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Beyond Building A Tree: Phylogeny Of Pitvipers And Exploration Of Evolutionary Patterns

Allyson Fenwick
University of Central Florida

BEYOND BUILDING A TREE: PHYLOGENY OF PITVIPERS AND EXPLORATION OF EVOLUTIONARY PATTERNS

by

ALLYSON M. FENWICK
B.S. – Michigan State University, 2003
B.A. – Michigan State University, 2003
M.S. – The University of Texas at Tyler, 2006

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ABSTRACT

As generic and higher-scale evolutionary relationships are increasingly well understood, systematists move research in two directions: 1) understanding species-level relationships with dense taxon sampling, and 2) evaluating evolutionary patterns using phylogeny. In this study I address both foci of systematic research using pitvipers, subfamily Crotalinae.

For direction one, I evaluate the relationships of 96% of pitvipers by combining independent sets of molecular and phenotypic data. I find the inclusion of species with low numbers of informative characters (i.e. less than 100) negatively impacts resolution of the phylogeny, and the addition of independent datasets has no effect on or a small benefit to confidence in estimated evolutionary relationships. Combined evidence is extremely useful in evaluating taxonomy; I use it with South American bothropoid pitvipers. Previous work found the genus *Bothrops* paraphyletic, but no study had included enough species to propose a taxonomic resolution. I resolve the relationships of 90% of bothropoid pitvipers, and support the paraphyly of *Bothrops* as previously defined, but find it consists of three well-supported clades distinguished by distinct habitats and geographic ranges. I propose the division of *Bothrops sensu lato* into three genera.

To address research direction two, I investigate the change in reproductive mode from egg-laying (oviparity) to livebearing (viviparity) in vipers, as well as the expansion of pitvipers through South America. I resolve the phylogeny and the divergence times for subgroups of interest then use model comparison and ancestral character state or

geographic range estimation to trace the evolution of reproductive mode or geographic range across evolutionary history. For vertebrates, the predominant explanation for the evolution of reproductive mode is Dollo's Law of unidirectional evolution. This law has been challenged for a number of characters in different systems, but the phylogenetic methods that found those violations were criticized. I find support for unidirectional evolution in two analyses and rejection of it in others, and therefore do not reject Dollo's Law for the evolution of reproductive mode in vipers. In the case of geographic range, dozens of hypotheses have been proposed to explain the great biodiversity in South America, but tests of these hypotheses are lacking. I define specific time- and space-based predictions for seven hypotheses based on geological and climatic events – uplift of the Andes Mountains, saltwater inundation of inland areas, change in river flow, and Pleistocene climate changes. I find some support for half of the hypotheses, including one allopatric, one parapatric, and one based on climate change. I conclude that the evolution of South American pitvipers is extremely complex.

Through fulfillment of both systematic research directions, I generated new knowledge about pitvipers and evolutionary processes. My methods of evaluating evolutionary patterns provide frameworks for different research questions in these areas, and I suggest that other researchers apply similar techniques to evaluate other portions of the Tree of Life.

To the family in my home,

the family who supported me from afar,

and those friends who became family

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INTRODUCTION: ROLES FOR PHYLOGENETICISTS IN BIOLOGICAL RESEARCH

Biological research has greatly benefited from phylogenetics. Phylogenies provide a general understanding of the diversification of groups over time, and therefore can be used to connect independent observations of related taxa and greatly magnify the utility of these observations. Understanding taxon relationships helps identify major evolutionary lineages and other factors important to conservation. Phylogenies of taxa can be compared to phylogenies of genes to better understand how gene families evolve across the Tree of Life. Researchers collecting observations of organismal responses to a factor of interest use phylogenetic trees to eliminate the "noise" of shared evolutionary history, allowing a better evaluation of the relationship between the factor and the response. Finally, phylogenetic trees are used to estimate characteristics of the extinct ancestors of extant taxa. Researchers collect observations of the traits of extant taxa, and then use phylogenetic trees to map the character states of ancestral taxa. Mapping the evolution of characters helps clarify general rules guiding change in these traits. In the specific case of geographic ranges, this research points to environmental or geologic factors driving diversity in various organisms within a region.

Historically, researchers who recovered phylogenies used them only to identify groups (systematics) and evaluate the biological relevance of names (taxonomy). The published trees were then used in other disciplines to test hypotheses. Systematics and taxonomy are important ways to quickly disseminate understanding of lineage

relationships to an audience much broader than those who will read the phylogenies, but as higher level relationships become well-resolved, the role of phylogeneticists must broaden. In herpetology in particular, most family and genus level relationships may soon be resolved (Wiens, 2008), therefore systematists must focus on 1) resolving species-level relationships and 2) using phylogenies to test hypotheses about evolutionary patterns and processes.

Species-level relationships

The most useful phylogenies for hypothesis testing are taxon-comprehensive. Using as many species as possible reduces the problem of species sampling bias and can enhance the estimation of character states in ancestral lineages. Greater density of taxon sampling increases accuracy of resolving phylogenies (Graybeal, 1998; Hillis, 1998; Poe and Swofford, 1999; Rannala et al., 1998; Wiens, 2003a, b; Wiens, 2005), which leads to greater accuracy in branch length estimation. As branch lengths represent the amount of evolutionary change that occurred between speciation events, they can be used to determine the dates of those speciation events. Accurate estimation of lineage divergence times is critical to character state reconstruction, biogeographic, and comparative studies (e.g. Pagel et al., 2004; Rutschmann, 2006 and references therein).

The most straightforward way to estimate relationships for all species in a group is to utilize all available forms of data for all species, following the principles of total evidence (de Queiroz, 1993; Kluge, 1989). These data most often include DNA and phenotypic characters. However, for some species DNA are not available. Specimens must be fresh, frozen, or specially preserved to yield usable DNA, and in the case of taxa

preserved in formalin such as some invertebrates, fishes, amphibians, and reptiles, rare species may have no specimens available for DNA sequencing (Hillis, 1987). Organismal collections such as natural history museums house specimen collections that date back over 100 years, and luckily these specimens yield phenotypic data that allow the inclusion of species in phylogenetic analysis even when no specially preserved individuals are available.

Although including as many species as possible has acknowledged benefits, researchers are concerned about the inclusion of species that lack genetic data because of the large amount of missing cells in the data matrix (e.g. Lemmon et al., 2009). Morphological datasets are often on the order of hundreds of characters, while most genetic datasets have several thousand characters (e.g. Wiens et al., 2005). As techniques for collecting genetic and genomic data improve, this discrepancy continues to increase. Phylogenetic placement of species with large amounts of missing data may be difficult to resolve (e.g. Anderson, 2001; Novacek, 1992; Wilkinson, 1995). Including taxa with missing data may also decrease accuracy of phylogenetic resolution overall, lessening confidence in the placement of other species. In contrast, simulations and some empirical studies suggest that large proportions of missing data may not adversely affect accuracy if the number of completely sampled characters is large enough, and may in fact rescue analyses from problems such as long-branch attraction (Wiens and Morrill, 2011 and citations therein). Therefore, including lineages with a large number of sampled morphological characters but lacking DNA data may be beneficial.

The use of morphological data alone and in combination with molecular evidence is important to the understanding of relationships among lineages as well as to the usability of phylogenies. Phenotypic characters not only increase taxon sampling, they also facilitate the placement of fossils, which tie phylogenies to absolute time (Hillis and Wiens, 2000). Branch lengths with absolute times are useful for testing biogeographic hypotheses as well as connecting other character changes to specific events (e.g. Lynch, 2009). Accuracy for the position of fossil taxa is increased by including molecular data (Wiens, 2009; Wiens et al., 2010), and incorporating fossil taxa can even change the position of living taxa (Wiens et al., 2010).

Early phylogenies were generally based on morphology, with more recent phylogenies based on molecular evidence (Wiens, 2008). The differences between these sources of evidence make incongruence between the inferred phylogenies extremely difficult to evaluate, introducing phylogenetic uncertainty to subsequent hypothesis testing. The addition of morphology to an established molecular dataset allows one to conduct both separate and combined evidence analyses. Combined evidence also provides suitable means to evaluate whether incongruence occurs due to problems within a character type or due to evolutionary processes acting on a lineage. Character problems may be resolved after analysis; evolutionary processes must be taken into account in hypothesis testing. For example, phylogenies of the palm-pitviper genus *Bothriechis* inferred based on allozyme and morphological data (Crother et al., 1992) suggested different patterns of Central American colonization than phylogenies based on mitochondrial DNA (mtDNA; Castoe et al., 2009 and references therein). Taggart et

al. (2001) compared and combined the allozyme dataset to mtDNA from Parkinson (1999) and new sampling. They concluded that it was inappropriate to combine mitochondrial and nuclear DNA evidence because introgression and/or incomplete lineage sorting may cause mtDNA phylogenies to not reflect the evolutionary history of the group. Further testing with an expanded dataset of mitochondrial haplotypes and nuclear loci by Castoe, Daza and Parkinson failed to reveal incongruence between mitochondrial and nuclear sites, or introgression or incomplete lineage sorting in mitochondrial haplotypes (unpublished; reported in Castoe et al., 2009). As the morphological data sampled by Crother et al. (1992) was limited, the expanded morphological dataset collected by this study should complete the story of congruence among datatypes for palm-pitvipers.

Evaluating evolutionary patterns

Once accurate, comprehensive species trees have been resolved, phylogeneticists should use their unique skill set to evaluate interesting evolutionary patterns. This role is becoming increasingly important as more accurate and more comprehensive phylogenies become available for a variety of organisms. Subfields of evolution such as character reconstruction and biogeography utilize data collection and analytical methods similar to those of phylogenetic reconstruction, and are good areas for expanded interest.

Phylogenies can be combined with the large amounts of natural history data about extant species accumulated in published literature to illuminate patterns of character evolution across ancestral taxa. Identifying these patterns enables inferences

of key innovations or other factors driving speciation (e.g. Lynch, 2009), and facilitates tests of long-assumed explanations of character change (e.g. Collin and Miglietta, 2008). Biogeographic work is also informed by reconstruction of ancestral ranges, but in addition a long history of study of extant species ranges has produced an array of hypotheses on how geologic and climatic change have driven speciation. These hypotheses can now be tested using time-calibrated, taxon-dense trees. In both character evolution and biogeographic studies, advances in computational methods and processing power have greatly expanded the use of phylogenetic information in estimating the evolution of geographic ranges and other characters (e.g. Pagel et al., 2004; Ree and Sanmartín, 2009). Recently adopted methods provide newly accurate estimates of confidence in the reconstruction of ancestral states and ranges, including estimates of uncertainty in relationships, branch lengths, character states, and confounding factors (e.g. Goldberg et al., 2011; Maddison et al., 2007; Pagel and Meade, 2006; Pagel et al., 2004).

Pitvipers as a model system

Pitvipers are an excellent system to meet the goals of this research program for theoretical and practical reasons. First, pitvipers can be a model system for testing evolutionary hypotheses because they contain a number of interesting natural history characters (see Campbell and Lamar, 2004; Greene, 2000). Groups have evolved to utilize various diets, modes of reproduction, and macro- and microhabitats. Pitvipers are beneficial to the study of biogeography because they range across the Americas and Southeast Asia and have greatly diversified over the past 20 million years (Castoe et al.,

2009). Second, a robust phylogeny and biologically relevant taxonomy of pitvipers is important because all species are venomous (Greene, 2000). Understanding evolutionary relationships of pitvipers is essential to antivenom production and aids in the selection of species to utilize as biological resources (Fry et al., 2003; Koh et al., 2006; Wüster, 1996; Wüster et al., 1997). Third, this group is extremely speciose, containing 213 species in at least 24 genera (www.reptile-database.org and references therein, accessed 19 May 2012). This diversity provides many species to test hypotheses in various fields. Fourth, a large set of morphological characters has been published for pitvipers (Appendix A). Many mitochondrial sequences are also available, providing a generous molecular dataset that can be expanded by including rare species and adding independent molecular datasets from nuclear genes. The combination of phenotypic and molecular data in this study results in three independent datasets for resolving species trees.

Study goals

The need for multiple approaches to understanding evolution and the suitability of pitvipers as a model system lead to my two main goals: build a robust and comprehensive phylogenetic hypothesis for pitvipers and investigate evolutionary patterns using phylogenies.

I resolve relationships of rare and newly described species based on phenotypic data, those with few known individuals and no available molecular data. I compare topologies based on morphological, molecular, and combined evidence. I provide insight into long-established questions of pitviper relationships, such as the earliest diverging

lineage among pitvipers, relationships among certain Asian groups, and the sister lineage of New World vipers. The comprehensive phylogenetic tree benefits not only my work but also those who investigate vipers in contexts such as comparative statistical analysis (Gartner, pers. comm.).

I evaluate conflicts between established taxonomy and evolutionary relationships, suggesting areas of further study or proposing taxonomic changes where accumulated evidence provides strong support for name changes. In this way I continue the long history of phylogenetics enlightening systematics and taxonomy to propose biologically relevant names.

I use subsets of the pitviper tree to evaluate interesting evolutionary patterns. Specifically, I use current methods to evaluate the prevailing hypothesis for the evolution of egg-laying and livebearing modes of reproduction in vertebrates: Dollo's Law (Dollo, 1893, 1905; Fitch, 1970; Neill, 1964; Tinkle and Gibbons, 1977). Vipers provide an excellent test of the evolution of reproductive mode because they are squamate reptiles, a group that contains the largest number of changes in reproductive mode among vertebrates (Blackburn, 1982). Current character reconstruction methods require taxon-comprehensive phylogenies, and therefore my trees provide an accurate estimation of confidence in the support for this hypothesis.

Several current methods for estimating the geographic ranges of ancestral taxa are related to those of character reconstruction and also rely on accurate, species-dense phylogenies of appropriate taxa. I consider a number of explanations for the great biodiversity in South America, defining specific predictions for locations and timing of

geographic range evolution in pitvipers. This group entered the continent in the mid-Miocene (Castoe et al., 2009), was present across the time period important to most hypotheses, and ranges from Central America to southern Argentina (Campbell and Lamar, 2004).

This work will benefit other evolutionary biologists by providing a framework for going beyond simply building trees. The tree and taxonomic changes will benefit countless researchers, because a key step to empirical study is understanding one's focal taxon. The results of my hypothesis testing will contribute to the ongoing discussion on the applicability of Dollo's Law and illuminate a set of relevant diversification drivers in the Neotropics.

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CHAPTER 2: COMPREHENSIVE TAXON SAMPLING WITH COMBINED MOLECULAR AND PHENOTYPIC EVIDENCE ESTIMATES THE PHYLOGENY OF PITVIPERS (SERPENTES: CROTALINAE)

Introduction

As the field of phylogenetics is benefiting from innovations in genome sequencing technology and advancements in the ability to analyze large datasets with computationally complex methods, two directions are emerging. One direction is phylogenomic, as new technology allows sampling of hundreds of thousands of characters, but financial considerations limit taxon sampling to few lineages. The other direction is expansive taxon sampling, with the goal of including all taxonomic units within the group of interest through using more cheaply available data. The second method is generally conducted using few genetic loci and may include other character types such as phenotype or behavior. This study explores the possibilities and challenges of the second method via resolving evolutionary relationships with two independent genetic datasets for the majority of the ingroup taxa, with a phenotypic dataset for all included species. We contribute an empirical example of the data matrices that will soon become common: a large number of species of varying completeness.

Taxon sampling

Taxon sampling is now not constrained by analytical limitations, but rather by limitations of specimen availability and data collection (Heath et al., 2008). A classic

example of this constraint is including fossils in phylogeny: a subset of phenotypic characters can be collected, but usable DNA can be retrieved only in rare cases (Hillis, 1987). Because molecular datasets are on the order of thousands of characters but phenotypic datasets generally consist of a few hundred characters, lineages represented by phenotypic data alone often have over 90% missing data in combined analyses (e.g. Gatesy et al., 2004; Manos et al., 2007). Therefore, one of the challenges in dense sampling is how to include lineages with large amounts of missing data. Because fossils are critical to placing evolutionary relationships in temporal context, accurate placement of fossils has been evaluated through simulation and some empirical examples (see Wiens and Morrill, 2011). These fossil studies suggest that taxa with large proportions of missing data can be accurately placed in phylogeny, and some observations suggest that they can change the estimated relationships of living taxa (Donoghue et al., 1989).

The requirement for resolution of these data-limited taxa is that they surpass a threshold number of complete characters (Wiens, 2003). However, because the focus in studies addressing the missing data problem has generally been the proportion of missing data (see review in Wiens and Morrill, 2011), few empirical studies have addressed how many complete characters are needed in absolute numbers. The likely relationship between taxon sampling and number of complete characters is complicated, and may be based on the amount of data present and phylogenetic issues specific to a given dataset, and therefore we need a variety of empirical studies to

evaluate the behavior of phylogenetic analysis under common sampling and analysis conditions.

Dense taxon sampling is beneficial because it returns results for a maximum number of lineages, which assists researchers working on various aspects of the biology of those lineages. For example, changing taxonomic classification to reflect evolutionary history requires nearly complete sampling (e.g. Fenwick et al., 2009). Similarly, dense species-level sampling is expected in comparative analysis (Harvey and Pagel, 1991), where many methods assume complete taxon sampling (e.g. Maddison et al., 2007). Fenwick et al. (2012) found different patterns of evolution of egg-laying and livebearing in vipers with denser taxon sampling compared to Lynch (2009). This is a pattern expected to repeat in various systems.

Dense taxon sampling also benefits phylogenetic estimation. Increased taxon sampling increases phylogenetic accuracy, sometimes through breaking long branches (Graybeal, 1998; e.g. Huelsenbeck, 1995; Kim, 1998; Poe and Swofford, 1999; Rannala et al., 1998). Inclusion of more taxa allows better usage of rapidly evolving characters (Hillis, 1998; Townsend and Leuenberger, 2011), and may even overcome some of the problems with single-gene phylogenies (Agnarsson and May-Collado, 2008). In dense character sampling with low taxon sampling, as seen in current phylogenomic studies, noise may swamp faint phylogenetic signal in areas of the tree that are difficult to recover (Philippe et al., 2011).

Combining datasets

The missing data problem in taxon sampling is often related to the issues of combining datasets, and this issue is of particular interest when combining molecular and phenotypic data. Molecular data are often available for thousands of characters but fewer taxa, while morphological datasets consist of up to hundreds of characters but can be complete for all taxa. Groups that are commonly preserved with formaldehyde, such as amphibians, reptiles, fishes, and some invertebrates, are notable because specimens prepared in this fashion cannot be readily used for PCR-based DNA sequencing with current technology (but see Kearney and Stuart, 2004; Kohlsdorf and Wagner, 2006), which results in thousands of specimens that cannot provide DNA but are available for phenotypic examination. Fossils provide the best known example of a need to find efficient ways of combining data, as morphology is generally the only data type available for these specimens. Recent work on the problem of placing fossils suggests that combining morphological and molecular data for fossils and extant taxa leads to more accurate placement of the fossils (Wiens, 2009; Wiens et al., 2010), and that morphological data can even change the position of extant taxa despite being a small fraction of the data matrix (Wiens et al., 2010).

