b) and Tropidophiidae (~81% of taxa with no sequence data) (Appendix B1). Of the 90 recognized boa taxa (Boidae; 58 species and 32 subspecies), we have at least one locus for 58 taxa (49 species, 9 subspecies). Of the 52 recognized python taxa (Pythonidae; 40 species and 12 subspecies), we have at least one locus for 37 taxa (33 species, 4 subspecies). This represents 84.5% species coverage for the boas (64.4% taxon coverage, including subspecies) and 82.5% species coverage for the pythons (71.1% taxon coverage).

In addition, we selected nine outgroup taxa based on the availability of sequence data and their relationships to the henophidian snakes: the basal *Typhlops jamaicensis*, *Leptotyphlops humilis*, and *Liotyphlops albirostris* (Scolecophidea) as well as *Achrochordus granulatus* (Acrochordidae), a caenophidian family sister to the superfamily Colubroidae (Pyron et al., 2013a; Wiens et al., 2008), and four colubroid snakes: *Bothrops asper* (Viperidae), *Micrurus fulvius* (Elapidae), *Lampropeltis getula* (Colubrinae), and *Thamnophis marcianus* (Natricinae). Two lizard species, *Iguana iguana* (Iguanidae) and *Anolis carolinensis* (Dactyloidae), were included as the most divergent outgroups to root the trees. We downloaded sequence data for each accession using the R package ape (Paradis et al., 2004) as Fasta files.

2.2. Sample collection and DNA sequencing

In a related study (Reynolds et al., 2013a) we generated 367 novel sequences from 18 boid taxa, and 119 of these sequences were included in this analysis. In addition, we obtained samples of 18 additional taxa from field collection, museum tissue collections, public reptile collections (zoos), and U.S. private reptile breeders (Table 1). Of these, six taxa have no previously published sequence data. Samples consisted of tissue biopsies preserved in 95% ethanol or frozen freshly-shed skins.

We initially assayed eight taxa for primer amplification using the polymerase chain reaction (PCR) across nine of the 11 loci (not the ribosomal subunit loci) included in this study. Of these nine, we obtained consistent amplification and sequence products from seven loci, including *CYTB*, *ntf3*, *bdnf*, *c-mos*, *bmp2*, *rag1*, and *odc* (Table 1). We sequenced taxa in Table 1 at each of the seven loci, generating 120 novel sequences (six sequences failed to amplify). We visualized PCR products by gel electrophoresis and purified and sequenced products (both strands) on an automated sequencer (ABI 3730XL) at Massachusetts General Hospital DNA Core Facility, Cambridge, MA. We assembled each gene region and manually verified ambiguous base calls using Sequencher 5.1 (Gene Codes) and we reconstructed haplotypes for polymorphic nuclear sequences using Phase v2.1 (Stephens et al., 2001; Stephens and Donnelly, 2003) We deposited all newly generated sequences in GenBank (accessions in Appendix B1).

2.3. Alignments

We aligned sequences for each gene independently using the ClustalW 2.1 algorithm (Larkin et al., 2007) implemented in

Table 1
Specimens, known origins, and museum numbers used to generate novel sequences in this study. See Appendix B1 for Genbank accession numbers. Taxa with an asterisk represent the first published sequence data generated for these species.

Taxa	Origin	Specimen ID
Aspidites ramsayi	–	**UMFS** 11343
Boa imperator	Reynolds et al. (2013b)	**RGR** BOIM1
*Candoia superciliosa**	Ngeruktabel I., Palau	**CAS** 236351
*Candoia superciliosa crombiei**	Ngeaur I., Palau	**CAS** 236457
Charina umbratica	San Bernardino Co., CA, U.S.A.	**MVZ** 230469
Eryx tataricus	–	**UMFS** 11688
*Eryx muelleri**	–	**UMFS** 11723
Bothrochilus albertsii	–	**UMFS** 11340
Simalia boeleni	–	**UMFS** 11003
Simalia nauta	Tanimbar I., Indonesia	**UMFS** 11352
Simalia tracyae	Halmahera I., Indonesia	**UMFS** 11014
*Python anchietae**	Pet Trade	**MVZ** 232856
Python curtus	Sumatra, Indonesia	**UMFS** 11257
Python sebae	–	**UMFS** 11459
*Tropidophis curtus**	Long I., Bahamas	**RGR** Tcurt1
Tropidophis greenwayi lanthanus	North Caicos, Turks and Caicos I.	**RGR** TropeN2
Tropidophis feicki	Prov. Pinar del Río, Cuba	**MVZ** 241301
*Tropidophis taczanowskyi**	Zamora Chinchipe, Ecuador	**UMMZ** 229269

CAS: California Academy of Science; **MVZ**: Museum of Vertebrate Zoology, UC Berkeley; **RGR**: author personal collection; **UMMZ** and **UMFS**: University of Michigan Museum of Zoology.

Mesquite 2.75 (Maddison and Maddison, 2011) using reference sequences and fine-tuning by eye. Because all loci except *12S*, *16S*, and *odc* are exons from protein-coding genes, alignment was straightforward except for the recombination activating gene (*rag1*). Sequence lengths for this locus varied widely, likely due to the use of differing internal sequencing primers, and included some regions with little overlap. Sequences with no overlap with the rest of the dataset were excluded. One *rag1* sequence (*Morelia viridis*, Genbank #EU366442) could not be aligned and was also excluded. We translated the protein-coding sequences to ensure that an open reading frame was included. We aligned *12S*, *16S*, and *odc* step-wise in batches of similar sequences (i.e., generated from the same study) to achieve consistent alignments and checked each alignment by eye. Some sequences included the complete *12S*/*16S* and adjacent tRNA regions. In order to incorporate these, we trimmed each subunit from the other and the adjacent tRNAs by aligning the sequence with known sequences and subsequently fine-trimming the initial sequence.

Our final concatenated alignment consisted of 7561 bp of sequence data from 127 in-group henophidian taxa, including 114 species and 13 additional subspecies, 55.6% and 25.0% of the species and subspecies included in our original database of the henophidian snakes, respectively. Missing data for individual genes varied widely, with 108 in-group taxa for *CYTB* (85.0%, 1110 bp), 81 taxa for *12S* (63.8%, 358 bp), 79 taxa for *c-mos* (62.2%, 714 bp), 74 taxa for *bdnf* (58.3%, 711 bp), 71 taxa for *16S* (55.9%, 541 bp), 71 taxa for *ntf3* (55.9%, 543 bp), 63 taxa for *rag1* (49.6%, 1023 bp), 52 taxa for *odc* (40.9.8%, 644 bp), 48 taxa for *bmp2* (37.8%, 648 bp), 28 taxa for *slc30a1* (22.0%, 576 bp), and 26 taxa for *gpr35* (20.5%, 693 bp). However, all taxa had at least one mtDNA gene sequence, and the average number of missing cells per taxon was 50.4% (range 0–90.9%). We have submitted our final alignment to the repository TreeBase (Study ID 14919).