Additional considerations for the use of all available sources of data in phylogeny reconstruction are more philosophical. First, the principle of total evidence suggests that a scientific hypothesis such as phylogeny should be based on all available evidence. Second, synapomorphy and homoplasy of morphological characters, those that are generally cited to define taxa, can only be determined by combined analysis (Assis and

Rieppel, 2011). The common technique of mapping morphological characters onto a molecular phylogeny in order to determine "synapomorphies" is not useful because it does not allow morphology to affect evolutionary relationships and does not result in true synapomorphies because node positions cannot be supported or refuted by the morphology. Third, as early phylogenies were generally based on morphology, with more recent phylogenies based on molecular evidence (Wiens, 2008), it is difficult to compare the hypotheses of relationship without a combined analysis. Without combined analysis, phylogenetic uncertainty is introduced to subsequent hypothesis testing.

Pitvipers as a model system

The phylogenetic considerations discussed above have been well evaluated using simulations and large-scale empirical examples (e.g. Wiens et al., 2010), but species- and genus-level datasets have yet to be fully explored. Pitvipers (subfamily Crotalinae) provide an excellent opportunity to examine taxon sampling and combined data. Crotalinae contains approximately 200 species in 27 genera (Guo et al., 2007; Malhotra and Thorpe, 2004; McDiarmid et al., 1999), providing a large taxon sample with a range of common and rare species. Evolutionary relationships of this group have been of interest for a long time, as all species are venomous and venom composition correlates with phylogenetic relationships (Fry et al., 2003; Koh et al., 2006; Wüster, 1996; Wüster et al., 1997). Due to this interest, morphological and molecular characters have been generated for a number of species, with the potential to efficiently fill in gaps. In addition, pitvipers are of interest as a model in comparative (e.g. Lynch, 2009, Fenwick

et al. in press) and biogeographic studies (Castoe et al., 2009; Crother et al., 1992; Daza et al., 2010; Werman, 2005; Wüster et al., 2002; Zamudio and Greene, 1997). Densely sampled and character-rich phylogenies would be of great utility to studies like these. For example, biogeographic hypotheses of Central American *Bothriechis* proposed by Crother et al. (1992) are quite different from those suggested by Castoe et al. (2009); combined evidence phylogeny may help to distinguish between these hypotheses.

Despite long interest in Crotalinae and the resolution of most within-genus relationships, intergeneric relationships are still largely unknown (see Castoe and Parkinson, 2006; Pyron et al., 2011). Poor resolution of these relationships may be due to the proposed quick radiation of pitvipers into contemporary genera, resulting in short phylogenetic branches that are difficult to resolve. These relationships have been mainly resolved with mitochondrial and some nuclear loci, with morphological data examined for relatively few taxa (see Gutberlet and Harvey, 2002).

In this study we combine mitochondrial, nuclear and morphological data to generate the most species-dense crotaline phylogeny to date. We evaluate the effect of including taxa with varying amounts of data complete and the results of combining different data types. We address outstanding questions in pitviper evolution and evaluate the phylogenetic positions of recently described species.

Materials and Methods

Morphological Data

We examined 205 of the 213 currently-recognized species of pitviper, or 96% (JCVI Reptile Database accessed 17 July 2012, www.reptile-database.org; Table 3). In accordance with current hypotheses of viper phylogeny (Pyron et al., 2011; Wüster et al., 2008), *Echis carinatus* was used as the far outgroup, with representatives of the major clades of true vipers as additional outgroups.

We examined scalation of 177 species, hemipenes of 127 species, and skeletal material for 114 species (Appendix B). When possible, specimens were acquired from throughout the range of each species. Character data for additional individuals were taken from published sources, allowing us to include morphological data for 204 species. Males and females were treated together. Some juveniles were coded for scale characters as scalation does not change with ontogeny (but see Shine et al., 2005; Tomović et al., 2008), but skeletal data were only collected from presumed adults.

One hundred morphological characters were included in this study (Appendix A). Most characters followed Fenwick et al. (2009), with some original to this study. Characters were coded using a combination of gap weighting for meristic characters (GW; Thiele, 1993), unscaled coding for polymorphic characters with three or fewer states (U; Campbell and Frost, 1993), and majority coding for polymorphic characters with more states (MC; Johnson et al., 1988). This combination uses the greatest amount of phylogenetic information and also captures polymorphism, but follows the requirement that characters used by MrBayes may have no more than six states. The

continuous character method involves using a range of one standard deviation around the mean of the character for each species in order to capture polymorphism.

Molecular Data

Previously published sequence data for mitochondrial loci 12S and 16S rRNA, cytochrome *b* (cyt-*b*), and NADH dehydrogenase subunit 4 (ND4), were obtained from GenBank (Appendix C). In addition, new sequences were obtained for 13 species following protocols described in Castoe & Parkinson (2006); these sequences have been deposited in GenBank (highlighted sequences in Appendix C). This provided a molecular dataset with at least one gene fragment included for each of 173 taxa, or 81% of currently-recognized species.

We also sequenced the nuclear recombination activating gene 1 (Rag1) for 97 species; these sequences have also been deposited in GenBank (Appendix C). We extracted DNA using a DNeasy kit (Quiagen), following manufacturer protocols. We amplified several overlapping fragments using a number of primers, most developed by Todd Castoe to be a strong match across macrostomate snakes (Table 1), and different thermocycler conditions (Table 2). Amplification was conducted in 21µl reaction volumes, with 7.9µl water, 2.1µl of 10x reaction buffer, 3mM MgCl, 1.35mM DNTPs, 0.75mM primers, 0.2 µl Taq polymerase, and 2.5µl of DNA template. Different brands of Taq were used, with Bioline BioXL Long (Bioline) used most often. Product was sequenced on a CEQ8000 or on an ABI 3730 by the Nevada Genomics Center (Reno, NV) and the University of Arizona Genetics Core (Tucson, AZ). All sequences were edited with Sequencher 4.8 (Gene Codes).

Table 1. Primers and PCR conditions for amplification of nuclear gene Rag1. Primer names containing tc refer to primers designed by T. Castoe; numbers refer to position in reference to human RAG1, final letter denotes forward (F) or reverse (R). Primers R13 and R18 designed by Groth and Barrowclough (1999). Thermocycler conditions for PCR programs follow this table. Primers with no PCR program listed were used for sequencing only.

Primer	Sequence (5'→3')	PCR program
R13	TCT GAA TGG AAA TTC AAG CTG TT	SLK1
R18	GAT GCT GCC TCG GTC GGC CAC CTT T	SLK1
Rag1_tc0225F	GCA GCT GTA ATG TCA CAA GTG C	Rag1-59 or SLK1
Rag1_tc0290F	TGA ATA AAA ATA GCT TGG CAR GAG AG	–
Rag1_tc0745F	ATT CAC AGC TGA GCA AAA AAC TCA GG	–
Rag1_tc1000F	AGC TAT TGC CCA TCC TGC C	SLK1
Rag1_tc1370R	CCA RTT CAT CTG CTT GTC TGT GC	SLK1
Rag1_tc1430F	TCA TCC AGC TGT TTG TTT GGC	Rag1-59 or Rag1-DN
Rag1_tc1870F	GGA GAT GTC AGT GAA AAG CAT GGC	Rag1-59
Rag1_tc2000R	TTA CAA CAC AAC TCT GAA TTG GG	Rag1-59 or SLK1
Rag1_tc2700R	AAA GGT CCA TTA ATT CTC TGA GGG	Rag1-59 or Rag1-DN

Table 2. Thermocycler conditions for amplification of fragments of nuclear gene Rag1. Primers cited here are listed in Table 1.

a)

SLK1		
use with primer pair R13 and R18, 225F and 1370R, 225F and 2000R, or 1000F and 2000R		
Step	Temperature	Time (min:sec)
1	94	3:30
2	94	0:40
3	start at 57, -0.2 per cycle	0:40
4	68	1:10
5	Goto 2, 35 times	
6	68	7:00
7	4	forever
8	End	

b)

Rag1-59		
use with primer pairs 225F and 2000R, 1000F and 2000R, 1430F and 2700R, or 1870F and 2700R		
Step	Temperature	Time (min:sec)
1	95	5:00
2	50	1:30
3	68	2:00
4	94	0:40
5	59	0:45
6	72	1:30
7	Goto step 4, 39 times	
8	72	5:00
9	4	forever
10	End	

c)

Rag1-DN		
use with primer pair 1430F and 2700R		
Step	Temperature	Time (min:sec)
1	95	5:00
2	50	1:30
3	68	2:00
4	94	0:40
5	57	0:45
6	72	1:30
7	Goto step 4, 9 times	
8	94	0:40
9	56	0:45
10	72	1:30
11	Goto step 8, 9 times	
12	94	0:40
13	55	0:45
14	72	1:30
15	Goto step 12, 9 times	
16	94	0:40
17	54	0:45
18	72	1:30
19	Goto step 16, 9 times	
20	72	5:00
21	4	forever
22	End	

Ribosomal RNA sequences 12S and 16S were aligned by Muscle in MEGA v5.0 (Tamura et al., 2011). Protein-coding sequences cyt-*b,* ND4, and Rag1 were aligned by eye in GeneDoc v.2.7 (Nicholas and Nicholas Jr., 1997), and no insertions, deletions, or internal stop codons were observed. For all sequences, alignment positions with data for fewer than half of all species were eliminated. Gaps in the alignment were treated as missing data in analyses. The final nucleotide alignments are available by request.

Phylogenetic Analyses

We reconstructed phylogenies using Bayesian inference (BI) with MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003). Prior work (e.g. Castoe and Parkinson, 2006) found no incongruence among mitochondrial genes, and this is expected as loci are inherited as a single linkage unit. We therefore combined all mtDNA into a single analysis. We analyzed Rag1 sequences separately, followed by combined DNA analysis and then combined morphological and molecular analysis. One set of combined evidence analyses included all taxa; others deleted taxa represented by less than 1% of the dataset to investigate the effect of including these extremely data-limited taxa. A final combined evidence analysis excluded taxa with only phenotypic data (2.2% of the matrix).

Based on the results of Castoe & Parkinson (2006), maximum partitioning of the molecular data set was done *a priori*, with all codon positions or stem and loop positions of each gene allocated independent models. Partitioning of rRNA genes was based on models of secondary structure for snake mitochondrial rRNAs (Parkinson, 1999). Each partition was independently analyzed using MrModelTest version 2.2 (Nylander, 2004) to estimate best-fit models of nucleotide evolution. The best-fit models were implemented in partitioned-model analyses of the combined datasets as described in Castoe & Parkinson (2006). The standard Mk model was used for the morphology partition. Preliminary analyses determined that there was no increase in likelihood score with the addition of the gamma-distributed rate variation parameter; therefore we

chose the simpler model. Models chosen for each partition are available from the authors.

Analysis with MrBayes used program defaults, with the exception of chain temperatures being set at half of the program's default to facilitate chain swapping. Chains were run for at least 5.0×10^6 generations, sampled every 500 generations. Tracer 1.5 (Rambaut and Drummond, 2009) was used to verify stationarity and define the burn-in period. If most parameters had not reached the recommended estimated sample size (ESS) of 200 by 5.0×10^6 generations, up to 1.0×10^7 total generations were run to assure adequate sampling. Summary statistics and consensus phylograms with nodal posterior probability support were estimated from the combination of both runs per analysis.

Results

The 12S alignment consisted of 422 base pairs (bp), 16S contained 505bp, cyt-*b* contained 716bp, and ND4 contained 668bp, for a total of 2311 mitochondrial characters (Table 3). Nuclear locus and independent dataset Rag1 contained 2199bp, for a total of 4510 DNA characters. The morphological dataset contained 100 characters, for a total of 4610 total characters. Both 12S and 16S had data for 75% of taxa, cyt-*b* had data for 85% of taxa, ND4 had data for 80% of taxa, and 86% of taxa had some mitochondrial data. Only 43% of species had Rag1 data, and no species had nuclear data but lacked mitochondrial characters. All 223 included species had some morphological data, and only four terminals (2%) had fewer than 46 characters, which represents 1% of the dataset. Thirty-two species (14%) had morphological data only, and therefore had

no more than 2.2% of the dataset complete. *Gloydius monticola* was represented by 368 characters of cyt-*b* and morphology, and was only 8% complete; all other species were over 10% complete.

Phylogenies recovered from individual datasets (Figures 1–3) showed varying amounts of resolution based on the number of complete or informative characters in each matrix. We defined resolution as the number of nodes supported by posterior probabilities ≥ 0.5. Morphology had the fewest supported nodes, followed by Rag1, with mitochondrial DNA the most resolved. These trees are in general agreement, with three strongly supported incongruences between the morphological phylogeny and the DNA-based trees. First, we found strong morphological support for the inclusion of *Azemiops feae* with *Causus* (*Pp*=1.0), compared to a sister relationship of *Azemiops* to pitvipers with mtDNA (*Pp*=1.0) and inclusion with pitvipers with Rag1 (*Pp*=0.54). Second, morphology supported a sister relationship of *Parias schultzei* with *Trimeresurus trigonocephalus* (*Pp*=0.99), but mtDNA found these two species within their respective genera (*Pp*=1.0), and they did not have nuclear data. Third, morphology supported a sister relationship of *Crotalus ravus* to *Sistrurus* (*Pp*=0.98), but mtDNA found *C. ravus* sister to the *C. triseriatus* group (*Pp*=0.98). Rag1 recovered *C. ravus* in a *C. triseriatus* group clade with that species and *C. lepidus* (*Pp*=0.97).

Table 3. Number of characters used for each species in phylogenetic analysis. Mitochondrial genes are 12S, 16S, cyt-*b*, and ND4, and consist of a single linkage unit. Rag1 is a nuclear locus and evolves independently. Morph indicates morphology. Numbers under matrix names are the number of nucleotide positions in alignment. Shading in the Total column highlights species with limited data: dark grey for species with <1% of characters filled, medium grey for 1–2% of characters filled, and light grey for 2–10% of characters filled. Numbers and proportions of species with data for each dataset are summarized at end of table.

Species	12S	16S	cyt-*b*	ND4	Total mtDNA	Rag1	total DNA	morph	total
	422	505	716	668	2311	2199	4510	100	4610
Agkistrodon bilineatus	406	491	714	665	2276	2191	4467	95	4562
Agkistrodon contortrix	407	491	716	668	2282	2199	4481	100	4581
Agkistrodon piscivorus	403	491	716	665	2275	2191	4466	100	4566
Agkistrodon taylori	403	492	716	668	2279	2199	4478	99	4577
Atheris ceratophora	402	490	716	668	2276	–	2276	91	2367
Atheris nitschei	402	491	715	668	2276	1186	3462	98	3560
Atheris squamigera	377	479	694	349	1899	850	2749	98	2847
Atropoides indomitus	390	–	711	667	1768	–	1768	68	1836
Atropoides mexicanus	409	491	716	665	2281	1819	4100	100	4200
Atropoides nummifer	405	489	711	667	2272	1627	3899	100	3999
Atropoides occiduus	405	492	711	667	2275	1032	3307	68	3375
Atropoides olmec	–	491	716	668	1875	1265	3140	68	3208
Atropoides picadoi	405	490	716	668	2279	2199	4478	98	4576
Azemiops feae	404	487	716	668	2275	2009	4284	86	4370
Bitis arietans	404	490	716	668	2278	2199	4477	100	4577
Bitis nasicornis	402	489	664	668	2223	2180	4403	95	4498
Bitis peringueyi	402	489	715	668	2274	873	3147	68	3215
Bothriechis aurifer	403	491	710	668	2272	2199	4471	100	4571
Bothriechis bicolor	403	491	716	668	2278	2199	4477	95	4572
Bothriechis lateralis	403	490	715	668	2276	1929	4205	100	4305
Bothriechis marchi	403	491	716	668	2278	2199	4477	100	4577
Bothriechis nigroviridis	402	490	713	668	2273	2199	4472	99	4571
Bothriechis rowleyi	403	491	716	668	2278	1690	3968	91	4059
Bothriechis schlegelii	404	476	716	668	2264	2199	4463	96	4559
Bothriechis supraciliaris	405	490	716	668	2279	2199	4478	68	4546
Bothriechis thalassinus	403	491	716	667	2277	2193	4470	64	4534
Bothriopsis bilineata	409	462	641	408	1920	2199	4119	95	4214
Bothriopsis chloromelas	409	491	714	662	2276	–	2276	61	2337

Species	12S	16S	cyt-*b*	ND4	Total mtDNA	Rag1	total DNA	morph	total
Bothriopsis medusa	–	–	–	–	0	–	0	61	61
Bothriopsis oligolepis	–	–	635	641	1276	–	1276	56	1332
Bothriopsis pulchra	409	–	716	662	1787	–	1787	87	1874
Bothriopsis taeniata	409	490	716	668	2283	1013	3296	99	3395
Bothrocophias campbelli	–	–	631	663	1294	–	1294	60	1354
Bothrocophias colombianus	–	–	–	–	0	–	0	61	61
Bothrocophias hyoprora	409	490	716	668	2283	873	3156	94	3250
Bothrocophias microphthalmus	409	491	714	663	2277	2199	4476	90	4566
Bothrocophias myersi	–	–	–	–	0	–	0	95	95
Bothropoides alcatraz	–	–	573	–	573	–	573	41	614
Bothropoides diporus	408	489	716	668	2281	1430	3711	67	3778
Bothropoides erythromelas	408	489	716	668	2281	778	3059	61	3120
Bothropoides insularis	409	490	716	668	2283	–	2283	62	2345
Bothropoides jararaca	409	465	602	236	1712	2191	3903	91	3994
Bothropoides lutzi	–	–	–	–	0	–	0	44	44
Bothropoides marmoratus	–	–	–	–	0	–	0	64	64
Bothropoides mattogrossensis	–	–	–	–	0	–	0	92	92
Bothropoides neuwiedi	–	–	639	668	1307	–	1307	96	1403
Bothropoides pauloensis	368	489	692	659	2208	2073	4281	62	4343
Bothropoides pubescens	272	411	122	437	1242	1240	2482	68	2550
Bothrops andianus	377	439	705	587	2108	–	2108	65	2173
Bothrops asper	409	490	715	668	2282	2166	4448	94	4542
Bothrops atrox	409	491	716	663	2279	1186	3465	94	3559
Bothrops barnetti	409	457	604	659	2129	–	2129	60	2189
Bothrops brazili	393	463	711	659	2226	2198	4424	94	4518
Bothrops caribbaeus	–	–	642	662	1304	–	1304	89	1393
Bothrops jararacussu	409	489	716	668	2282	2193	4475	89	4564
Bothrops lanceolatus	–	–	642	662	1304	–	1304	67	1371
Bothrops leucurus	325	484	712	659	2180	1186	3366	62	3428
Bothrops lojanus	–	–	–	–	0	–	0	56	56
Bothrops marajoensis	–	–	642	665	1307	–	1307	8	1315
Bothrops moojeni	407	490	640	535	2072	2199	4271	92	4363
Bothrops osbornei	–	–	642	668	1310	–	1310	56	1366
Bothrops pictus	–	456	631	659	1746	–	1746	65	1811

Species	12S	16S	cyt-*b*	ND4	Total mtDNA	Rag1	total DNA	morph	total
Bothrops punctatus	–	–	642	668	1310	–	1310	89	1399
Bothrops roedingeri	–	–	–	650	650	–	650	8	658
Bothrops sanctaecrucis	–	–	–	–	0	–	0	56	56
Bothrops venezuelensis	–	–	–	–	0	–	0	67	67
Calloselasma rhodostoma	402	491	716	668	2277	1059	3336	98	3434
Causus defilippi	402	480	716	668	2266	1943	4209	67	4276
Causus resimus	402	486	716	668	2272	2199	4471	97	4568
Causus rhombeatus	402	484	716	653	2255	1723	3978	100	4078
Cerastes cerastes	378	402	660	623	2063	832	2895	98	2993
Cerastes gasperettii	350	382	597	–	1329	–	1329	61	1390
Cerrophidion godmani	405	491	711	667	2274	805	3079	92	3171
Cerrophidion petlalcalensis	405	492	708	667	2272	1179	3451	59	3510
Cerrophidion sasai	405	491	716	668	2280	2181	4461	59	4520
Cerrophidion tzotzilorum	367	489	711	667	2234	1178	3412	93	3505
Cerrophidion wilsoni	–	–	708	667	1375	–	1375	91	1466
Crotalus adamanteus	404	490	716	668	2278	807	3085	100	3185
Crotalus aquilus	405	479	544	602	2030	–	2030	98	2128
Crotalus atrox	405	491	716	667	2279	1610	3889	100	3989
Crotalus basiliscus	405	477	563	632	2077	–	2077	100	2177
Crotalus catalinensis	405	477	563	–	1445	–	1445	71	1516
Crotalus cerastes	405	478	565	–	1448	–	1448	100	1548
Crotalus cerberus	–	–	600	629	1229	–	1229	62	1291
Crotalus culminatus	–	–	618	607	1225	–	1225	66	1291
Crotalus durissus	405	478	563	506	1952	1298	3250	100	3350
Crotalus enyo	405	479	559	–	1443	–	1443	100	1543
Crotalus ericsmithi	–	–	–	–	0	–	0	68	68
Crotalus horridus	405	478	564	623	2070	2199	4269	100	4369
Crotalus intermedius	367	457	673	655	2152	2025	4177	73	4250
Crotalus lannomi	–	–	–	–	0	–	0	51	51
Crotalus lepidus	378	478	563	668	2087	2199	4286	98	4384
Crotalus mitchellii	404	478	564	–	1446	–	1446	100	1546
Crotalus molossus	405	491	716	668	2280	1237	3517	100	3617
Crotalus oreganus	405	477	563	629	2074	–	2074	99	2173
Crotalus polystictus	405	476	563	–	1444	–	1444	98	1542

Species	12S	16S	cyt-*b*	ND4	Total mtDNA	Rag1	total DNA	morph	total
Crotalus pricei	405	479	563	–	1447	–	1447	98	1545
Crotalus pusillus	378	479	504	602	1963	–	1963	98	2061
Crotalus ravus	405	489	716	668	2278	897	3175	98	3273
Crotalus ruber	405	478	563	668	2114	–	2114	100	2214
Crotalus scutulatus	405	478	563	629	2075	–	2075	100	2175
Crotalus simus	375	371	660	624	2030	1446	3476	92	3568
Crotalus stejnegeri	–	–	–	–	0	–	0	99	99
Crotalus tancitarensis	–	–	–	–	0	–	0	61	61
Crotalus tigris	405	491	716	666	2278	2115	4393	84	4477
Crotalus totonacus	–	–	618	632	1250	–	1250	68	1318
Crotalus transversus	405	–	274	–	679	–	679	61	740
Crotalus triseriatus	410	479	563	602	2054	873	2927	100	3027
Crotalus tzabcan	–	–	618	632	1250	–	1250	61	1311
Crotalus viridis	401	–	600	629	1630	–	1630	100	1730
Crotalus willardi	405	476	557	638	2076	1817	3893	100	3993
Cryptelytrops albolabris	398	492	638	661	2189	1743	3932	100	4032
Cryptelytrops andersoni	388	446	635	618	2087	–	2087	49	2136
Cryptelytrops cantori	387	464	645	653	2149	870	3019	63	3082
Cryptelytrops cardamomensis	–	–	–	–	0	–	0	55	55
Cryptelytrops erythrurus	372	443	699	616	2130	1226	3356	94	3450
Cryptelytrops fasciatus	383	477	647	641	2148	–	2148	27	2175
Cryptelytrops honsonensis	–	–	–	–	0	–	0	35	35
Cryptelytrops insularis	382	456	685	621	2144	–	2144	81	2225
Cryptelytrops kanburiensis	385	481	587	600	2053	–	2053	63	2116
Cryptelytrops labialis	–	–	–	–	0	–	0	49	49
Cryptelytrops macrops	405	476	646	624	2151	2185	4336	81	4417
Cryptelytrops pupureomaculatus	397	483	707	652	2239	2198	4437	98	4535
Cryptelytrops rubeus	–	–	–	–	0	–	0	71	71
Cryptelytrops septentrionalis	384	476	643	524	2027	–	2027	63	2090
Cryptelytrops venustus	405	475	643	634	2157	–	2157	79	2236
Daboia russelii	–	382	597	–	979	–	979	100	1079
Daboia siamensis	398	490	636	667	2191	2114	4305	68	4373
Deinagkistrodon acutus	393	490	710	668	2261	2161	4422	100	4522
Echis carinatus	372	401	660	620	2053	836	2889	68	2957

Species	12S	16S	cyt-*b*	ND4	Total mtDNA	Rag1	total DNA	morph	total
Echis pyramidum	372	401	660	620	2053	803	2856	68	2924
Garthius chaseni	380	489	640	657	2166	–	2166	61	2227
Gloydius blomhoffii	387	486	716	653	2242	2191	4433	100	4533
Gloydius brevicaudus	397	429	632	640	2098	–	2098	100	2198
Gloydius halys	403	489	716	668	2276	–	2276	98	2374
Gloydius himalayanus	–	–	–	–	0	–	0	66	66
Gloydius intermedius	391	478	701	634	2204	–	2204	98	2302
Gloydius monticola	–	–	309	–	309	–	309	59	368
Gloydius saxatilis	394	464	711	656	2225	2189	4414	93	4507
Gloydius shedaoensis	403	489	708	668	2268	2191	4459	48	4507
Gloydius strauchi	404	490	716	668	2278	2199	4477	74	4551
Gloydius tsushimaensis	394	488	703	662	2247	947	3194	54	3248
Gloydius ussuriensis	404	490	716	668	2278	2096	4374	68	4442
Himalayophis tibetanus	364	482	613	645	2104	–	2104	81	2185
Hypnale hypnale	403	490	716	668	2277	772	3049	71	3120
Hypnale nepa	–	–	–	–	0	–	0	71	71
Hypnale zara	–	–	–	–	0	–	0	71	71
Lachesis acrochorda	407	491	582	658	2138	2191	4329	91	4420
Lachesis melanocephala	–	–	276	252	528	–	528	63	591
Lachesis muta	402	489	716	668	2275	2199	4474	98	4572
Lachesis stenophrys	403	490	716	668	2277	2124	4401	98	4499
Macrovipera lebetina	356	401	597	575	1929	–	1929	68	1997
Mixcoatlus barbouri	385	488	713	653	2239	–	2239	71	2310
Mixcoatlus browni	409	491	660	667	2227	–	2227	70	2297
Mixcoatlus melanurus	405	490	713	668	2276	2199	4475	100	4575
Ophryacus undulatus	346	491	713	668	2218	2199	4417	100	4517
Ovophis monticola	405	461	716	668	2250	2129	4379	98	4477
Ovophis okinavensis	404	490	716	668	2278	2199	4477	100	4577
Parias flavomaculatus	405	477	643	645	2170	–	2170	96	2266
Parias hageni	397	485	619	620	2121	–	2121	81	2202
Parias malcolmi	397	480	318	637	1832	–	1832	61	1893
Parias schultzei	405	477	647	629	2158	–	2158	66	2224
Parias sumatranus	380	461	709	592	2142	–	2142	95	2237
Peltopelor macrolepis	–	–	–	–	0	–	0	77	77

Species	12S	16S	cyt-*b*	ND4	Total mtDNA	Rag1	total DNA	morph	total
Popeia barati	358	459	542	607	1966	–	1966	39	2005
Popeia buniana	376	405	610	610	2001	–	2001	47	2048
Popeia fucata	405	477	609	633	2124	–	2124	61	2185
Popeia nebularis	257	481	570	409	1717	–	1717	66	1783
Popeia popeiorum	395	486	632	662	2175	–	2175	84	2259
Popeia sabahi	385	466	316	666	1833	–	1833	92	1925
Popeia toba	–	–	–	–	0	–	0	59	59
Porthidium arcosae	405	492	716	666	2279	2199	4478	61	4539
Porthidium dunni	405	492	714	668	2279	–	2279	59	2338
Porthidium hespere	–	–	716	665	1381	–	1381	61	1442
Porthidium lansbergii	377	402	618	668	2065	–	2065	61	2126
Porthidium nasutum	405	489	711	668	2273	2199	4472	100	4572
Porthidium ophryomegas	405	490	716	668	2279	1690	3969	99	4068
Porthidium porrasi	405	491	711	667	2274	–	2274	61	2335
Porthidium volcanicum	–	–	–	–	0	–	0	61	61
Porthidium yucatanicum	384	370	711	667	2132	1186	3318	95	3413
Protobothrops cornutus	394	487	635	647	2163	–	2163	50	2213
Protobothrops elegans	405	491	716	668	2280	–	2280	96	2376
Protobothrops flavoviridis	405	491	715	668	2279	–	2279	100	2379
Protobothrops jerdonii	404	492	716	668	2280	–	2280	95	2375
Protobothrops kaulbacki	409	479	702	575	2165	–	2165	61	2226
Protobothrops mangshanensis	385	491	638	659	2173	–	2173	47	2220
Protobothrops maolanensis	–	–	–	–	0	–	0	49	49
Protobothrops mucrosquamatus	397	464	640	657	2158	1985	4143	98	4241
Protobothrops sieversorum	384	491	639	661	2175	–	2175	61	2236
Protobothrops tokarensis	405	491	716	668	2280	2199	4479	76	4555
Protobothrops trungkhanhensis	–	–	–	–	0	–	0	40	40
Protobothrops xiangchengensis	408	480	715	605	2208	–	2208	41	2249
Rhinocerophis alternatus	407	491	716	668	2282	2026	4308	95	4403
Rhinocerophis ammodytoides	409	491	716	659	2275	2188	4463	73	4536
Rhinocerophis cotiara	408	491	716	592	2207	1177	3384	83	3467
Rhinocerophis fonsecai	–	–	642	668	1310	–	1310	56	1366
Rhinocerophis itapetiningae	386	490	708	459	2043	748	2791	80	2871
Rhinocerophis jonathani	–	–	–	–	0	–	0	84	84

Species	12S	16S	cyt-*b*	ND4	Total mtDNA	Rag1	total DNA	morph	total
Sinovipera sichuanensis	408	479	624	648	2159	–	2159	54	2213
Sistrurus catenatus	405	490	716	667	2278	2166	4444	100	4544
Sistrurus miliarius	403	489	716	668	2276	851	3127	100	3227
Trimeresurus andalasensis	–	–	–	–	0	–	0	45	45
Trimeresurus borneensis	398	482	647	657	2184	–	2184	93	2277
Trimeresurus brongersmai	–	–	–	–	0	–	0	66	66
Trimeresurus gracilis	404	491	706	667	2268	2199	4467	91	4558
Trimeresurus gramineus	404	461	647	555	2067	–	2067	63	2130
Trimeresurus malabaricus	401	475	638	512	2026	–	2026	77	2103
Trimeresurus puniceus	404	459	632	522	2017	–	2017	84	2101
Trimeresurus strigatus	–	–	–	–	0	–	0	68	68
Trimeresurus trigonocephalus	375	485	639	629	2128	–	2128	98	2226
Trimeresurus wiroti	–	–	522	–	522	–	522	66	588
Tropidolaemus huttoni	–	–	–	–	0	–	0	47	47
Tropidolaemus laticinctus	–	–	–	–	0	–	0	57	57
Tropidolaemus philippensis	–	–	–	–	0	–	0	61	61
Tropidolaemus subannulatus	404	489	716	668	2277	2186	4463	96	4559
Tropidolaemus wagleri	396	486	708	660	2250	–	2250	93	2343
Vipera ammodytes	372	401	660	623	2056	–	2056	63	2119
Viridovipera gumprechti	399	487	698	662	2246	–	2246	81	2327
Viridovipera medoensis	375	445	646	652	2118	–	2118	68	2186
Viridovipera stejnegeri	391	485	588	662	2126	–	2126	98	2224
Viridovipera truongsonensis	389	466	703	626	2184	–	2184	39	2223
Viridovipera vogeli	393	489	641	661	2184	–	2184	83	2267
Viridovipera yunnanensis	399	480	699	546	2124	–	2124	83	2207
total individuals with data	168	167	190	179	191	97	191	223	223
proportion of individuals with data	0.75	0.75	0.85	0.80	0.86	0.43	0.86	1.00	1.00

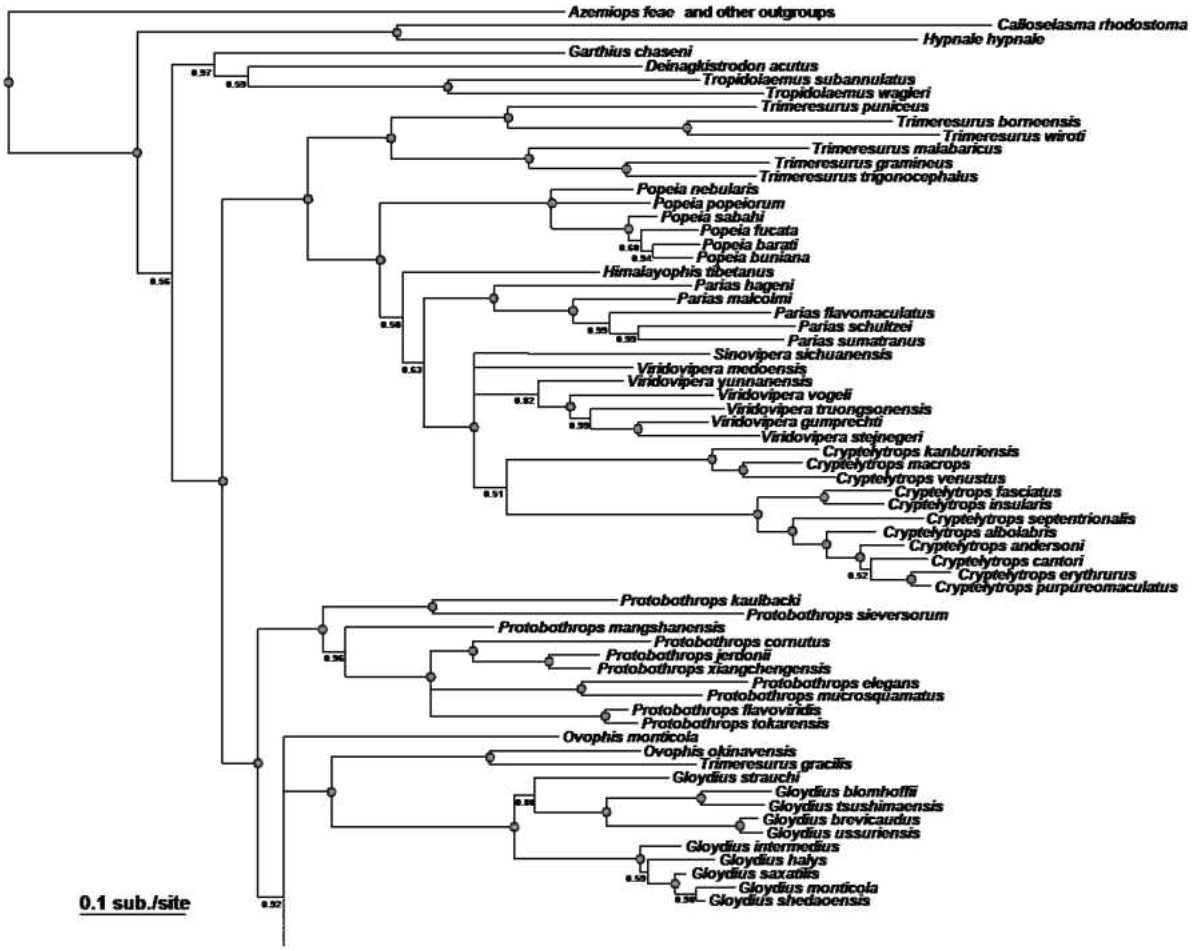


Figure 1. Bayesian MCMC 50% majority rule consensus phylogram compiled from analysis of 2311bp of mitochondrial sequences. Posterior probabilities shown adjacent to nodes; probabilities of 1.0 are indicated by gray-filled circles.