2.4. Phylogenetic analyses

We conducted phylogenetic analyses using ML (Felsenstein, 1981) in the program RAxML v7.4.2 (Stamatakis, 2006) implemented in the graphical front-end raxmlGUI v1.3 (Silvestro and Michalak, 2012). We partitioned the concatenated 11-gene matrix by gene and used the GTRGAMMA model for all genes and partitions. Previous studies using these genes in snakes have identified the GTR + Γ or the GTR + Γ + I as the best-fitting substitution models (Pyron et al., 2011; Reynolds et al., 2013a); however, the use of the invariant sites parameter (I) has been recommended against in RAxML as invariant sites are accounted for in the GTRGAMMA rate categories (Stamatakis, 2006). We used the rapid bootstrapping algorithm with 1000 bootstrap (BS) replicates followed by the thorough ML search option with 100 independent searches. Similar to, though more conservative than, previous studies (e.g., Pyron et al., 2011, 2013a) we consider BS values above 70% to indicate well-supported clades (Felsenstein, 2004; Taylor and Piel, 2004).

We also conducted phylogenetic inference using the Metropolis-coupled Markov chain Monte Carlo (MCMC) algorithm implemented in MrBayes 3.2 (Ronquist et al., 2012). We partitioned the concatenated 11-gene matrix by locus and selected the best-fit model of molecular evolution for each locus using Akaike's Information Criterion implemented in ModelTest Server (Posada, 2006) or Bayesian information criterion in jModelTest2 (Darriba et al., 2012; Guindon and Gascuel, 2003) [Table 2]. Each locus was unlinked to allow values for transition/transversion ratio, proportion of invariant sites, and among-site rate heterogeneity to vary across partitions. The six-chain MCMC was run for 10 million generations with 25% burn-in and the trace files were examined to confirm convergence of the chains. We consider posterior probability (PP) values $\geqslant$ 0.95 to indicate significant support at a given node. Bayesian inference ran for 160 h on an Intel® 3.4 GHz quad-core i7 processor on a Macintosh® Imac.

To investigate whether missing data led to changes in topology or nodal support, we tested the effect of removing loci with limited coverage by selecting from the full matrix only those genes with approximately 50% or more of the taxa represented as sequence data (49.6–85.0% coverage). This dataset consisted of 5000 bp from seven genes – the mitochondrial *CYTB*, *12S* and *16S*; as well as the nuclear *bdnf*, *ntf3*, *c-mos*, and *rag1* genes. We then ran the ML and MCMC analyses on the reduced dataset as above.

3. Results and discussion

Overall we recovered a well-resolved tree of henophidian snakes, with greater than 78% of nodes with strong (BS > 70%) support, and average nodal support of 84% (Fig. 1). Similarly, the Bayesian tree was well resolved, with 78.4% of nodes strongly (PP $\geqslant$ 0.95) supported, and average nodal support of PP = 0.954 (Appendix B2). Missing data in supermatrices have been generally shown to have little effect on topology and support in resulting phylogenetic trees (Driskell et al., 2004; Philippe et al., 2004; Pyron et al., 2011; Pyron et al., 2013a,b; Thomson and Shaffer, 2010; Wiens et al., 2005; but see Lemmon et al., 2009; Zhang et al., 2013). Our matrix contained only 50.4% missing cells, while similar studies have included matrices with >80% average missing cells and yet have still achieved consistent topologies and strong support values (e.g., Pyron et al., 2013b; but see Zhang et al., 2013). However, it remains important to demonstrate that these parameters are not heavily influenced by loci with a large number of missing cells, as some simulation studies (e.g., Lemmon et al., 2009) have suggested can be possible. Recently, Zhang et al. (2013) found that missing data contributed to ambiguous placement of entire clades, which would represent a serious problem for some phylogenetic studies. In the present study, we suspect that missing data has not caused major errors in the topology of our tree (such as the misplacement of entire clades) as our trees are topologically consistent with other smaller studies based on complete matrices of one or a small number of genes. Furthermore, our reduced loci

Table 2
Genes and primers used to generate novel sequence data in this study, as well as selected best-fit models of evolution and percentage of coverage in the matrix for all 11 genes. Primers are not listed (NA) for genes for which no new sequences were generated. See Appendix B1 for GenBank accession numbers associated with novel and mined sequences.

Gene	Abbreviation	Length (bp)	Ploidy	Primers	Selected model
12S ribosomal RNA	*12s*	358	N	NA	GTR + I + G
16S ribosomal RNA	*16s*	541	N	NA	TIM2 + I + G
Cytochrome b	*CYTB*	1120	N	Burbrink et al. (2000)	HKY + I + G
Oocyte maturation factor	*c-mos*	718	2n	Noonan and Chippendale (2006a)	K81uf
Brain-derived neurotrophic factor	*bdnf*	711	2n	Wiens et al. (2008)	TrN
Neurotrophin-3	*ntf3*	545	2n	Wiens et al. (2008)	TrN + I
Bone morphogenetic protein 2	*bmp2*	648	2n	Wiens et al. (2008)	TrNef + G
Recombination activating protein-1	*rag1-in*	1023	2n	F-5′-GCAGCTTTGGTGGCTGCCCT R-5′-ACAGTGCAGTGCATCTATTGAAGGC	HKY + I
Ornithine decarboxylase	*odc*	628	2n	Friesen et al. (1999)	HKY + G
Solute carrier family 30 member 1	*slc30a1*	576	2n	NA	HKY + I + G
G protein-coupled receptor 35	*gpr35*	693	2n	NA	TIM3 + G

datasets resulted in nearly identical topologies to the full datasets (Appendices B3 and B4), though with slightly lower average nodal support. For the ML analysis, 73.8% of nodes had strong support, with an average nodal support of 82.7%. For the Bayesian analysis, 79.2% of nodes had strong (PP > 0.95) support, with an average nodal support of PP = 0.951.