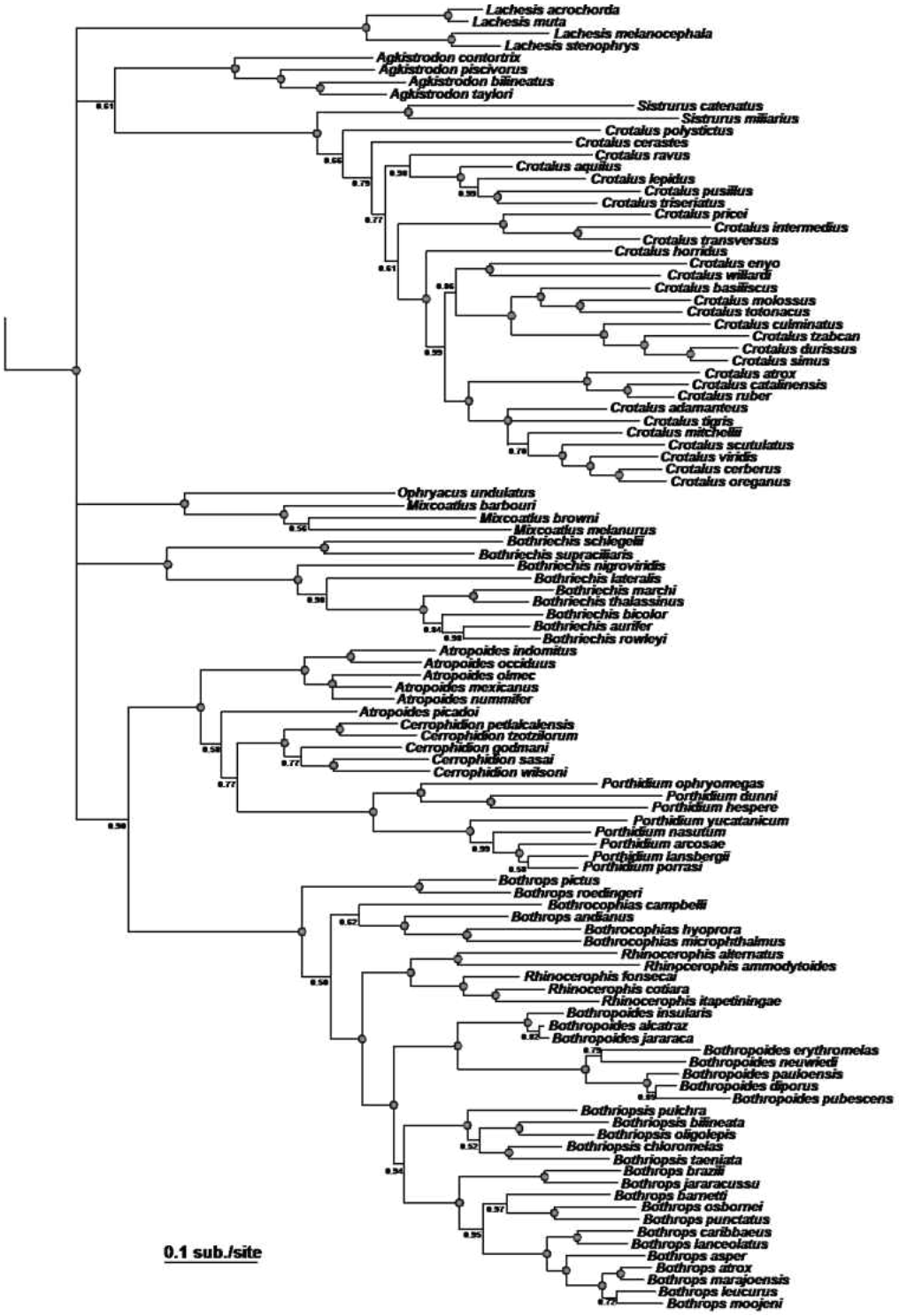


Figure 1 continued

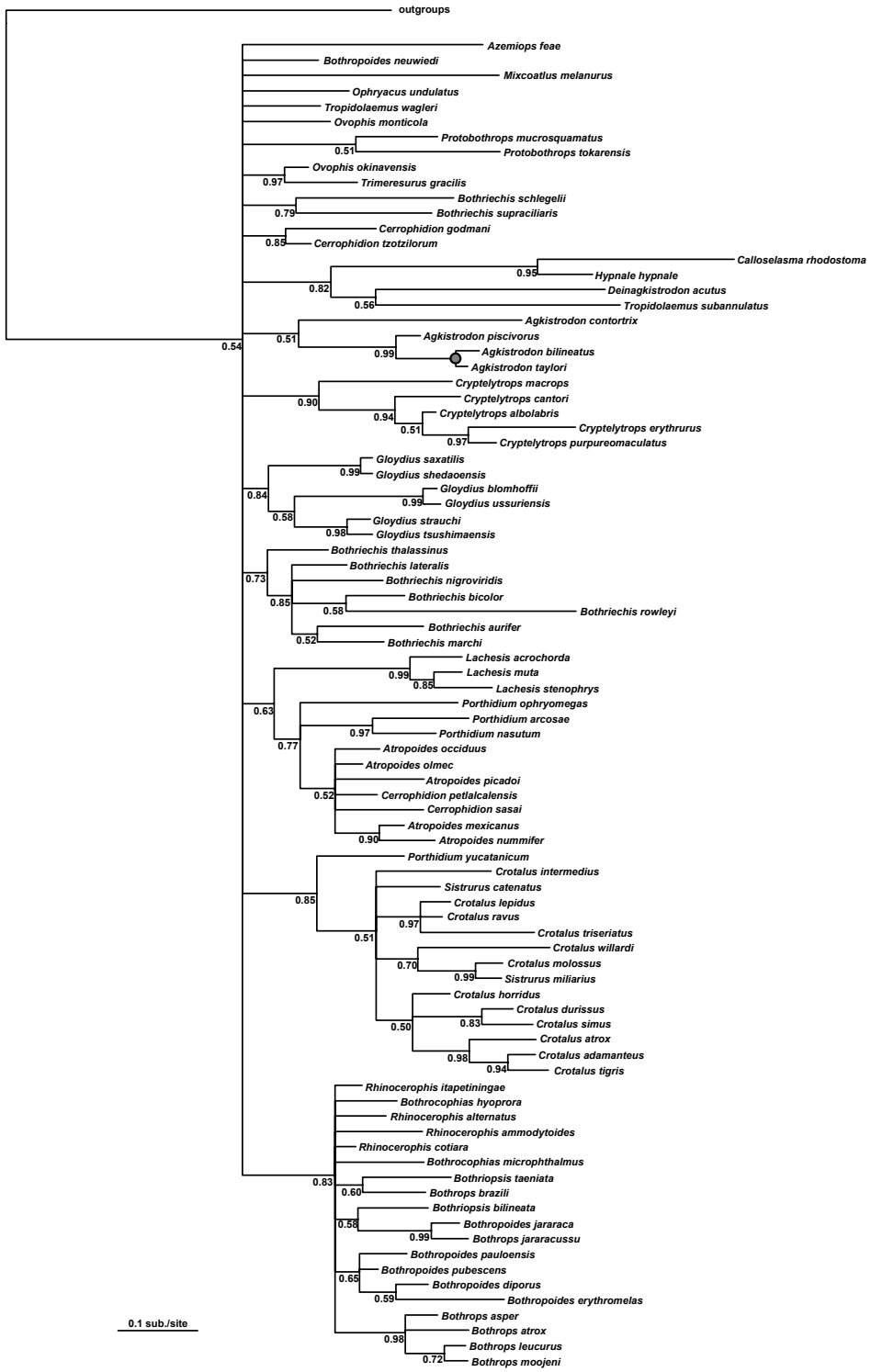


Figure 2. Bayesian MCMC 50% majority rule consensus phylogram compiled from analysis of 2199bp of nuclear sequence of the Rag1 gene. Posterior probabilities shown adjacent to nodes; probabilities of 1.0 are indicated by gray-filled circles. Nodes with less than 50% posterior probability support have been collapsed.

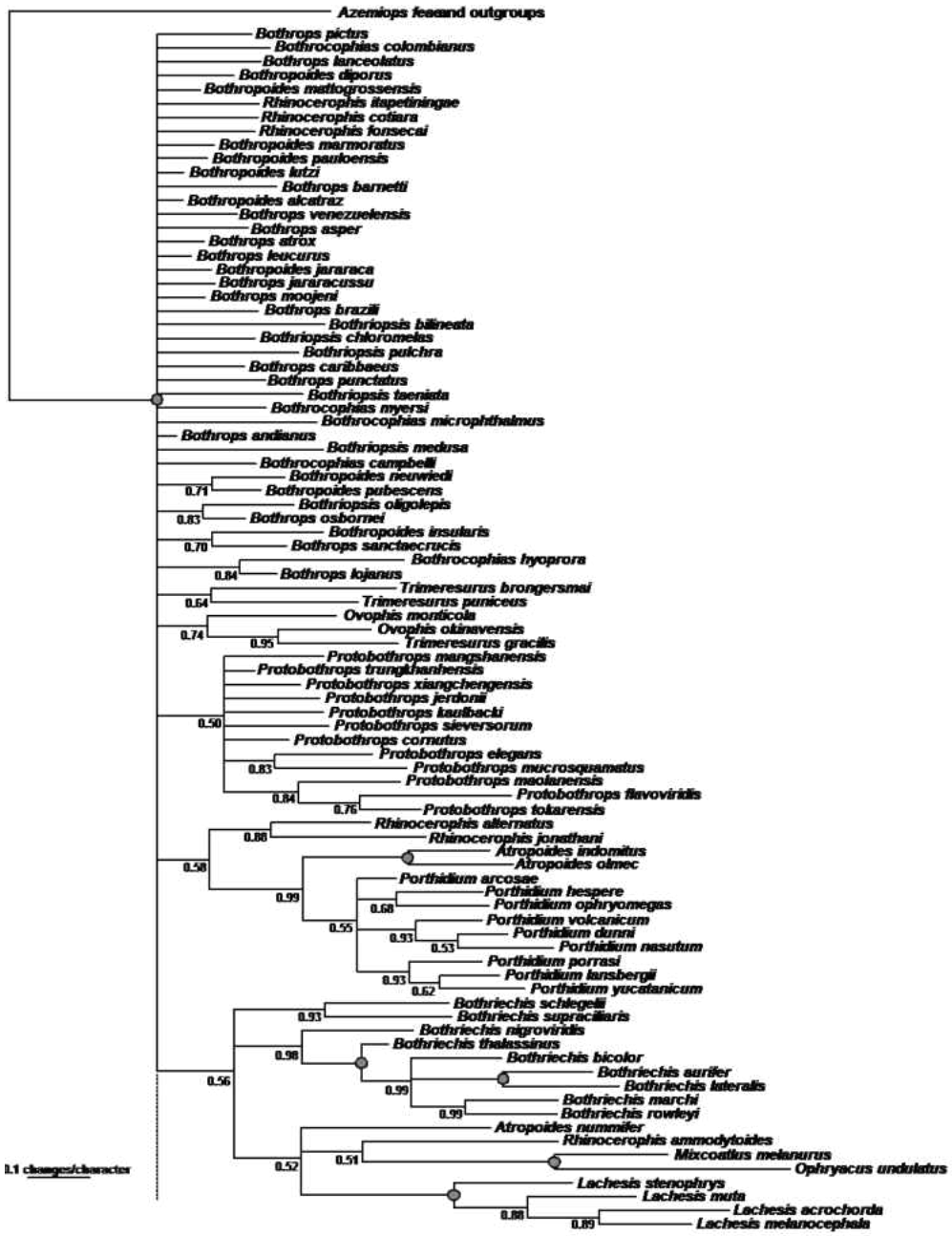


Figure 3. Bayesian MCMC 50% majority rule consensus phylogram compiled from analysis of 100 morphological characters. Posterior probabilities shown adjacent to nodes; probabilities of 1.0 are indicated by gray-filled circles. Nodes with less than 50% posterior probability support have been collapsed.

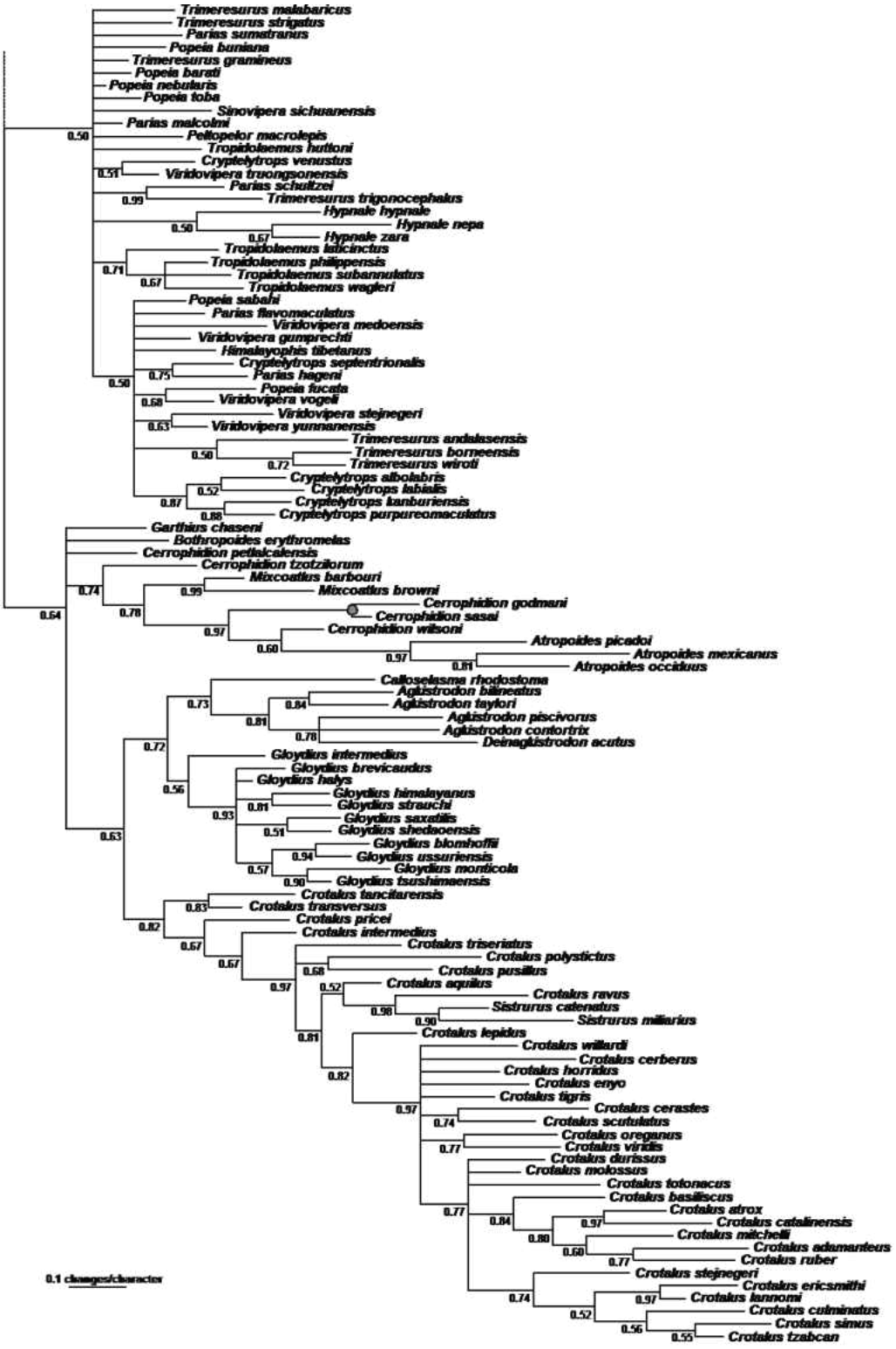


Figure 3 continued

Combined analysis of the two DNA datasets resulted in phylogeny similar to the mtDNA tree (Figure 4). We found one strongly supported incongruence: combined analysis resolved a clade of *Bothriechis bicolor* and *B. rowleyi* (*Pp*=1.0), with *B. aurifer* sister (*Pp*=0.99), but mitochondrial DNA resolved *B. rowleyi* and *B. aurifer* together (*Pp*=0.98), with *B. bicolor* sister (*Pp*=0.84). Overall we found slightly more resolution in combined DNA analysis than mtDNA. For example, we found low support for a clade of *Sinovipera* and *Viridovipera* (*Pp*=0.75) which was lacking in the single-gene analyses. We also found low support for a sister relationship between *Lachesis* and a strongly-supported clade of *Ophryacus* and *Mixcoatlus* (*Pp*=0.75), and moderate support for a sister relationship between this clade and one of North American genera (*Agkistrodon, Crotalus* and *Sistrurus, Pp*=0.90); both sister relationships were not found in single-gene analyses. In fact, in Rag1 analysis *Lachesis* was sister to most *Porthidium, Atropoides,* and *Cerrophidion* species with lower support than in combined DNA analysis (*Pp*=0.63). Combined DNA supported the inclusion of *Atropoides picadoi* with its congeners (*Pp*=0.96), in contrast to low mtDNA support for the species being sister to *Cerrophidion* and *Porthidium* (*Pp*=0.58) and lack of resolution in Rag1 analysis.

The addition of morphology led to reduced resolution compared to DNA-based analyses. We found one strongly-supported conflict with combined DNA in the analysis with Rag1 and morphology (not shown): *Bothriechis aurifer* was sister to *B. lateralis* (*Pp*=1.0) in agreement with morphology (*Pp*=1.0); Rag1 found low support for a clade of *B. aurifer* and *B. marchi* (*Pp*=0.52). We found no strongly-supported conflicts in the analysis with mtDNA and morphology (not shown).

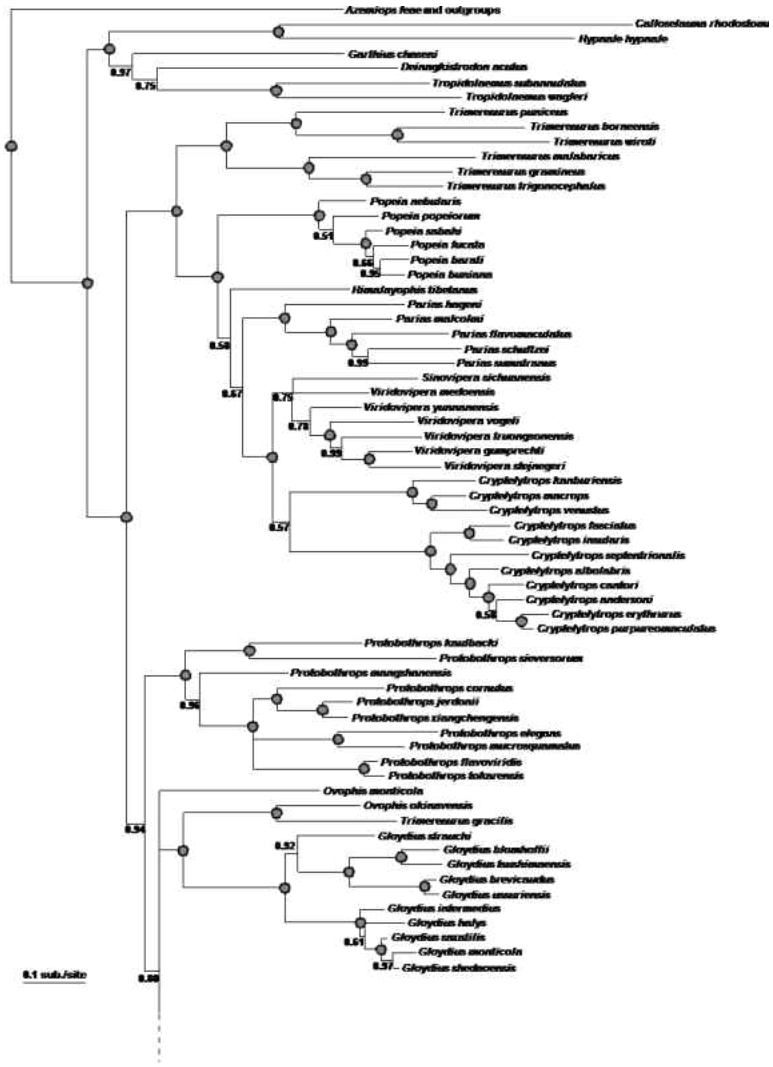


Figure 4. Bayesian MCMC 50% majority rule consensus phylogram compiled from analysis of 2311bp of mitochondrial sequences and 2199bp of nuclear sequence of the Rag1 gene. Posterior probabilities shown adjacent to nodes; probabilities of 1.0 are indicated by gray-filled circles. Nodes with less than 50% posterior probability support have been collapsed.

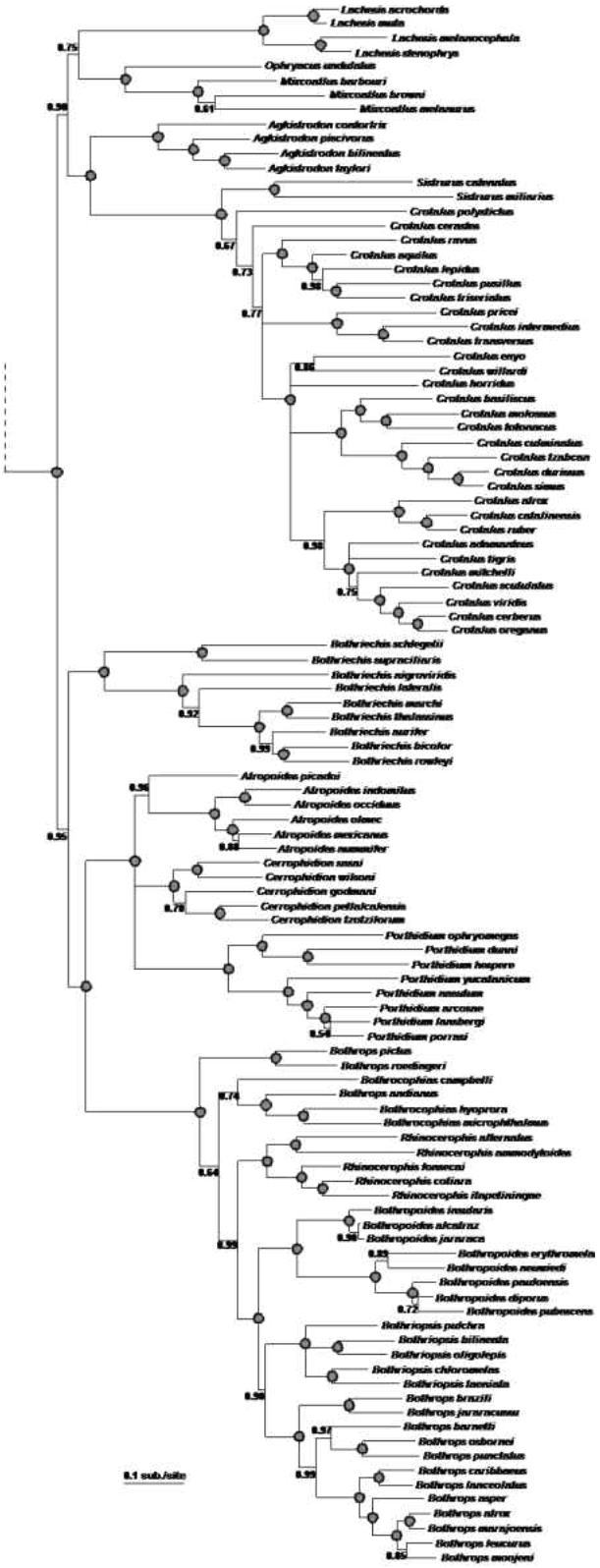


Figure 4 continued

Combining mtDNA, Rag1, and morphological datasets but excluding species with morphological data only led to a phylogeny that had similar resolution to that based on only mtDNA and Rag1 (Figure 5). This is our preferred analysis for resolution of genera and of species that are at least partially complete for the DNA matrix. We find strong support (*Pp*=1.0) for monophyly of all genera except *Viridovipera* (*Pp*=0.75), *Cryptelytrops* (*Pp*=0.74), *Crotalus* (*Pp*=0.92), and *Bothrocophias* (*Pp*=0.99).

Inclusion of species represented by morphological data only led to decreased resolution compared to molecular analyses, but we again found no strongly supported incongruence among the analyses (Figure 6). We found strong support for eight genera and moderate support for one, with low support for *Hypnale* (*Pp*=0.52), *Tropidolaemus* (*Pp*=0.50), *Protobothrops* (*Pp*=0.54), *Bothriechis* (*Pp*=0.66), *Porthidium* (*Pp*=0.69), eight species of *Cryptelytrops* (*Pp*=0.50), eight species of *Bothropoides* (*Pp*=0.52), and thirteen species of *Bothrops* (*Pp*=0.63). We also found low support for two clades of *Trimeresurus* excluding *T. strigatus* and *T. brongersmai* (*Pp*=0.70 and 0.52) and two clades of *Rhinocerophis* excluding *R. alternatus* (*Pp*=0.60 and 0.62). Monophyly of *Crotalus* was not supported but most species groups had some support. Finally, we found strong support for *Ovophis okinavensis* + *Trimeresurus gracilis* (*Pp*=1.0) and *Crotalus enyo + C. willardi* (*Pp*=0.99), with low support for *Bothrops pictus + B. roedingeri* (*Pp*=0.82) and three species of *Bothrocophias* plus *Bothrops andianus* and *B. lojanus* (*Pp*=0.62).

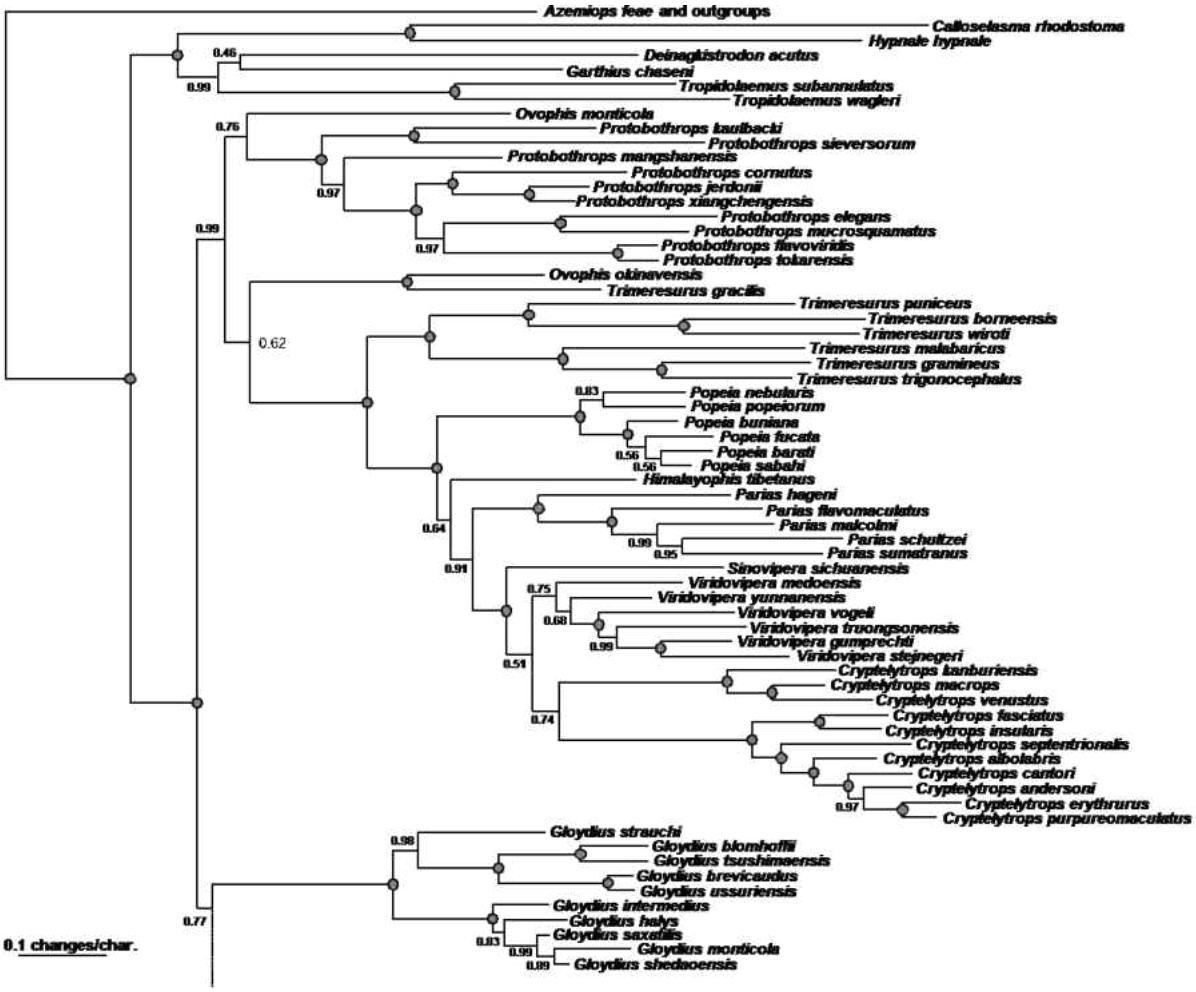


Figure 5. Bayesian MCMC 50% majority rule consensus phylogram compiled from analysis of 2311bp of mitochondrial sequences, 2199bp of nuclear sequence of the Rag1 gene, and 100 morphological characters. Only species represented by DNA data are included; this is the preferred analysis for systematic interpretation. Posterior probabilities shown adjacent to nodes; probabilities of 1.0 are indicated by gray-filled circles. Nodes with less than 50% posterior probability support have been collapsed.

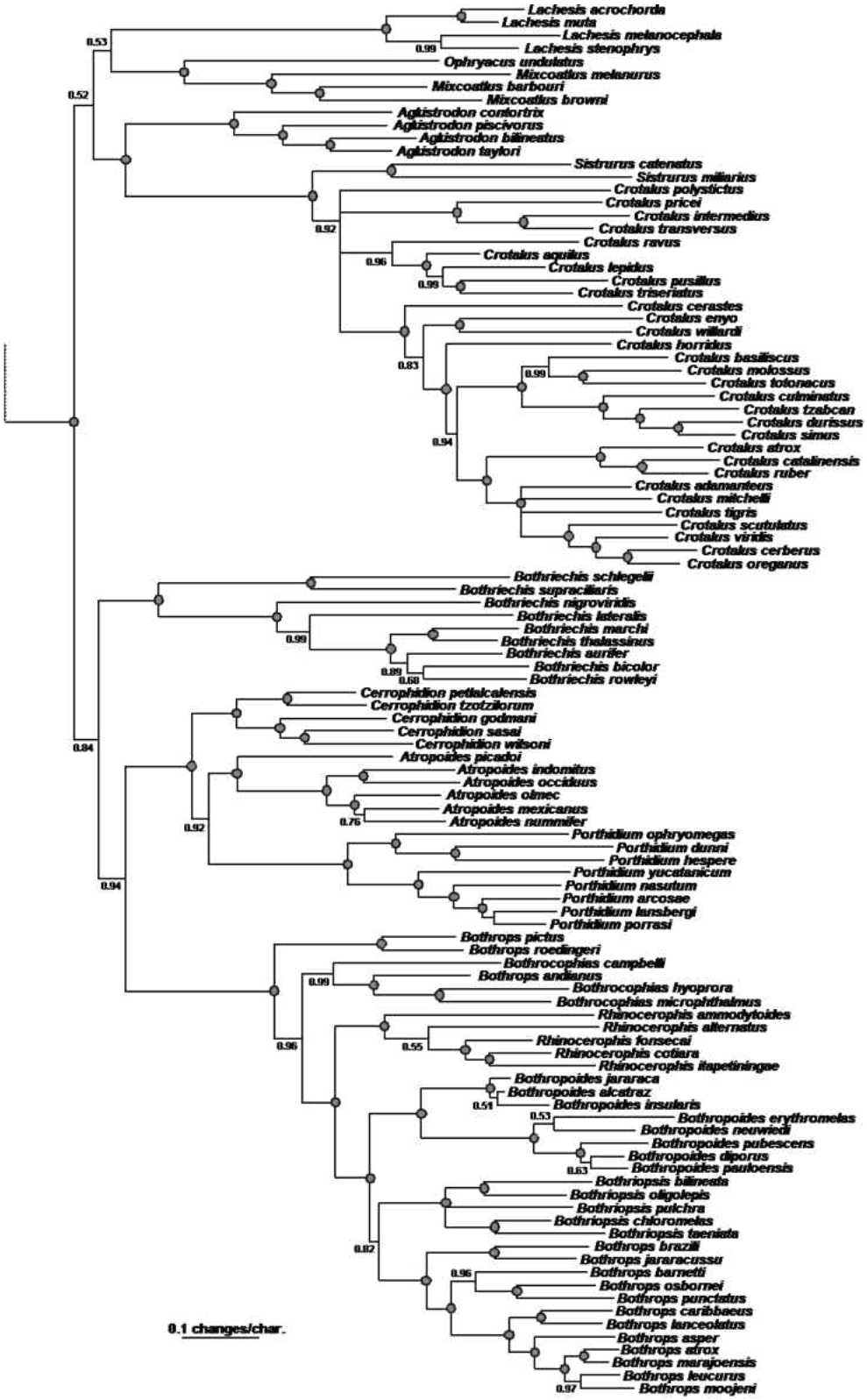


Figure 5 continued.

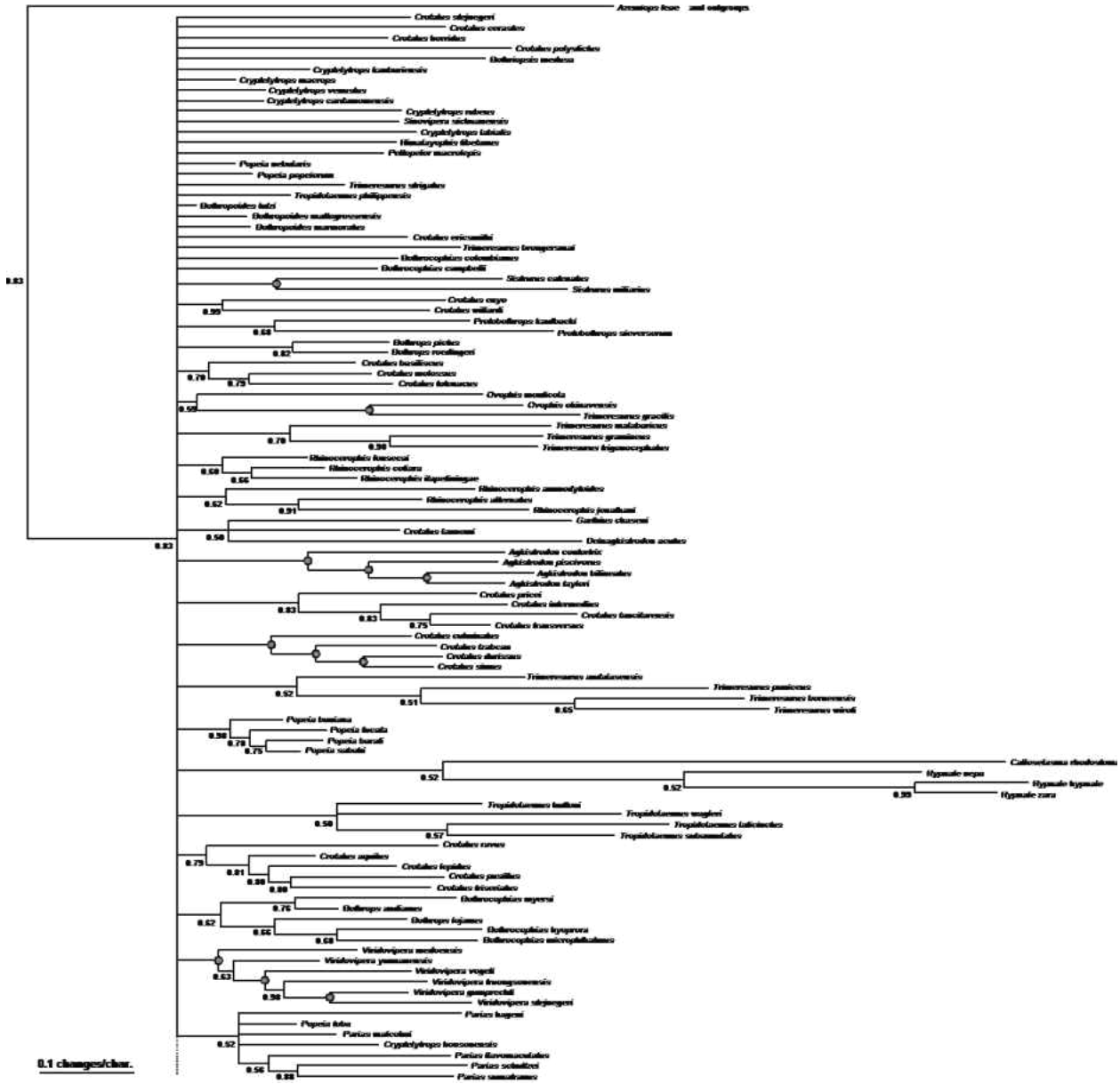


Figure 6. Bayesian MCMC 50% majority rule consensus phylogram compiled from analysis of 2311bp of mitochondrial sequences, 2199bp of nuclear sequence of the Rag1 gene, and 100 morphological characters. All available species are represented, including species complete for morphological characters only. Posterior probabilities shown adjacent to nodes; probabilities of 1.0 are indicated by gray-filled circles. Nodes with less than 50% posterior probability support have been collapsed.