3.1. Henophidian families

The majority of the higher-level relationships among families in our analyses are similar to those found in many other recent studies (e.g., Pyron and Burbrink, 2012; Pyron et al., 2013b; Vidal et al., 2007, 2009; Wiens et al., 2008, 2012). We found strong support for a basal relationship of the South American/Greater Antillean clade containing the Aniliidae and Tropidophiidae to the rest of the alethinophidian snakes. The monotypic Amazonian Aniliidae (*Anilius scytale*) remains a highly divergent sister taxon (~90 Mya; Vidal et al., 2009) to the Tropidophiidae, a monophyletic family composed of the mainland genus *Trachyboa* (two species) and the diverse *Tropidophis* (Curcio et al., 2012; Hedges, 2002; Wilcox et al., 2002). Although we do not have sequence data for four of the five mainland species of *Tropidophis* (*T. battersbyi* [a likely synonym for *T. wrighti*, Hedges, *in litt.*], *T. grapiuna*, *T. preciosus* and *T. paucisquamis*), we found a basal relationship for the mainland species *T. taczanowskyi* relative to the West Indian radiation in the Bayesian (but not the ML) analyses, which suggests that the genus *Tropidophis* might be paraphyletic. We also found support (BS = 75, PP = 1.0) for monophyly of the Cuban species (*T. feicki*, *T. melanurus*, *T. pardalis*, and *T. wrighti*; four of the 16 species sampled), which corroborates the proposed impressive radiation of this genus within the island of Cuba (Hedges, 2002; Hedges and Garrido, 2002), rather than multiple colonizations of the island by different members of the genus. In the ML analysis, we found a close relationship between the Hispaniolan *T. haetianus* and Bahamian *T. curtus* species (BS = 87). Interestingly, *T. greenwayi* (Turks and Caicos I.) appears to be basal to the rest of the Greater Antillean radiation represented here (see also Wilcox et al., 2002), though in the MCMC analysis this species is found to be sister to *T. haetianus* (PP = 1.0). This situation is similar to that of the West Indian boas (*Chilabothrus*), whereby the Great Bahamas Bank boas are derived more recently from a Hispaniolan ancestor and not from the southern Bahamas boa (Reynolds et al., 2013a). The relationships of the Cayman Island and Jamaican *Tropidophis* remain unclear, as no sequences are available for these species, although unpublished evidence suggests phylogeographic concordance among these taxa (Hedges, *in litt*; Hedges and Garrido, 2002). As ~81% of the taxa in this genus have no published sequence data, this group represents an excellent target for further study, and inferred relationships would likely change with the inclusion of additional taxa. Given the possible paraphyly in *Tropidophis*, we suggest that the available name *Ungalia* Gray 1842 might be used for the South American species should future analyses support a paraphyletic relationship among tropidophids. However, owing to the discordant topology in our trees and the substantial number of missing taxa we refrain from specifically renaming this group pending further investigation.

Our analyses suggest weak support for a sister relationship between the Mauritian Bolyeriidae (†*Bolyeria multocarinata* and *Casarea dussumieri*) and the Malaysian family Xenophidiidae (*X. acanthognathus* and *X. schaeferi*; Wallach and Gunther, 1998), which is consistent with analyses of the mtDNA *CYTB* gene (Lawson et al., 2004) and multilocus studies (e.g., Pyron and Burbrink, 2012; Pyron et al., 2013b). We found support for a sister relationship between the Anomochilidae and the Cylindrophiidae (BS = 91); however, support (controlling for the difference between bootstrap and Bayesian posterior probability support values) was not as high in the MCMC analysis (PP = 0.92). Similar studies have found Anomochilidae to be basal to the radiation of Cylindrophiidae and Uropeltidae (Pyron et al., 2013a), while others have found Uropeltidae to be the basal family (Pyron and Burbrink, 2012) and a sister relationship between Anomochilidae and Cylindrophiidae (Gower et al., 2005; Pyron et al., 2013b). Similar to numerous other studies over the last few decades (Bossuyt et al., 2004; Cadle et al., 1990; Gower et al., 2005; Pyron et al., 2013a,b), we found support for paraphyly of *Rhinophis* and *Uropeltis*, though no authors have revised the taxonomy given the still-limited taxon sampling in these diverse and enigmatic species (Pyron et al., 2013a,b).

3.2. Pythonidae

The monogeneric families Xenopeltidae and Loxocemidae have been shown previously (Pyron et al., 2013a,b; Vidal et al., 2007; Wiens et al., 2008) to be basal to the radiation of the pythons, having diverged 70 Mya and 43 Mya, respectively (Vidal et al., 2009). We recovered the monotypic Central American Loxocemidae (*Loxocemus bicolor*) as sister to the in-group pythons, while we recovered the East Asian Xenopeltidae (*X. hainanensis* and *X. unicolor*) as sister to the clade (Pythonidae, Loxocemidae) in both our ML and MCMC analyses. Among the pythons, we found the African and southern Asian genus *Python* to be a monophyletic clade basal to the rest of the pythons (Lawson et al., 2004; Rawlings et al., 2008; Pyron et al., 2013b). Within this genus, we found support for a basal placement of the small-bodied West African *P. regius* (contrary to Pyron et al., 2013b), a derived clade of large-bodied species (*P. bivittatus* and *P. molurus*) from southern Asia, and a derived clade of the small-bodied Southeast Asian blood pythons (*P. brongersmai* and *P. curtus*). This relationship suggests an evolution of gigantism separate from other giant members of the

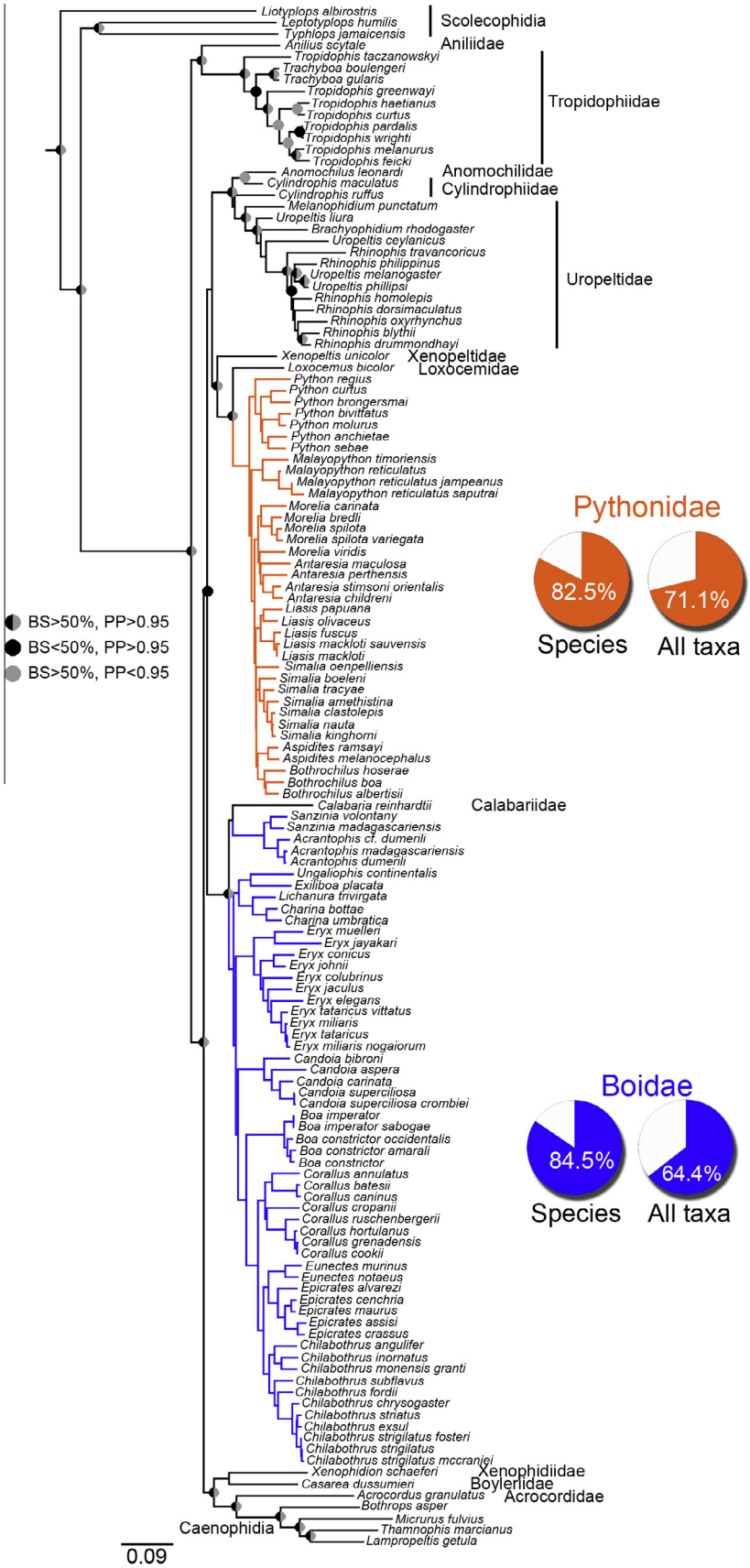

Fig. 1. Maximum likelihood tree for the henophidian snakes with revised taxonomy. Support values at each node are bootstrap proportions from maximum likelihood (BS > 50%, above; gray) and posterior probabilities from Bayesian analyses (PP > 0.95, below; black). Nodes with black and gray are supported in both ML and Bayesian analyses. See Fig. 2 for expanded trees for Pythonidae and Boidae with support values. Pie charts show the percentage of species and of all taxa (species + subspecies) included in the tree.

Australasian Pythonidae (*Malayopython* and *Morelia*). However, *Python regius* is represented only by mtDNA in our dataset, hence it remains to be seen whether this relationship is also supported by nuclear data. Interestingly, we generated novel sequence data for the small-bodied Kalaharian *P. anchietae*, recovering a relationship with the giant African rock python *P. sebae*. This suggests either independent evolution of large body size in *Python* or the reversal from a large ancestor of the giant snakes *P. molurus*, *P. bivittatus*, and *P. sebae* (all 3–7.5 m TL) to the relatively small *P. anchietae* (<2 m TL).

Recently, Rawlings et al. (2008) used the genus *Broghammerus* for the monophyletic clade containing the Southeast Asian *B. reticulatus* and the Lesser Sundan endemic *B. timoriensis* to resolve the apparent paraphyly of the genus *Python*. Like Rawlings et al. (2008) and Pyron et al. (2013b), we found support for the distinction of this clade (BS = 96, PP = 1.0). However, though used by Rawlings et al. (2008) in a peer-reviewed publication, the genus name *Broghammerus* Hoser 2004 is technically invalid, as it resulted initially from a non-peer reviewed writing that included no formal data or analyses (Kaiser et al., 2013). Though Rawlings et al. (2008) redescribed the genus in a peer-reviewed publication based on apparently sound molecular and morphological data, these authors did not formalize their description as required by Article 16.1 of the ICZN. Furthermore, consensus from the herpetological community suggests that invalid names should be abandoned (Kaiser et al., 2013). Hence, a new name is needed for this clade (Pyron et al., 2013b), and no suitable synonym is available. Following articles 10.3, 10.4, 11.8, and 42 of the ICZN, we ascribe the genus name *Malayopython* (Appendix A) to the clade containing the species *M. reticulatus* and *M. timoriensis*, after the location of the neotype of *M. reticulatus reticulatus* in Rengit, West Malaysia (Auliya et al., 2002) [holotype is lost, Kluge, 1993]. Within this genus, we found support for distinction between two species *M. reticulatus* and *M. timoriensis* (BS = 99, PP = 1.0). Our inclusion of three subspecies of *M. reticulatus* suggests that phylogeographic structure might exist between the nominate and widespread subspecies (*M. r. reticulatus*; Southeast Asia and Indonesia), and the island endemic subspecies *M. r. jampeanus* (Tanahjampea Island, Indonesia) and *M. r. saputrai* (Salajar Island, Indonesia), though the latter are minimally divergent (though strongly supported-BS = 100, PP = 1.0). Further investigation of this group, including more extensive sampling, is warranted.

Similar to other studies (Pyron et al., 2013b; Rawlings et al., 2008; but see Carmichael, 2007 and Rawlings et al., 2004), we found paraphyly of the genera *Apodora* and *Liasis*, with strong support (BS = 98, PP = 1.0) for two clades: the widespread Australian endemic *L. olivaceaus* and the Papuan endemic *A. papuana* (olive pythons); and the widespread Australian *L. fuscus* and the Indonesian/Papuan *L. mackloti* (water pythons). Hence, based on our study, as well as other work suggesting this paraphyly (e.g., Rawlings et al., 2008), we recommend subsuming the genus *Apodora* Kluge, 1993 into *Liasis* Gray 1842. The olive pythons (*L. olivaceaus*) might further be split into an eastern Australian species and a western Australian species (Rawlings et al., 2004); however, additional work, including more extensive sampling and an explicit test of this hypothesis, is needed. Similar to Rawlings et al. (2004), we found support in the ML tree (BS = 94) for the subspecific distinction of the Sawu Island water pythons (*L. mackloti sauvensis*) and the Timor water pythons (*L. m. mackloti*).