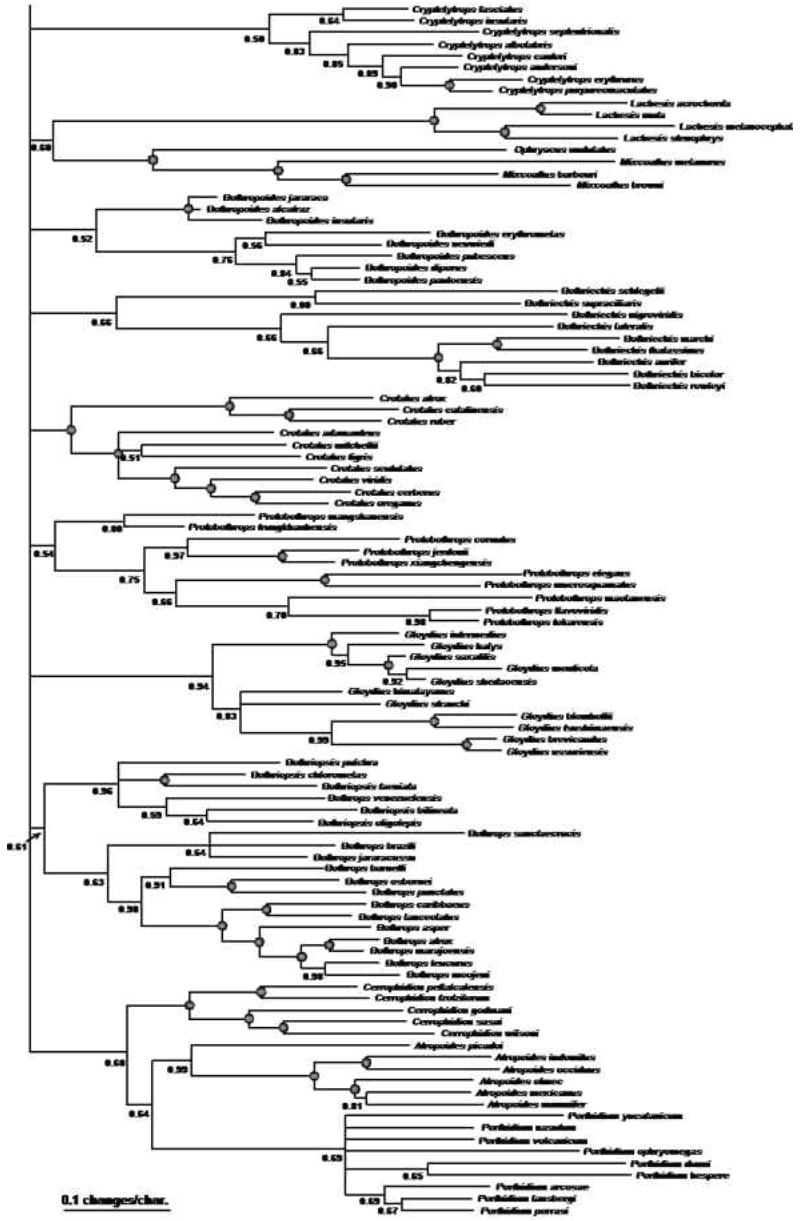


Figure 6 continued

We investigated how the completeness of a species affected its placement in the tree based on combined mtDNA, Rag1, and morphology and using all taxa. The morphological matrix represented 2.2% of the dataset, and the 32 species that were represented by morphology only made up 14% of taxa. These morphology-only species were disproportionately represented among the unresolved terminals, making up 56% of these branches (Figure 7). Considering this group of species alone, 14 were unresolved (44%) and four were in groups inconsistent with their taxonomy (12%). However, 14 species were in groups consistent with their taxonomy (44%). The pattern held when considering the four species with 1% or less of the data matrix complete: one species was unresolved, one was in an unexpected group based on taxonomy, but two were in groups consistent with their taxonomy. Analysis of all taxa except those with less than 1% of the data matrix represented failed to converge after $1x10^7$ generations (phylogram not shown).

As expected from the morphological data-only results, species with 10% or less matrix completeness were overrepresented in the unresolved taxa (Figure 7). Although unresolved taxa made up 11% of the tree, 42% of the minimally-complete species were unresolved. Species with 90% or more matrix completeness were underrepresented, with only 3% of the maximally complete species being unresolved. Species of intermediate completeness among unresolved species were generally found in proportion to their presence in the dataset overall.

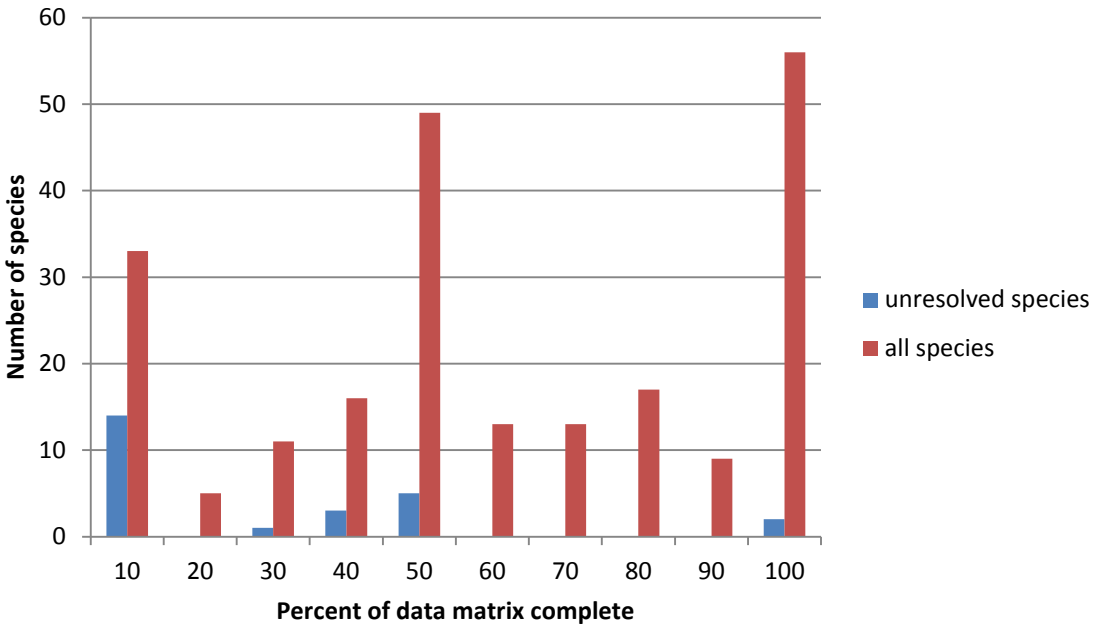


Figure 7. Histogram of data completeness for all species included in study compared to completeness for unresolved species. Minimally complete species are overrepresented among unresolved species and maximally complete species are underrepresented.

We also discovered that the inclusion of highly incomplete taxa had a negative effect on support of genus-level clades (Table 4). On average, genera with more than one species included in the analysis had posterior probability support of 0.92, but only had support of 0.52 with the inclusion of the complete morphological dataset. In every case, the addition of highly incomplete species decreased support for monophyly of the genus, and in half of the cases genera were not recovered as monophyletic in combined DNA and morphological analysis. Of the nine genera in which all species had DNA data, the addition of morphology maintained support in six cases, increased support in one case and decreased it in a second. In only one case did the addition of morphology result in a genus not being recovered in the majority-rule phylogram.

Table 4. Relationship of data matrix completeness to support for generic-level clades. Minimum completeness is measured as the minimum proportion of the DNA matrix (4510 characters) complete for any species in the group with DNA data, or the minimum proportion of the total matrix (4610 characters) complete for any species in the group. For groups including species with morphological data only, analysis of those species results in a decrease in support for that group. For groups where all species have DNA data, only two groups have decreased support with the addition of morphology, two have increased support, and the rest are unchanged.

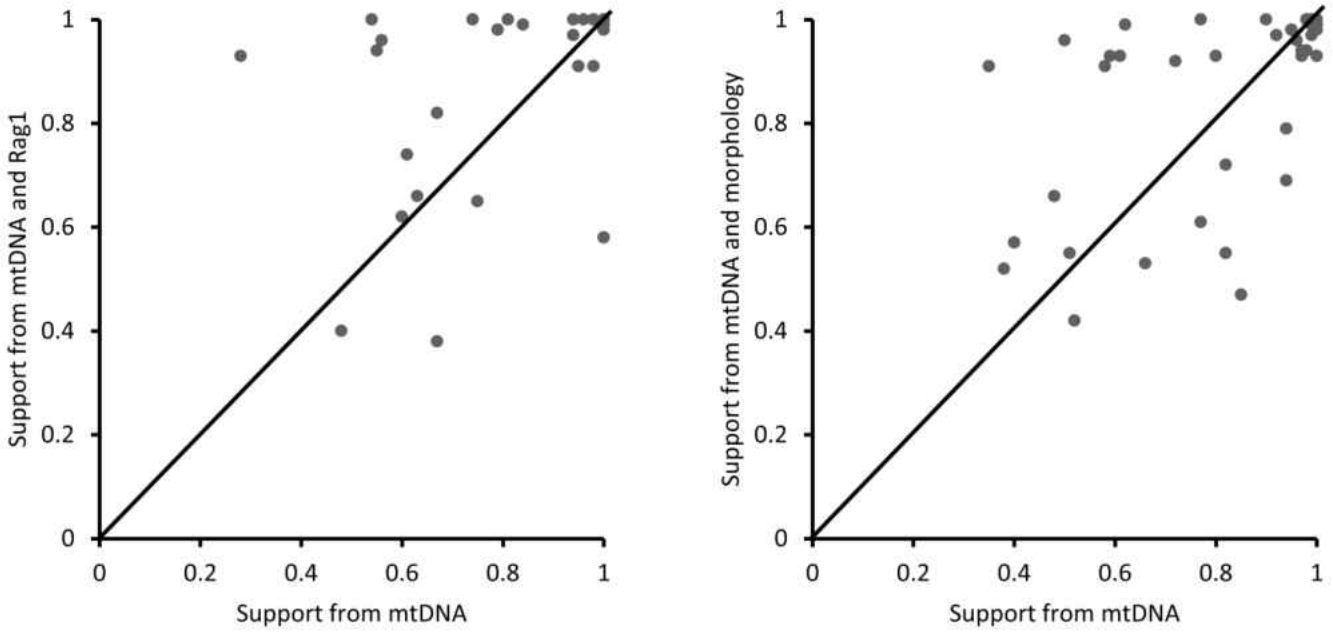
Genus	DNA support	Minimum DNA completeness	Combined support	Minimum overall completeness
Groups including species with morphological data only				
Bothriopsis	1.00	0.283	0.96*	0.013
Bothrocophias	0.74	0.287	0.23*	0.013
Bothropoides	1.00	0.127	–	0.010
Bothrops	1.00	0.144	0.63	0.012
Crotalus	0.67	0.150	–	0.011
Cryptelytrops	0.57	0.449	–	0.008
Gloydius	1.00	0.068	0.94	0.014
Hypnale	n/a, single ind.	0.676	0.52	0.015
Popeia	1.00	0.381	–	0.013
Porthidium	1.00	0.306	0.69	0.013
Protobothrops	1.00	0.480	0.40	0.009
Rhinocerophis	1.00	0.290	–	0.018
Trimeresurus	1.00	0.116	–	0.010
Tropidolaemus	1.00	0.499	–	0.010
Groups where all species have DNA data				
Agkistrodon	1.00	0.990	1.00	0.990
Atropoides	0.96	0.392	0.99	0.398
Bothriechis	1.00	0.880	0.66	0.880
Cerrophidion	1.00	0.305	1.00	0.318
Lachesis	1.00	0.117	1.00	0.128
Mixcoatlus	1.00	0.494	1.00	0.498
Parias	1.00	0.406	–	0.411
Sistrurus	1.00	0.693	1.00	0.700
Viridovipera	0.35	0.470	1.00	0.474
Average	0.92	0.391	0.52	0.216

* indicates genera include species of questionable taxonomic assignment

– indicates clades do not exist in majority rule phylogram

We compared analyses with the same number of species but different datasets. In 55 of 80 nodes (68%) for nuclear gene Rag1 and 105 of 146 nodes (72%) for morphology, relationships were strongly supported by mtDNA (*Pp*=1.0) and the addition of a dataset did not change the values (Figure 8). Two other nodes had strong support with no change after addition of morphology (*Pp*=0.99, 0.96). We classify strong support

as posterior probabilities 0.95–1, moderate support 0.90–0.94 and low support ≤0.89. Overall, the addition of Rag1 increased support for 17 nodes, and decreased support for only eight nodes. We found six increases from low to high values (*Pp*=0.54 to 1, 0.56 to 0.96, 0.74 to 1, 0.79 to 0.98, 0.81 to 1, and 0.84 to 0.99), two increases from low to moderate values (*Pp*=0.28 to 0.93 and 0.55 to 0.94), and two increases from moderate to high values (*Pp*=0.94 to 97 and 0.94 to 1). In four cases support increased but values stayed low, and in three cases support was high and increased. One node was strongly supported by mtDNA and decreased with the addition of Rag1 (*Pp*=1 to 0.58), and two others decreased from strong to moderate support (*Pp*=0.95 to 0.91 and 0.98 to 0.91). In two cases values decreased but remained high, and in three others values were low and decreased.



(a) (b)

Figure 8. Comparison of nodal posterior probability support between Bayesian analysis of mitochondrial DNA of pitvipers and analysis of same species but additional data: (a) nuclear gene Rag1, (b) morphological characters. Values on 1:1 axis represent no change with addition of dataset, values above axis represent increased support with addition of data, and values below axis represent decreased support with addition of data. Addition of nuclear data results in a net increase of node support, but morphology yields no net benefit to nodal support.

Overall, the addition of morphology resulted in increased support for 20 nodes and decreased support for 21 nodes. We found three increases from low to high values (*Pp*=0.50 to 0.96, 0.62 to 0.99, 0.77 to 1.0), six increases from low to moderate values (*Pp*=0.35 to 0.91, 0.58 to 0.91, 0.59 to 0.93, 0.61 to 0.93, 0.72 to 0.92, 0.80 to 0.93), and two increases from moderate to high values (*Pp*=0.90 to 1.0 and 0.92 to 0.97). Four nodes increased but remained poorly supported, and five nodes had strong support and increased. In no cases did support decrease from high to low values, but we found four decreases from strong to moderate support (*Pp*=1.0 to 0.93, 0.98 to 0.94, 0.97 to 0.94, 0.97 to 0.93), and two decreases from moderate to low support (*Pp*=0.94 to 0.69 and 0.94 to 0.79). Seven nodes decreased but retained strong support, and six nodes had low support and decreased.

Discussion

Taxon sampling

In contrast to the many studies finding increased accuracy with increased taxon sampling (Graybeal, 1998; e.g. Huelsenbeck, 1995; Kim, 1998; Poe and Swofford, 1999; Rannala et al., 1998), we find lowered resolution of our phylogeny with maximum taxon sampling. This is likely an issue of inclusion of taxa with minimal data, below the theoretical threshold cited by Wiens (2003) for accurate placement in phylogeny. Wiens and Morrill (2011) reviewed multiple empirical examples which found incomplete taxa consistently placed into expected genus- or higher-level taxa, often with strong support.

Huelsenbeck (1991) recovered relationships for eight taxa based on 100 simulated characters, and found taxa with only 25 characters were problematic in parsimony analysis. Wiens and Reeder (1995) found supporting evidence with a similarly small dataset. Wiens and Morrill (2011) review a number of examples that support the assertion that large amounts of missing data are mainly problematic when the overall number of characters is small. They also find, in an analysis of eight empirical datasets, that only two showed a significant positive relationship between completeness and branch support, suggesting that missing data are not necessarily a problem.

In our empirical example of far more taxa and more characters, we focus on species with 46 or fewer complete characters (1% of the dataset), 100 or fewer (2.2%), and 461 or fewer (10%). We find that inclusion of highly incomplete species had a detrimental effect on genus-level support in all cases (Table 4). This was not due to the inclusion of morphology, because the analysis including only species with greater than 2.2% of the dataset complete resolved strong support for all except three genera, and moderate support for one of these groups. Analysis including species with greater than 1% of the dataset represented failed to converge after twice the number of generations sampled in most analyses, suggesting that some taxa still included were problematic to analysis.

Dragoo and Honeycutt (1997) suggested that the effect of missing data on species placement may relate more to the relationships of taxa involved and phylogenetic signal in the dataset than to the amount of missing data, and our results reflect this assertion. Clades supported by many characters from certain datasets may

be able to withstand the addition of taxa with large amounts of missing data while maintaining their phylogenetic positions (Dragoo and Honeycutt, 1997). In our work, we find that addition of highly incomplete taxa was detrimental in all cases even though most genera had full posterior probability support from DNA evidence (Table 4). This suggests the negative effects of the incomplete taxa overwhelmed any effects of relationships.

Interestingly, we do not find patterns that allow one to distinguish which highly incomplete taxa will be problematic in analysis. Slightly less than half of species with morphological data only were placed in the correct genera, and this pattern held for species represented by less than 1% of the entire dataset, or 46 characters. This suggests that these taxa should not be excluded prior to analysis.

Missing data may be more problematic when a taxon has no close relatives (Dragoo and Honeycutt, 1997). This is a particular issue for one monotypic genus in this study: *Peltopelor.* The phylogenetic placement of *Peltopelor macrolepis* has been of recent interest, with Malhotra and Thorpe (2004) suggesting it is closely related to *Popeia* based on hemipenial morphology, and Guo et al. (Guo et al., 2010) suggesting it is related to *Trimeresurus* or *Cryptelytrops* based on skull morphology. This is the first study to include *Peltopelor macrolepis* in phylogenetic analysis, and we find it unresolved in combined morphology and DNA analysis. Based on morphology alone, we find low support for its inclusion in a group with several genera of Asian pitvipers (*Pp*=0.50). As an example of a way to treat limited-data species, we conducted one analysis based on combined evidence using all taxa represented by DNA data plus *P.*

macrolepis (phylogram not shown), and recovered it within *Cryptelytrops* with low support (*Pp*=0.43), sister to *C. macrops* and *C. venustus* with low support (*Pp*=0.62). This suggests that inclusion of limited-data species one at a time may not always be informative.

Combining datasets

As more loci and other characters sets are used in phylogenetics, the issue of combinability is increasingly important. The simplest strategy for resolving conflict among datasets is to follow Kluge's (1989) call to use total evidence in combined analysis. Some suggest this is the best method even when a problematic data partition is successfully identified (Baker and DeSalle, 1997), and this is the method we follow in this study. Using observations of incongruence among single-locus phylogenies, we find little conflict among our datasets, and we do not observe loss of resolution in conjunction with combining these datasets. This suggests that in future when genomic methods are available for large numbers of pitvipers, the information will be able to be analyzed with little conflict. It also supports the combinability of morphological with molecular data in phylogenetic analysis, in contrast to the practice in Asian pitviper studies of estimating evolutionary relationships with DNA data and using morphology only in multivariate statistical analysis to define distinct morphotypes (e.g. Malhotra et al., 2011a).

With the potential problems of adding taxa based on a limited number of phenotypic characters (e.g. Lemmon et al., 2009), it may be tempting to infer the phylogenetic positions of these taxa from analyses of morphology only. This approach

has been refuted by simulation and empirical studies (Wiens and Reeder, 1995; Wiens, 2009; Wiens et al., 2010) that found molecular data mainly benefited the accuracy of placing fossil taxa in phylogeny. Our results did not find major changes in placement of taxa with DNA data with the addition of morphological data and species lacking DNA, but the differences in resolution and support between the tree based on morphology (Figure 3) and that based on three independent datasets (Figure 6) support the inclusion of molecular data with phenotypic characters when available.

Wiens et al. (2005) found that adding an incomplete set of nuclear data to a mitochondrial dataset seemed to improve the results. In our study, we added the nuclear gene Rag1, which was sequenced for 43% of species, and was on average 79% complete for those terminals. In agreement with Wiens et al. (2005), we find a small beneficial effect of adding our incomplete nuclear gene to the dataset, with an increase in mean posterior probability from 0.928 to 0.955. We find increases in support for twice the number of nodes that had decreases in support, with eight nodes increasing to strong confidence in relationships but only three nodes losing strong support. We find some increase in variability of support values with the addition of morphological data, but no net positive or negative effect.

Pitviper phylogenetic relationships

Newly described species

Two genera and many species have been described since the publication of the most recent pitviper phylogenies (Castoe and Parkinson, 2006; Pyron et al., 2011).