We did not find support for the distinction of the *Aspidites* and *Leiopython*/*Bothrochilus* clades. To the contrary, our results suggest a close relationship among these taxa, a finding similar to other studies (McDowell, 1975; Rawlings et al., 2008). However, this result stands in contrast to previous suggestions (e.g., Kluge, 1993) that *Aspidites* is sister to all other pythons. Based on a multilocus mtDNA and morphological combined analysis, Rawlings et al. (2008) recommended subsuming the genus *Leiopython* Hubrecht 1879 into *Bothrochilus* Fitzinger 1843 (resurrected by Kluge, 1993) [see also: McDowell, 1975]. Our analyses support the arrangement of Rawlings et al. (2008), as we found support for the distinction of *L. hoserae nomen dubium* (similar to Schleip (2008)) from *B. boa*/*L. albertisii* based on mtDNA in our ML analysis (BS = 95), but not in our Bayesian analysis (PP = 0.59). However, given the limited divergence of these taxa and the findings of similar studies (e.g., Rawlings et al., 2008; Schleip, 2008), we suggest the genus *Bothrochilus* include the species *B. boa*, *B. albertisii*, and *B. hoserae*. The specific epithet *hoserae* was considered *nomen nudum* given its original appearance in non-peer reviewed work with no data or analyses to support the name. However, Schleip (2008) provided an extensive formal description of *Leiopython* (=*Bothrochilus*) *hoserae*, and this epithet has been accepted by Schleip and O'Shea (2010) as well as Kaiser et al. (2013). Hence, we retain the epithet *hoserae* in the interest of stability. It should be noted that other species in this genus are currently recognized based on morphological and geographic distinction (*B. bennettorum*, *B. fredparkeri*, *B. huonensis*, and *B. biakensis*; Schleip, 2008), but no published molecular phylogeny exists. Hence, a larger-scale molecular phylogenetic analysis, including additional markers, would be of great utility in further characterizing this group.

A number of studies have suggested that taxonomy in the genus *Morelia* does not reflect actual evolutionary relationships (e.g., Pyron et al., 2013b; Rawlings et al., 2008). For instance, Rawlings et al. (2008) suggested that *Morelia* might be paraphyletic, and identified three lineages: (1) *M. boeleni*, (2) *M. carinata* + *M. viridis*, and (3) *M. amethistina* + *M. bredli* + *M. oenpelliensis* + *M. spilota*. We added the species *M. tracyae*, *M. clastolepis*, *M. nauta*, and *M. kinghorni* to our analysis and recovered a slightly different arrangement. We found support (BS = 92, PP = 0.99) for the Australasian/Indonesian clade of scrub (amethystine) pythons (*M. oenpelliensis*, *M. boeleni*, *M. tracyae*, *M. amethistina*, *M. clastolepis*, *M. kinghorni*, *and M. nauta*) and a clade of the carpet and tree pythons (*M. bredli*, *M. carinata*, *M. spilota*, *and M. viridis*), which is sister to the children's (dwarf) pythons (*Antaresia*). Within the scrub pythons, we found a basal placement of the enigmatic *M. oenpelliensis* and *M. boeleni*, and we found strong support for the distinction of the species *M. tracyae*, *M. amethistina*, and *M. clastolepis*, though not the closely-related derived species *M. kinghorni*, *and M. nauta* (BS = 57, PP = 0.93) described in Harvey et al. (2000). It should be noted that Harvey et al. (2000) suggest that *M. amethistina* likely comprises a cryptic species complex, a sentiment which is echoed by O'Shea (2007). Among the tree pythons, we did not find strong support for the placement of *M. carinata* or *M. viridis* (other research suggests that the latter is likely two species: *M. viridis* and *M. azurea*; Rawlings and Donnellan, 2003) relative to the rest of the clade; however, we did find support for the distinction of the carpet pythons *M. bredli* and *M. spilota* (BS = 100, PP = 1.0), as well as the distinction of the subspecies *M. s. spilota* and *M. s. variegata* (BS = 100, PP = 0.88). Additional subspecies are described in *M. spilota*, and a more extensive analysis would determine whether this widespread species is in fact a species complex. Our analysis supports a close relationship between the tree, carpet, and children's pythons, but we are unable to recover strong support among these species, likely due to the availability of only mtDNA sequences for *M. carinata* and most species of *Antaresia*. Additional sampling of markers should help to resolve the species' relationships in this clade. However, it is clear that *Morelia* is likely paraphyletic with respect to the other Australasian/Indonesian pythons, and we recommend resolving this paraphyly with a new generic name for the scrub python clade (*M. oenpelliensis*, *M. boeleni*, *M. tracyae*, *M. amethistina*, *M. clastolepis*, *M. kinghorni*, *and M. nauta*). Wells and Wellington (1984) proposed the name *Australiasis nomen nudum* to describe the scrub pythons, though this name is technically invalid in their publication as the description did not conform to

ICZN convention, including sufficient data and analysis (i.e., Kaiser et al., 2013). The available subgeneric name *Simalia* Gray 1849 exists, which was originally used to describe both *Liasis mackloti* and *Simalia* (=*Morelia*) *amethistina*, but was then synonymized with *Liasis* Gray (Schleip and O'Shea, 2010). According to the suggestions proposed by Kaiser et al. (2013) we use the available name *Simalia* to describe the scrub python clade and include a formal description in Appendix A.

3.3. Boidae

Among the boas, we found well-supported relationships largely consistent with previous studies. In our full 11-gene analysis (though not in the reduced dataset) we found weak support for a sister relationship of the non-boid *Calabaria* to the Madagascan boids. As this is not well supported (BS = 46, PP = 0.59) and inconsistent with previous studies, which have all found *Calabaria* to be basal to the rest of the boid radiation (but see Pyron et al., 2013b), we consider *Calabaria* as the closest extant relative to the Boidae. Among Malagasy species we found strong support for the distinction of *Sanzinia* and *Acrantophis*, although *S. madagascariensis* is quite divergent from the subspecies *S. m. volontany*. This is consistent with the previous suggestion that *S. m. volontany* should be elevated to specific status despite an apparent lack of diagnostic morphological differences (Orozco-Terwengel et al., 2008). We advocate elevation of this taxon to full species (*S. volontany*), and recommend a more thorough species-tree analysis among these taxa. The genus *Acrantophis* likely needs some revision, as we found *A. madagascariensis* and *A. dumerili* to be only slightly divergent (though with strong support: BS = 100; PP = 1.0), and found a topology that differs from that in Orozco-Terwengel et al. (2008). *Acrantophis* cf. *dumerili* (Tolangaro, Madagascar; Orozco-Terwengel et al., 2008) is basal to *A. madagascariensis* and *A. dumerili* in our analysis, though the relationship is reversed in Orozco-Terwengel et al. (2008). This is likely due to the inclusion of only two available genes (*CYTB* and *c-mos*) and a single individual in our analysis. Further studies with additional genes, individuals and localities are needed to define species boundaries in this genus.

Similar to recent higher-level analyses (e.g., Pyron et al., 2013a,b), the Central American *Ungaliophis* and *Exiliboa* are recovered as sister taxa to the North American boids *Charina* and *Lichanura*, with support for the distinction of *C. bottae* and *C. umbratica*. The only previous phylogenetic study including both of these taxa used only the mtDNA *ND4* gene to elevate *C. umbratica* from southern California (Rodríguez-Robles et al., 2001). With the first published sequence data for the African species *Eryx muelleri*, we found strong support (BS = 100, PP = 1.0) for the placement of this species as sister to the south Asian *E. jayakari*. Indeed, we found evidence for interdigitation of *Eryx* species between Africa and south Asia suggesting repeated dispersal events, but one node (*E. colubrinus*) lacks strong support in the ML analysis (BS = 43). We found no evidence to support the continued usage of the generic name *Gongylophis* Boulenger (Tokar, 1995) for the species *E. colubrinus*, *E. muelleri*, and *E. conicus*, due to the polyphyly created by this name. Samples from the Asian taxa *E. miliaris* and *E. tataricus* (novel sequence data, specimen UMFS 11688) were not found to be reciprocally monophyletic, although our specimen of *E. tataricus* is originally from the pet trade, hence the identification could be questionable. Nonetheless, this finding is supported by recent morphological work suggesting that *E. tataricus* and *E. miliaris* represent the same species, at least in northeastern Iran (Eskandarzadeh et al., 2013). These authors also suggested that Iranian *E. jaculus* and *E. elegans* are conspecific. Although we did find support for the distinction of *E. tataricus vittatus*, these taxa have very similar ranges (Uetz and Hošek, 2013) and a phylogeographic study combined with a species-tree analysis is certainly needed to shed more light on what is likely a larger species complex.

The long-enigmatic radiation of boas in the Pacific (*Candoia*) has recently become better characterized (Austin, 2000; Noonan and Chippindale, 2006a; Noonan and Sites, 2010), and we were able to add sequence data from two taxa (*C. superciliosa* and *C. s. crombiei*) that had no previously published sequences. The Melanesian/Micronesian *C. bibroni* was recovered as basal to the rest of the radiation (Austin, 2000), with the highly similar Palauan *C. superciliosa* and *C. s. crombiei* sister to *C. carinata* (Smith et al., 2001). We found support (BS = 72) for the distinction between the widespread *C. carinata* and the geographically isolated Palauan species.

Among western hemisphere boids, we found support for the recognition of *B. imperator* (suggested by Hynková et al. (2009); see also Reynolds et al. (2013b)) and recommend the epithet *B. imperator*, though we recognize the need for a phylogenetic study across the wide range of *B. constrictor* sensu lato. Relationships among *Corallus* have been well-studied recently (Colston et al., 2013; Henderson and Hedges, 1995; Henderson et al., 2013), including the finding that West Indian species are nested within the wide ranging *C. hortulanus*. Our analysis also recovers this topology, yet Henderson et al. (2013) have refrained from subsuming these species (*C. grenadensis* and *C. cookii*) due to morphological and ecological differences in addition to the unique locations of these populations. We also found support for the distinction between Guyanian *C. caninus* and Amazonian *C. batesii* (Henderson et al., 2009; Vidal et al., 2005), though this relationship is complicated by the unclear origins of sequence data on Genbank. Our sequences for *C. batesii* were generated from a known specimen in a related study (Reynolds et al., 2013a); however, it is possible that some Genbank sequences labeled as *C. caninus* might actually be from Amazonian (*C. batesii*) specimens, even though we attempted in each case to select sequences from known specimens. Henderson et al. (2013) showed a more divergent relationship between *C. batesii* and *C. caninus*, but it is not clear where the phylogenetic data for *C. batesii* originated in Henderson et al. (2013) [the phylogeny was reported to be directly from Colston et al. (2013), but this paper did not explicitly include *C. batesii*]. Among the South American *Eunectes* and *Epicrates*, we recovered similar relationships to previous studies (e.g., Reynolds et al., 2013a; Rivera et al., 2011), with support for the distinction of the five mainland species of *Epicrates*. We were only able to include two of the four recognized species of *Eunectes*, and we attempted to include a sample from the type specimen of *Eu. beniensis* (AMNH 101924), but this specimen appears to have been formalin-fixed as we were not able to obtain usable DNA from a tissue subsample. In the West Indies, we found a slightly different topology than a recent study (Reynolds et al., 2013a). However, Reynolds et al. (2013a) included multiple individuals of each taxon in a species-tree framework with different genetic loci. In particular, we found a strongly-supported clade consisting of the Cuban (*Chilabothrus angulifer*) and Puerto Rican (*C. inornatus* and *C. monensis*) *Chilabothrus*, similar to Rivera et al. (2011) and contrary to the basal placement of *C. angulifer* in Reynolds et al. (2013a) relative to the rest of the West Indian radiation.

3.4. Biogeographic implications

The results from our phylogenetic analyses suggest some interesting and heretofore unrecognized biogeographic patterns. While it is beyond the scope of the present study to conduct time-calibrated historical biogeographic analyses, we discuss some biogeographic implications and propose some testable hypotheses for future study. Among the pythons, we find a basal placement for the West African *Python regius*, indicating a possible origin of this genus (and pythonids) in Africa followed by dispersal to Europe

(†*P. europaeus*; Szyndlar and Rage, 2003) and Asia, consistent with Rawlings et al. (2008). This is contrary to previous suggestions of an origin of pythons in Southeast Asia (Underwood and Stimson, 1990) or Australasia (Kluge, 1993). Our analyses suggest continued dispersal east through Asia to the Indonesian archipelago, followed by arrival in Australasia. Given the shallow branches in our phylogeny (Fig. 2), likely owing to rapid speciation during colonization of the greater Indo-Australian archipelago (Rawlings et al., 2008), it is difficult to resolve whether colonization occurred from Australia back to Melanesia; however, this scenario is suggested and would be an interesting hypothesis to test (see Fig. 3).