Several of these descriptions were not accompanied by DNA sequences and most have not been included in phylogenetic analysis. Below we discuss the placement of newly recognized species included in large-scale phylogeny for the first time. We focus on combined evidence analysis excluding taxa with morphology only because the analysis with maximal taxa lacked resolution, but we discuss results of other analyses when alternate relationships are supported.

For genera and species in which mitochondrial data have been analyzed, our combined mtDNA, nuclear and morphological analysis generally supports prior results. We find *Sinovipera* sister to a clade of *Viridovipera* and *Cryptelytrops* (Guo and Wang, 2011), and we support the monophyly of *Mixcoatlus* (Jadin et al., 2011). We find *Atropoides indomitus* sister to *A. occiduus* (Smith and Ferrari-Castro, 2008). We find *Popeia buniana* related to *P. fucata*, *P. sabahi,* and *P. barati* (Grismer et al., 2006; Sanders et al., 2006), although this does not support subsuming all of these species under the name *P. sabahi* as suggested by Sanders et al. (2006).

In two cases, our combined evidence results do not agree with prior work. Jadin et al. (2012) elevated two lineages formerly described as *Cerrophidion godmani* to species status: *C. sasai* and *C. wilsoni*. They found *C. godmani s.s.* sister to *C. petlalcalensis* and *C. tzotzilorum*, with a clade of *C. sasai* and *C. wilsoni* sister to that group. We find the same relationships in combined DNA analysis, but find strong support for a clade of *C. godmani, C. wilsoni* and *C. sasai* in combined DNA and morphological analysis. Second, *Protobothrops maolanensis* was described on the basis of morphology (Yang et al., 2011), and its phylogenetic position was recently evaluated

on the basis of mtDNA (Liu et al., 2012). Although their molecular data were unavailable for this study, we evaluate the phylogenetic position of this species on the basis of morphology, the first time its phenotype was included in phylogenetic analysis. Liu et al. (2012) found strong support for the inclusion of *P. maolanensis* in a clade with *P. mucrosquamatus* and *P. elegans*. In combined analysis with all available taxa we find *P. maolanensis* sister to *P. flavoviridis* and *P. tokarensis* with low support (*Pp*=0.70), with this clade sister to *P. mucrosquamatus* and *P. elegans* with low support (*Pp*=0.66). This relationship may change with the combination of molecular and morphological data.

Our phylogenetic results for species described on the basis of phenotype alone agree less with prior work than the results described above. We find no supported phylogenetic position for *Bothropoides marmoratus* (Silva and Rodrigues, 2008). We find strong support for a sister relationship between newly described longtail rattlesnake *Crotalus ericsmithi* and equally rare *C. lannomi*, but no support for a clade including the third species of longtailed rattlesnake, *C. stejnegeri*, a relationship expected by Campbell and Flores-Villela (2008). In combined evidence analysis these relationships break down, but in analysis of rattlesnakes alone (Fenwick, Diamond, LaDuc, and Parkinson, unpub. data), a clade of all three longtailed species has low support (*Pp*=0.87).

The last few years were especially fruitful for species descriptions of Asian pitvipers. We find low combined evidence support for a sister relationship between *Tropidolaemus laticinctus* and *T. subannulatus* as expected by Kuch et al. (2007), but find *T. laticinctus* sister to *T. subannulatus, T. philippensis,* and *T. wagleri* based on morphology alone. We find *P. trungkhanhensis* sister to *P. mangshanensis* with low

support (*Pp*=0.80), in disagreement with Orlov et al. (2009) and Yang et al. (2011). We find *Trimeresurus andalasensis* part of a *T. puniceus* group, sister to that species*, T. borneensis,* and *T. wiroti*, in partial agreement with describers David et al. (2006). *Popeia toba* was described for a group from northern Sumatra closely related to *P. sabahi* (David et al., 2009), and *Cryptelytrops honsonensis* was described from southern Vietnam phenotypically similar to *C. venustus* (Grismer et al., 2008). In combined analysis we found low support for a clade of these new species and *Parias* lineages (Pp=0.52), in disagreement with both describers. In morphological analysis we found low support for their inclusion in a clade of a number of Asian pitvipers (Pp=0.50). Malhotra et al. (2011b) described *Cryptelytrops cardamomensis* and *C. rubeus*, mentioning they were morphologically similar to *C. macrops*. Based on phylogenetic analysis of morphology we find strong support for a sister relationship between the two newly described species (*Pp*=0.98), but strangely find *P. popeiorum* sister to this clade with strong support (0.98) and only find low support for *Cryptelytrops macrops* and *C. erythrurus* sister to these species (*Pp*=0.41). Combined molecular and morphological analysis did not resolve the phylogenetic positions of these species.

A few species have been described very recently, and we could not collect data in time to include them in the current analysis: *Bothrops ayerbi* (Folleco-Fernández, 2010; in Spanish)*, Gloydius lianjilii* (Jiang and Zhao, 2009; in Chinese)*,* and *Popeia phuketensis* (Sumontha et al., 2011). We look forward to evaluating their evolutionary relationships in the future.

Ongoing issues in pitviper phylogeny

One of the longstanding questions in pitviper phylogeny is which groups diverged first in the evolution of pitvipers. Based on combined DNA data we find strong support for a basal clade of pitvipers (*Pp*=1.0) containing a subclade of *Calloselasma* and *Hypnale* (*Pp*=1.0) and another subclade of *Garthius, Deinagkistrodon,* and *Tropidolaemus* (*Pp*=0.99). This clade is supported in both full-dataset and taxon-limited analyses, and when data-limited taxa are excluded it is sister to a clade of all other pitvipers. This topology is in agreement with Castoe and Parkinson (2006) and Pyron et al. (2011).

A second question has been the sister group to the clade of New World pitvipers. Malhotra et al. (2010) supported *Gloydius* as the sister group, but with sparse sampling of New World species and had strong support with only one of their methods of coding introns. Based on combined evidence with some taxa excluded we find low support for *Gloydius* as the sister group (*Pp*=0.77). Based on DNA evidence we find low support (*Pp*=0.80) for a clade of *Gloydius* and *Trimeresurus gracilis* + *Ovophis okinavensis* or for *Ovophis monticola* to be sister to New World pitvipers. We find moderate support (*Pp*=0.94) for either of these clades or *Protobothrops* to be sister to the American radiation. These constitute all of the previously proposed sister groups for American vipers (Malhotra et al., 2010). We expect additional sampling of nuclear loci will be the most effective way to resolve this relationship.

The species *Trimeresurus gracilis* and *Ovophis okinavensis* are in need of taxonomic revision, as their phylogenetic positions sister to each other and separate

from their currently-assigned genera are well understood based on mtDNA data (e.g. Malhotra and Thorpe, 2004). Malhotra and Thorpe (2004) suggested these species could be included with *Gloydius*, but investigation was ongoing. We find strong support for the clade of *T. gracilis* and *O. okinavensis* in all analyses, but only found the sister relationship to *Gloydius* in mtDNA (*Pp*=1.0), combined mtDNA and nuclear (*Pp*=1.0), and combined mtDNA and morphological analyses (*Pp*=0.67). Rag1 alone did not recover support for a sister group to this clade, and Rag1 with morphology found it in a group of several Asian genera. Morphological and combined morphological and DNA data with all taxa recovered the group sister to *Ovophis monticola* with low support (*Pp*=0.74 and 0.59, respectively). Combined morphological and DNA data with some taxa excluded resolved this clade in a group with *Protobothrops* and the genera of the *Trimeresurus* group elevated by Malhotra and Thorpe (2004). This clade may deserve its own genus-level designation and we encourage continued investigation into these relationships.

The assignment of *Atropoides picadoi* to its current genus has been problematic, as mitochondrial data placed it sister to *Porthidium* and *Cerrophidion* (Castoe and Parkinson, 2006) or included it in *Atropoides* with low support (Castoe et al., 2009; Castoe et al., 2005). Our mtDNA results find low support for the pattern of Castoe and Parkinson (*Pp*=0.58). The most recent morphological analysis recovered *A. picadoi* sister to the other *Atropoides* species with strong support (Jadin et al., 2010). We contribute nuclear data and combined evidence analysis to this case, and although we find only low Rag1 support for a clade of *Atropoides* including *A. picadoi* along with *Cerrophidion* species (*Pp*=0.52), we find combined mitochondrial, nuclear and morphological data

strongly support the inclusion of *A. picadoi* in its current genus with all taxa or with some excluded (*Pp*=0.97 and 1.0, respectively). This supports the importance of combined evidence analysis compared to combining tree topologies.

New observations

We find that *Cryptelytrops* consists of two supported clades that are not always recovered as monophyletic. For example, based on mtDNA, combined DNA, and taxon-limited combined DNA with morphology we find strong support for a clade of *C. macrops, C. venustus* and *C. kanburiensis* (*Pp*=1.0), and equally strong support for a clade of *C. fasciatus, C. insularis, C. septentrionalis, C. albolabris, C. andersoni, C. cantori, C. erythrurus,* and *C. purpureomaculatus.* We find only weak support for the sister relationship of these two clades (*Pp*=0.51, 0.57 and 0.74, respectively). Combined mtDNA, nuclear and morphological data with all taxa find weak support for the latter clade (*Pp*=0.50), weaker support for the former clade including new species *C. cardamomensis* and *C. rubeus* (*Pp*=0.30), and no support for a relationship between these clades.

Bothrops pictus and *B. roedingeri* were placed *incertae sedis* by Fenwick et al. (2009) when they proposed a new generic arrangement for bothropoid pitvipers. The former species was the only one that could be included in phylogeny, and was found sister to all bothropoid genera except *Bothrocophias* based on combined mtDNA and morphological evidence. With the addition of a mitochondrial gene for *B. roedingeri*, we recover a strongly supported clade of *B. pictus* and *B. roedingeri* in taxon-limited combined DNA and morphology analysis (*Pp*=1.0). We expect that with further

investigation these two species will constitute another major lineage of South American pitvipers that deserves genus-level recognition.

Fenwick et al. (2009) recovered *Bothrops andianus* in *Bothrops* based on morphological data, but Carrasco et al. (2012) recovered it in *Bothrocophias* based on a different analysis of morphology. This was one of the arguments against accepting the taxonomy of Fenwick et al. We have included mtDNA data for this species for the first time, and support the results of Carrasco et al. However, we do not support their recommendation to lump South American bothropoids into two genera, and will discuss our relevant results and arguments in a forthcoming paper (Fenwick and Parkinson in prep.)

Finally, this is the first study to include morphology in a large-scale phylogenetic context for Asian pitvipers. We find low resolution of relationships in taxon-dense sampling and combined evidence analysis, but taxon-limited sampling strongly supports the monophyly of almost all genera recognized by Malhotra and Thorpe (2004). The only genera that lack posterior probabilities of 1.0 are *Viridovipera* (*Pp*=0.75) and *Cryptelytrops* (*Pp*=0.74). The lack of support for *Cryptelytrops* was discussed above and may be due to the combination of two distinct lineages in one genus. The lack of support for *Viridovipera* may have to do with its close relationship to *Sinovipera* and a lack of data to fully resolve the relationships among species within these two genera and *Cryptelytrops*. Detailed analysis of this clade is certainly warranted, but our results support the taxonomic conclusions of Malhotra and Thorpe.

Conclusions and future directions

In ten years we predict that phylogenetic analyses will be able to include whole genomes for many taxa, but the taxon-dense methods described here will still be necessary. In the case of rare species of traditionally formalin-preserved groups, genomic data will likely be unavailable. Most fossil taxa will also lack genetic data and therefore will be complete for an increasingly small fraction of the data matrix. Fortunately, in our study of approximately 200 species, we find that species with over 100 characters are generally placed in expected phylogenetic positions.

Overall, we find that including a number of species with minimal data in analysis can be detrimental to phylogenetic resolution, but that the effects of these data-limited species cannot be predicted *a priori*. In the cases where understanding the relationships of these data-limited species is key, resolving their placement by including a single data-limited taxon with the more complete dataset may be beneficial but will not necessarily resolve the position of that taxon with confidence. Other *a posteriori* methods, such as the rogue taxa methods often used in supertree analysis, may also be helpful in this case. More investigation of common threshold values for empirical datasets would be welcome, but our results placing a number of data-limited taxa in expected positions argue against eliminating terminals before analysis.

The effect of missing data on estimates of divergence times is an area that needs to be fully investigated, although current evidence suggests that divergence date reconstructions are not misled by missing data (Wiens and Morrill, 2011). In this study we chose to eliminate alignment positions with high proportions of missing data, but

future work could investigate the effect of including those characters in analysis. Pitvipers are a useful model for biogeographic analysis (i.e. Castoe et al., 2009; Daza et al., 2010, Fenwick, Parkinson, Wuster, and Venegas, unpub. data) and a highly accurate estimate of their phylogeny and divergence dates will benefit a number of downstream users.

Outside of the issue of placing data-limited species, we find combining datasets to be beneficial to analysis. The congruence of trees based on the nuclear locus and on phenotypic data with the well-studied mitochondrial phylogeny suggests that relationships that are currently understood represent species tress and not only gene trees. We generally support recent taxonomic changes based on mtDNA data. We particularly highlight the inclusion of phenotypic data for Asian pitvipers in phylogenetic analysis for the first time. Phenotype is of ongoing importance in understanding many Asian groups, but has generally been used only in the context of clustering or ordination analysis to distinguish distinct populations and define species. We use independent datasets to support recent taxonomic changes in Asian snakes, and suggest future research include phenotype in phylogenetic analysis.

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CHAPTER 3: MORPHOLOGICAL AND MOLECULAR EVIDENCE FOR PHYLOGENY AND CLASSIFICATION OF SOUTH AMERICAN PITVIPERS, GENERA BOTHROPS, BOTHRIOPSIS, AND BOTHROCOPHIAS (SERPENTES: VIPERIDAE)

Introduction

The South American pitviper clade of *Bothrops, Bothriopsis,* and *Bothrocophias* is distributed throughout South America and continental islands and includes species that range into Central America, Mexico, and the Caribbean (Campbell & Lamar, 2004). The monophyly of these bothropoids has been supported by several phylogenetic analyses (e.g., Castoe & Parkinson, 2006; Castoe, Sasa & Parkinson, 2005; Gutberlet & Campbell, 2001; Parkinson, Campbell & Chippindale, 2002). The clade contains 47 species: five toadheaded pitvipers (*Bothrocophias*), six forest-pitvipers (*Bothriopsis*), and 36 lanceheads (*Bothrops*) (Campbell & Lamar, 2004). Among phylogenetic hypotheses for the group, common relationships appear (Table 5 and references therein). For example, *Bothrocophias* is generally found to be monophyletic (Castoe & Parkinson, 2006; Gutberlet & Campbell, 2001; Gutberlet & Harvey, 2002; but see Wüster et al., 2002) and sister to *Bothrops + Bothriopsis*. *Bothriopsis* is also supported as monophyletic (Wüster et al., 1999b; Wüster et al., 2002), but *Bothrops* is paraphyletic with respect to the forest-pitvipers (Campbell & Lamar, 1992; Castoe & Parkinson, 2006; Gutberlet & Harvey, 2002; Parkinson, 1999; Parkinson et al., 2002; Salomão et al., 1997; Vidal et al., 1997; Wüster et al., 2002).

Table 5. Content of clades recovered by phylogenetic studies of *Bothrops, Bothriopsis,* and *Bothrocophias* species. Species names have been changed to reflect current classification. Lines delineate clades recovered by the studies; names in bold are group names given by the authors.

Werman (1992)	Salomão et al. (1999)	Wüster et al. (2002)	Gutberlet & Harvey (2002)	Castoe & Parkinson (2006)
		Bothrocophias hyoprora	*Bothrocophias campbelli*	*Bothrocophias hyoprora*
		B. microphthalmus	*B. hyoprora*	*B. microphthalmus*
		Bothrocophias campbelli	*B. microphthalmus*	
Bothrops atrox	*Bothrops atrox*	*Bothrops atrox*	*Bothrops asper*	*Bothrops asper*
B. brazili	*B. brazili*	*B. asper*	*B. atrox*	*B. atrox*
B. jararacussu	*B. colombiensis*	*B. brazili*		*B. jararacussu*
B. leucurus	*B. isabelae*	*B. caribbaeus*		
B. moojeni	*B. jararacussu*	*B. colombiensis*		
	B. leucurus	*B. isabelae*		
	B. marajoensis	*B. jararacussu*		
	B. moojeni	*B. lanceolatus*		
	Bothriopsis bilineata	*B. leucurus*		
	Bothriopsis taeniata	*B. marajoensis*		
	Bothrops caribbaeus	*B. moojeni*		
	B. lanceolatus	*B. punctatus*		
Bothriopsis taeniata		*Bothriopsis bilineata*	*Bothriopsis bilineata*	*Bothriopsis bilineata*
		B. pulchra		*B. chloromelas*
		B. taeniata		*B. taeniata*
Bothrops jararaca	*Bothrops jararaca*	*Bothrops neuwiedi* [*sensu* Silva (2004)]	*B. neuwiedi*	*Bothrops diporus*
	B. insularis		*B. alternatus*	*B. erythromelas*
Bothrops neuwiedi (*sensu lato*)	*Bothrops alternatus*	*B. erythromelas*		*B. insularis*
	B. cotiara	*B. jararaca*		
B. alternatus	*B. fonsecai*	*B. insularis*		*Bothrops alternatus*
B. erythromelas		*Bothrops alternatus*		*B. ammodytoides*
B. itapetiningae		*B. cotiara*		*B. cotiara*
		B. fonsecai		
		B. itapetiningae		

Within *Bothrops*, several species groups have been repeatedly recovered and named (Table 5): a *Bothrops alternatus* group*, B. neuwiedi* group*, B. jararaca* group*, B. atrox* group*,* and *Bothriopsis*. Numerous ecological and evolutionary studies (e.g., Araújo & Martins, 2006; Martins et al., 2001; Martins, Marques & Sazima, 2002) traditionally use these species groups as well, recognizing *alternatus, neuwiedi, jararaca, atrox, jararacussu* (part of the *atrox* group in Table 5), and *taeniatus* (=*Bothriopsis*) groups.

Although the clade contains 47 species, the most comprehensive studies to date included eight (morphology: Gutberlet & Harvey, 2002), eleven (morphology and allozymes: Werman, 1992), and 28 species (mitochondrial DNA: Wüster et al., 2002). While these studies have generally recovered the same clades within the South American pitviper complex, the different species included in these phylogenies may lead to confusion about the content of clades (compare Castoe & Parkinson, 2006; Salomão et al., 1999). In addition, species in certain sparsely sampled regions like the Pacific versant of the Andes have been rarely included in phylogenetic hypotheses (*Bothrops pictus* included in Wüster et al., 2002; *B. roedingeri, B. andianus, B. lojanus* not included in phylogenetic analysis), making it difficult to evaluate the classification of these species.