Among the boids, we find support for the basal placement of the Madagascan boids, similar to Noonan and Sites (2010) suggesting a Gondwanan origin for the boids sensu stricto in the late Cretaceous. However, Noonan and Sites (2010) suggested Asia as a more likely origination, as many extinct boids are known from the Eocene of Europe (Rage, 1984) and other studies have found a sister relationship between Afro-Asian and Melanesian boids (Noonan and Chippindale, 2006a). Our tree lacks support to determine the latter relationship, and hence we cannot provide additional insight into the suggested possibility of a Beringian migration of ancestral boids from North America through the western Pacific Rim (i.e., Noonan and Sites, 2010). However, determining the origins of basal North American boids (e.g., *Charina*, *Lichanura*, †*Paraepicrates*, †*Pseudoepicrates*, etc.) would shed light on dispersal routes during the Eocene. Possible boid dispersal routes include Gondwanan dispersal through Australia–South America–Madagascar–Antarctica (Noonan and Chippindale, 2006b), Eocene dispersal across the North Atlantic (Noonan and Sites, 2010), and Beringian dispersal through the Pacific Rim. Selective extinctions, such as in Australia, would be required to explain some of these movements, but fossil records suggest that boids have remained a diverse group since the Eocene in some areas, such as North America and Europe, with ample evidence of extinctions (e.g., Rage, 1984). Afro-Eurasian sand boas (*Eryx*) provide interesting biogeographic patterns, and our inclusion of sequence data for a novel taxon (*E. muelleri*) suggests that the two egg-laying boids (*E. muelleri* and *E. jayakari*) are sister but not continentally co-distributed. The former is an African species, while *E. jayakari* is known from the Arabian Peninsula, a pattern that likely represents a relatively ancient range restriction to the Sahara and Arabian deserts. We also find evidence for at least two dispersal events from Africa to Asia in the ercyine boas, a finding that would be especially interesting if divergence dates could be estimated. However, as previously mentioned this group is likely plagued by taxonomic inconsistencies, poor distributional knowledge, and cryptic diversity.

The historical biogeography of the Central and South American boids is well studied (Colston et al., 2013; Reynolds et al., 2013a), and our results support these other analyses. In Melanesia and Micronesia, our inclusion of sequence data for a novel taxon (*C. superciliosa*) suggests that this Palauan species is derived from New Guinea. Furthermore, we find support for the hypothesis put forth by Austin (2000) that the Pacific boas are derived from the Fijian *C. bibroni*, and not from Melanesian species. Given the absence of boid fossils from Australia or Southeast Asia, it is unclear whether this pattern is a consequence of range contraction following extinction of other lineages.

3.5. Conclusions

Like many previous studies, we found low support for the placement of some families in the henophidian tree. Given the large number of molecular markers applied to higher level relationships within the Squamata (e.g., Pyron et al., 2013b; Wiens et al., 2012), it is not clear whether increased marker sampling will improve resolution of the placement of families such as Bolyriidae Calabariidae, and Xenophidiidae. However, improved taxon sampling

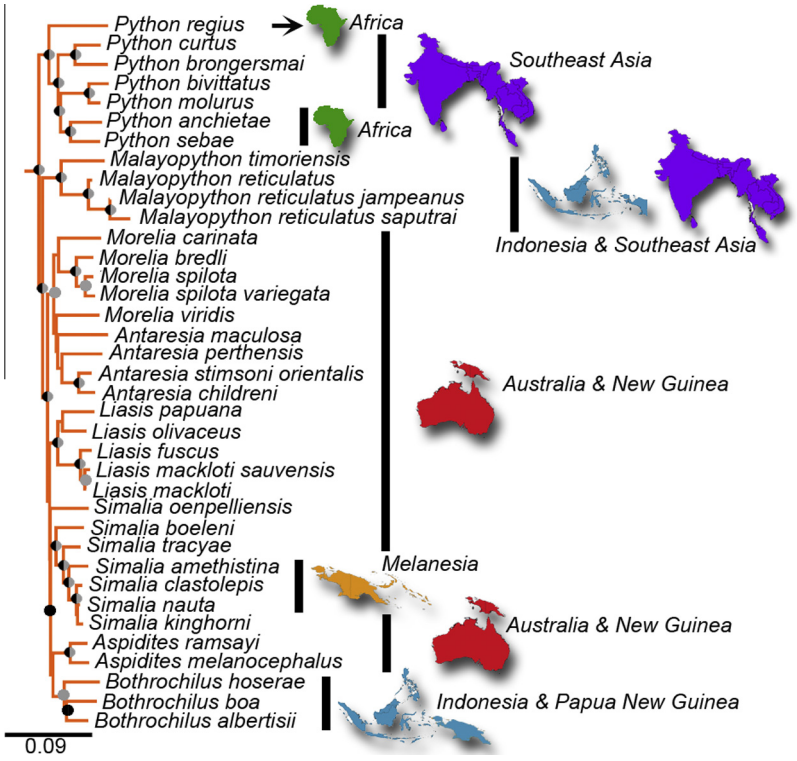

Fig. 2. Maximum likelihood tree for the Pythonidae with revised taxonomy pruned from the larger tree. Support values at each node are as in Fig. 1. The generalized ranges for each species are color-coded and shown to the right of the tree.

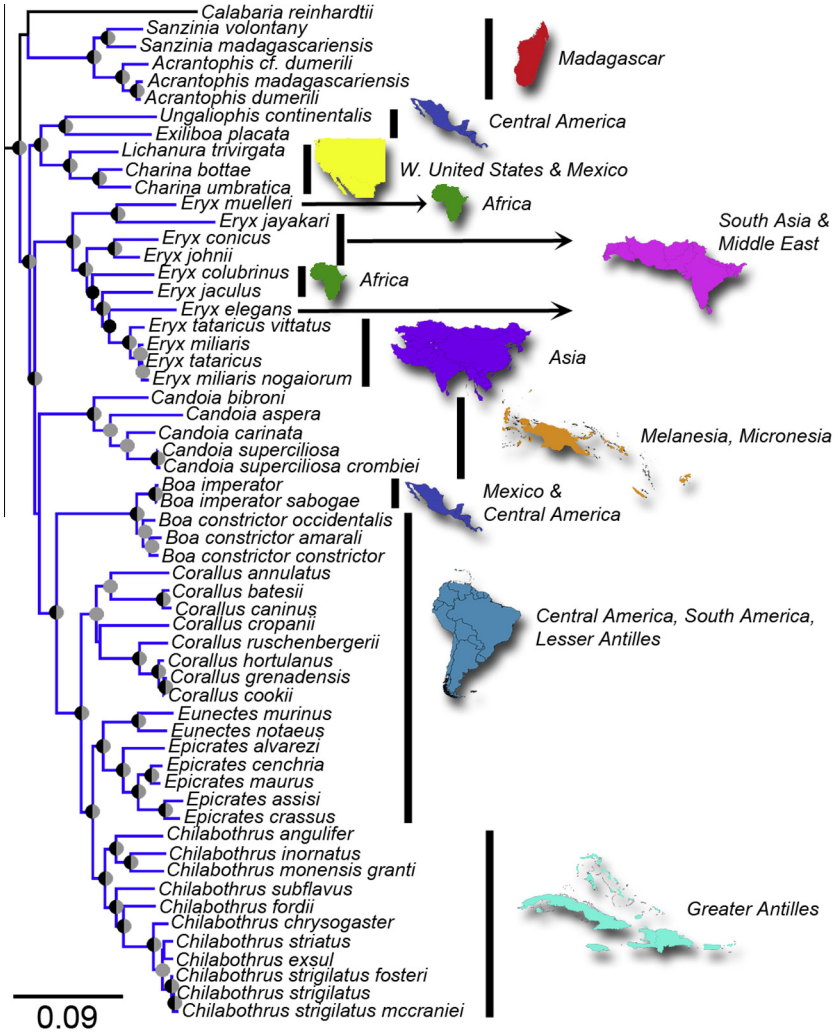

Fig. 3. Maximum likelihood tree for the Boidae with revised taxonomy pruned from the larger tree. Support values at each node are as in Figs. 1 and 2. The generalized ranges for each species are color-coded and shown to the right of the tree.

would likely clarify relationships among the enigmatic families Anomochilidae, Uropeltidae, and Cylindrophiidae.

A fruitful avenue for future research would be to implement a gene tree-species tree framework for these groups to assess whether there is genuine topological discordance between the gene trees of different, independently segregating genetic loci ("coalescent trees" *sensu* Felsenstein) within the containing species tree owing to processes such as incomplete lineage sorting or horizontal gene flow (e.g., Carstens and Knowles, 2007; Degnan and Rosenberg, 2009; Edwards et al., 2007). Unfortunately, MCMC species-tree methods require a large amount of computational time to achieve convergence, even on multi-processor computing clusters, and also require much more extensive sampling of individuals within species to construct robust coalescent trees. Furthermore, missing data in individual coalescent trees (a consequence of the supermatrix approach) might lead to problems in estimating a species-tree (Thomson et al., 2008), as the use of inconsistently sampled coalescent trees would become tantamount to using a "supertree" approach. Because we cannot access tissues for many species of boas and pythons, these analyses remain out of reach. Yet these types of intraspecific and intrageneric studies would be of great utility to conservation and to higher-level Tree-of-Life studies. Given that boas and pythons are a globally imperiled group (Bohm et al., 2013; IUCN, 2012), improved understanding of species boundaries would greatly improve conservation efforts. We call on other researchers to consider collaborating in the exchange of data and tissue samples to better characterize boa and python evolutionary relationships, and we hope that our study provides a first step forward in this path.

Acknowledgments

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Appendix A. Summary of taxonomic changes

ZooBank Registration: urn:lsid:zoobank.org:act:097BD9DD-4FA3-4525-8E3B-7EC2234DE475.

Malayopython gen. nov.
Constrictor Wagler 1830
Type species '*Constrictor schneideri* Wagler' (erroneous citation of *Python schneideri* Merrem 1820, = *Python reticulatus* (Schneider 1801)), designated by Fitzinger 1826. Primary homonym of *Constrictor* Laurenti 1768
Python Merrem 1820
Broghammerus Hoser 2004 *nomen nudum*
Broghammerus Rawlings et al., 2008 *nomen dubium*
Neotype: ZFMK 32378, Rengit, West Malaysia (Auliya et al., 2002)
Definition and diagnosis: see Rawlings et al. (2008)
Included species: *reticulatus* Schneider 1801, *timoriensis* Peters 1876

Simalia Gray 1849
Boa Schneider 1801
Type species '*Boa amethistina* Schneider
Python Daudin 1803
Constrictor Wagler 1830
Liasis Gray 1842
Simalia Gray 1849
Aspidopython Meyer 1874
Liasis Günther 1879
Australiasis nomen nudum Wells and Wellington, 1984
Morelia Kluge, 1993
Holotype: MCZ 9600 (*Liasis clarki*)
Definition: The clade comprising *Simalia amethistina* (Schneider 1801), and all species that share a more recent common ancestor with *Simalia amethistina* than with other pythonid taxa.
Diagnosis: see species descriptions in Kluge (1993) and Harvey et al. (2000).
Included species: amethistina Schneider 1801; *boeleni* Brongersma 1953; *clastolepis* Harvey et al., 2000; *kinghorni* Stull 1933; *nauta* Harvey et al., 2000; *oenpelliensis* Gow 1977; *tracyae* Harvey et al., 2000.

Proposed novel generic compositions:
Pythonidae: *Bothrochilus*: *B. boa*, *B. albertisii*, *B. bennettorum*, *B. biakensis*, *B. fredparkeri*, *B. hoserae*, *B. huonensis*; ***Liasis***: *L. fuscus*, *L. mackloti*, *L. olivaceus*, *L. papuana*; ***Malayopython***: *M. reticulatus*, *M. timoriensis*; ***Morelia***: *M. bredli*, *M. carinata*, *M. spilota*, *M. viridis*; ***Simalia***: *S. amethistina*, *S. boeleni*, *S. clastolepis*, *S. kinghorni*, *S. nauta*, *S. oenpelliensis*, *S. tracyae*; **Boidae**: ***Boa***: *B. constrictor*, *B. imperator*; ***Sanzinia***: *S. madagascariensis*, *S. volontany*.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.11.011.

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