The knowledge that *Bothrops* is paraphyletic has led to taxonomic arguments about how to revise the content of this genus. Some suggest synonymizing *Bothriopsis* with *Bothrops* and also mention the possibility of synonymizing the small, cohesive sister-genus *Bothrocophias* with *Bothrops* (Salomão et al., 1997; Wüster et al., 2002). Others propose dividing *Bothrops* into smaller monophyletic genera (Castoe &

Parkinson, 2006; Gutberlet & Campbell, 2001; Harvey, Aparicio & Gonzales, 2005; Parkinson, 1999). There is no completely objective criterion for distinguishing between these options, but a comprehensive phylogeny provides the best information for evaluating taxonomic alternatives.

An accurate and stable taxonomy for South American pitvipers is critical, as all species are venomous and several are known to cause human fatalities (Russell, 1980; Warrell, 2004). Venom composition generally has a phylogenetic component (Wüster, 1996; Wüster, Golay & Warrell, 1997), and because most biologists primarily receive phylogenetic information through classification (Frost et al., 2006) a naming system based on a well-supported hypothesis of evolutionary relationships can benefit antivenom production and treatment of envenomation. In addition, the taxonomy will enlighten research in comparative biology, trait evolution, historical biogeography, and other fields.

We believe the current taxonomy has persisted because, as mentioned above, no phylogenetic hypothesis of South American pitvipers has yet considered a significant array of taxa. In this study, we achieve almost complete taxon sampling through the use of both morphological and molecular data. Most taxa are included on the basis of morphological characters as well as one or more gene fragments and a few are included on the basis of morphology only. In the case of South American pitvipers, as well as in many other clades, some rare taxa are available only as formalin-preserved museum specimens and acquiring samples for DNA analyses has been prohibitively difficult. Morphological characters can be observed for almost all taxa and united with available

molecular characters in a combined evidence analysis. In addition, we applied as much DNA sequence data as possible to the analysis to achieve a robust combined evidence phylogeny. Therefore the primary goal of the present work is a phylogenetic analysis of 90% of the currently recognized taxa in the genera *Bothrops, Bothriopsis* and *Bothrocophias* using a morphological and multigene mitochondrial dataset. This is the most taxon- and character-comprehensive study to date on this group of venomous snakes. The phylogeny recovered allows us to identify the major evolutionary lineages in this speciose group, and determine the species composition of each major lineage. We evaluate previous taxonomic suggestions and propose a systematic revision of the group that recognizes evolutionarily, ecologically and morphologically distinct lineages as genera.

Materials and Methods

Morphological Data

Forty-three taxa of *Bothrops* (31 species), *Bothriopsis* (seven taxa of six species), and *Bothrocophias* (five species) were examined, slightly over 90% of currently recognized species. In addition, the subspecies *Bothriopsis b. bilineata* and *B. bilineata smaragdina* were treated as separate terminal taxa. Species in the South American pitviper clade unavailable to this study were *Bothrops lutzi, B. muriciencis, B. pirajai*, and *B. roedingeri*. Species were included in phylogenetic estimation if: (1) we had sequence data for at least one individual; (2) we had data from more than one type of morphological character, or (3) we had scalation data for at least eight individuals (the

average number of individuals examined). Five species failed these criteria and were therefore excluded from all analyses: *Bothrocophias colombianus, Bothriopsis medusa, Bothriopsis oligolepis, Bothrops lojanus,* and *B. pubescens* (Table 6). In accordance with current hypotheses of crotaline phylogeny (Castoe & Parkinson, 2006), *Atropoides picadoi* and *Cerrophidion godmani* were used as near outgroups, and *Agkistrodon contortrix* was chosen as a far outgroup.

We examined scalation of 42 species, hemipenes of 21 species, and skulls or skeletons for 13 species (Table 6 and Appendix E). When possible, specimens were acquired from throughout the range of each species. Scale and hemipenial data for *Bothrops alcatraz* were taken from the description of the holotype (Marques, Martins & Sazima, 2002). Observations of color pattern were taken from color plates in Campbell & Lamar (2004). Males and females were treated together. Some juveniles were coded for scale characters as scalation does not change with ontogeny, but skeletal data were only collected from presumed adults.

Eighty-five morphological characters were included in this study (Appendix A). Sixty-seven characters were taken from Gutberlet (1998b) and Gutberlet & Harvey (2002), with additional characters from Werman (1992) and Wüster et al. (1996), and some original to this study. Ordering of characters was taken from the maximum ordering of Gutberlet & Harvey (2002) and ordering in Werman (1992), using both intermediacy and adjacency as justification for ordering.

Table 6. Numbers of individuals examined/sequenced for data used in this study. Asterisks denote species not included in phylogenetic estimation.

Species	Scalation	Hemipene morphology	Osteology	12S	16S	Cyt b	ND4
Agkistrodon contortrix	10	1	3	3	3	4	4
Atropoides picadoi	4	3	2	1	1	3	5
Cerrophidion godmani	10	–	1	1	1	1	1
Bothrops alcatraz	1	1	–	–	–	5	–
Bothrops alternatus	11	4	1	4	4	6	5
Bothrops ammodytoides	9	4	–	1	1	1	1
Bothrops andianus	10	2	–	–	–	–	–
Bothrops asper	21	2	4	1	1	2	2
Bothrops atrox	23	6	6	1	1	5	4
Bothrops barnetti	10	1	–	–	–	–	–
Bothrops brazili	7	1	5	1	1	2	2
Bothrops caribbaeus	10	–	–	–	–	1	1
Bothrops cotiara	10	–	1	1	1	2	2
Bothrops diporus	10	5	–	1	1	1	1
Bothrops erythromelas	1	–	–	1	1	3	2
Bothrops fonsecai	10	–	–	–	–	1	1
Bothrops insularis	10	2	–	1	1	3	2
Bothrops isabelae	–	–	–	–	–	1	1
Bothrops itapetiningae	13	–	–	1	1	2	2
Bothrops jararaca	9	–	1	1	1	10	9
Bothrops jararacussu	10	3	2	1	1	3	2
Bothrops jonathani	1	1	–	–	–	–	–
Bothrops lanceolatus	10	–	–	–	–	1	1
Bothrops leucurus	10	2	–	1	1	1	1
Bothrops lojanus *	6	–	–	–	–	–	–
Bothrops marajoensis	–	–	–	–	–	1	1
Bothrops mattogrossensis	14	2	–	–	–	–	–
Bothrops moojeni	10	1	1	4	4	6	5
Bothrops neuwiedi	10	–	–	–	–	2	2
Bothrops osbornei	2	–	–	–	–	1	1
Bothrops pauloensis	5	–	–	1	1	1	1
Bothrops pictus	10	1	–	–	–	1	1
Bothrops pubescens *	4	–	–	–	–	–	–

Species	Scalation	Hemipene morphology	Osteology	12S	16S	Cyt b	ND4
Bothrops punctatus	9	1	–	–	–	1	1
Bothrops sanctaecrucis	9	–	–	–	–	–	–
Bothrops venezuelensis	5	2	–	–	–	–	–
Bothrocophias campbelli	2	–	–	–	–	1	1
Bothrocophias colombianus *	2	–	–	–	–	–	–
Bothrocophias hyoprora	14	1	1	1	1	2	2
Bothrocophias microphthalmus	8	–	1	1	1	2	2
Bothrocophias myersi	12	1	1	–	–	–	–
Bothriopsis b. bilineata	7	1	–	–	1	1	–
Bothriopsis b. smaragdina	10	–	–	1	1	2	2
Bothriopsis chloromelas	3	–	–	1	1	1	1
Bothriopsis medusa *	1	–	–	–	–	–	–
Bothriopsis oligolepis *	1	–	–	–	–	–	–
Bothriopsis pulchra	8	–	1	–	–	1	1
Bothriopsis taeniata	7	1	1	1	1	2	2

For parsimony analyses characters were coded using two different methods: generalized frequency coding (GFC) as described by Smith & Gutberlet (2001) or gap weighting (Thiele, 1993) and majority coding (Johnson, Zink & Marten, 1988). Generalized frequency coding was developed to extend the frequency bins method of Wiens (1995) to apply not only to binary characters, but to multistate and meristic characters. It is thought to extract maximal phylogenetic information available in patterns of polymorphism within terminal taxa because it codes the entire frequency distribution of a character within a taxon. Under this method, we processed data through the program FastMorphology GFC (Chang & Smith, 2001) and used unequal subcharacter weighting as recommended by Smith & Gutberlet (2001). This method divides the weight of one character by the number of subcharacters used, then divides the weight of each subcharacter by the number of steps between the lowest and

highest frequency bin included in it, allowing rare subcharacters greater weight than common subcharacters. Smith & Gutberlet (2001) found that unequal subcharacter weighting performed better than the alternative of equal subcharacter weighting.

Bayesian methods that are currently available provide no straightforward means to include frequency-based characters, so likelihood-based analyses were conducted using gap weighting for meristic characters (Thiele, 1993) and majority coding for binary and multistate characters (Johnson et al., 1988). Coding was done using Microsoft Excel. Gap weighting is used for meristic characters and assigns states to taxa according to their range-standardized means (Thiele, 1993). Since MrBayes allows a maximum of six ordered character states, the range of a character was divided into six bins and states 0–5 were assigned to each taxon. Majority coding is used for binary or multistate characters and simply assigns to the terminal taxon the character state found in the majority of samples. Gap weighting and majority coding (GW/MC) methods approximate or ignore polymorphism within species; they are therefore expected to provide less phylogenetic information than frequency methods such as GFC (Smith & Gutberlet, 2001).

Molecular Data

Previously published sequence data for 12S and 16S rRNA, NADH dehydrogenase subunit 4 (ND4), and cytochrome *b* (cyt-*b*) were obtained from GenBank. In addition, new sequences were obtained for eight species as described in Castoe & Parkinson (2006). This provided a molecular dataset with at least one gene fragment included for

each of 35 taxa, or approximately 75% of currently-recognized species (**Error! Reference source not found.**).

All sequences were aligned by eye and using ClustalW (Thompson, Higgins & Gibson, 1994). For conservatism in determining evolutionary relationships, when more than one sequence was available for a species, aligned sequences were combined into a majority-rule consensus sequence. When two or more nucleotides were found in equal proportions, standard IUPAC codes for uncertainty were used. Alignment of protein-coding genes was straightforward with no insertions or deletions. No internal stop codons were found in either protein-coding fragment. Alignment of rRNA genes was based on models of secondary structure for snake mitochondrial rRNAs (Parkinson, 1999). Novel sequences were deposited in GenBank (**Error! Reference source not found.**) and the final nucleotide alignment is available by request. Gaps in the alignment were treated as missing data in analyses.

Table 7. Species used, voucher data, collecting locality, and GenBank accession numbers for each taxon. Accession numbers with asterisks are sequences original to this study. Institutional abbreviations are listed in Leviton, Gibbs, Heal & Dawson (1985). Field series tags: AM = Anita Malhotra, Cadle=John Cadle, CLP = Christopher Parkinson, DPL = Dwight P. Lawson, HWG = Harry Greene, ITS = Marcio Martins Itarapina series, MM = Marcio Martins, Moody = Scott Moody, MSM = Mahmood Sasa, OP = Omar Pesantes, PT = Robert Espinoza, Reno collection, RG = Nelson da Silva, Xingó Hydroelectric project, RH = Richard Heighton, and WW = Wolfgang Wüster.

Species	Field tag	Voucher	Locality	Source	GenBank accession numbers			
					12S	16S	cyt-*b*	ND4
Agkistrodon contortrix	Moody 338	–	USA, Ohio, Athens Co.	Parkinson 1999, Parkinson et al. 2002	AF057229	AF057276	AY223612	AF156576
Agkistrodon contortrix	HWG 2218	–	USA, Texas, Terrell Co.	Parkinson, Zamudio, & Greene 2000	AF156587	AF156566		AF156577
Agkistrodon contortrix	RH 54411	–	USA, North Carolina, Union Co.	Heise et al. 1995	Z46473	Z46524		
Agkistrodon contortrix	–	–	Unknown	Zamudio & Greene 1997			U96022	U96034
Agkistrodon contortrix	–	–	Unknown	Vidal & Lecointre 1998			AF039268	
Agkistrodon contortrix		ROM 2331	bought commercially in FL, USA	Cullings et al. 1997			U65678	
Agkistrodon contortrix	–	UMMZ 199957	USA, South Carolina, Berkeley Co.	Kraus, Mink, & Brown 1996				U41868
Atropoides picadoi	CLP 45	MZUCR 11156	Costa Rica, Alajuella, Varablanca	Parkinson 1999 Parkinson et al. 2002	AY057208	AF057255	AY223583	
Atropoides picadoi	MSM 10350	–	Costa Rica:, San José, Bajo la Hondura	Castoe et al. 2005			DQ061197	DQ061222
Atropoides picadoi	–	UTA R-23837	Costa Rica, San Jose, Bajo la Hondura	Castoe et al. 2003			AY220324	AY220347
Atropoides picadoi	–	UTA R-24821	Costa Rica, Heredia, Sarapiqui	Castoe et al. 2003			AY220323	AY220346
Atropoides picadoi	–	UMMZ 177000	Costa Rica, Heredia, Cantón de Sarapicí	Kraus et al. 1996				U41872
Cerrophidion godmani	–	UTA R-40008	Guatemala, Baja Verapaz	Castoe & Parkinson 2006	DQ305419	DQ305442	AY220325	AY220348

Species	Field tag	Voucher	Locality	Source	GenBank accession numbers			
					12S	16S	cyt-*b*	ND4
Bothrops alcatraz	–	CBGM baz001–005	Brazil, São Paulo, Ilha de Alcatrazes	Grazziotin et al. 2006			AY865820–AY865824	
Bothrops alternatus	DPL 2879	–	–	Parkinson et al. 2002	AY223660	AY223673	AY223601	AY223642
Bothrops alternatus	–	IB 55314	Brazil, Paraná, Pinhão	Wüster et al. 2002			AF292579	AF292617
Bothrops alternatus	WW 59	–	Brazil, Paraná	Malhotra & Thorpe, 2000			AF191583	
Bothrops alternatus	MM 2E5'	released after sampling	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867249*	EU867261*	EU867273*	EU867285*
Bothrops alternatus	MM FE2	released after sampling	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867250*	EU867262*	EU867274*	EU867286*
Bothrops alternatus	ITS 358	–	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867251*	EU867263*	EU867275*	EU867287*
Bothrops ammodytoides	–	MVZ 223514	Argentina, Neuguen	Parkinson et al., 2002	AY223658	AY223671	AY223595	AY223639
Bothrops asper	CLP 50	MZUCR 11152	Costa Rica	Kraus et al. 1996, Parkinson 1999, Parkinson et al. 2002	AF057218	AF057265	AY223599	U41876
Bothrops asper	–	Belize Zoo live collection	Belize, Western Highway	Wüster et al. 2002			AF292600	AF292638
Bothrops atrox	WW 743	–	–	Parkinson et al., 2002	AY223659	AY223672	AY223598	AY223641
Bothrops atrox	–	FHGO live 1424	–	Wüster unpublished 1991			AF292604	AF292642
Bothrops atrox	–	–	Brazil, Acre	Puorto et al. 2001			AF246268	AF246277
Bothrops atrox	–	–	Suriname	Puorto et al. 2001			AF246267	AF246278
Bothrops atrox	–	–	French Guiana, Petit Saut	Vidal & Lecointre 1998			AF039263	
Bothrops brazili	–	FHGO 982	Ecuador, Morona Santiago, Macuma	Wüster et al. 2002			AF292597	AF292635

Species	Field tag	Voucher	Locality	Source	GenBank accession numbers			
					12S	16S	cyt-*b*	ND4
Bothrops brazili	–	USNM RWM 17831	Venezuela, Amazonas		EU867252*	EU867264*	EU867276*	EU867288*
Bothrops caribbaeus	–	released after sampling	Saint Lucia	Wüster et al. 2002			AF292598	AF292636
Bothrops cotiara	WW	–	Brazil	Parkinson 1999	AF057217	AF057264	AY223597	AY223640
Bothrops cotiara	–	IB live 3829	Brazil, Santa Catarina, Herval d'Oeste	Wüster et al. 2002			AF292581	AF292619
Bothrops diporus	PT 3404	–	Argentina, La Rioja, Castro Barros	Castoe & Parkinson 2006	DQ305431	DQ305454	DQ305472	DQ305489
Bothrops erythromelas	RG 829	–	Brazil, Alagóas, Piranhas	Kraus et al. 1996, Parkinson 1999, Parkinson et al. 2002	AF057219	AF057266	AY223600	U48177
Bothrops erythromelas	–	CBGM ber001	–	Grazziotin et al. 2006			AY865653	
Bothrops erythromelas	–	IB 55541	Brazil, Bahia, Guanambi	Wüster et al. 2002			AF292588	AF292626
Bothrops fonsecai	–	IB 55543	Brazil, São Paulo, Campos do Jordão	Wüster et al. 2002			AF292580	AF292618
Bothrops insularis	WW	–	Brazil, São Paulo, Isla Queimada Grande	Parkinson 1999, Parkinson et al. 2000, Parkinson et al. 2002	AF057216	AF057263	AY223596	AF188705
Bothrops insularis	–	CBGM bis007	Brazil, São Paulo, Isla Queimada Grande	Grazziotin et al. 2006			AY865660	
Bothrops insularis	–	–	Brazil, São Paulo, Isla Queimada Grande	Wüster et al. 2002			AF292590	AF292628
Bothrops isabelae	–	–	–	Wüster unpublished 2000			AF292603	AF292641
Bothrops itapetiningae	–	IB live 4982	Brazil, Distrito Federal, Brasília	Wüster et al. 2002			AF292582	AF292620

Species	Field tag	Voucher	Locality	Source	GenBank accession numbers			
					12S	16S	cyt-*b*	ND4
Bothrops itapetiningae	ITS 427	–	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867253*	EU867265*	EU867277*	EU867289*
Bothrops jararaca	–	IB 55592–55593	Brazil, Santa Catarina, São Bento do Sul	Wüster, Duarte, & Salomão 2005			AY122851–AY122855	AY122858–AY122862
Bothrops jararaca	–	BBBSP 926	Brazil, Paraná, Piracuara	Wüster et al. 2005			AY122857	122864
Bothrops jararaca	–	BBBSP 918	Afonso Clâudio, Espírito Santo	Wüster et al. 2005			AY122856	122863
Bothrops jararaca	–	–	Brazil, Paraná, Piracuara	Wüster et al. 2002			AF292589	AF292627
Bothrops jararaca	MM (19)6	released after sampling	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867254*	EU867266*	EU867278*	EU867290*
Bothrops jararacussu	DPL 104	–	–	Parkinson et al., 2002	AY223661	AY223674	AY223602	AY223643
Bothrops jararacussu	–	IB 55313		Wüster et al. 2002			AF292596	AF292634
Bothrops jararacussu	–	–	–	Wüster unpublished 1991			AF191585	
Bothrops lanceolatus	–	–	Martinique	Wüster et al. 2002			AF292599	AF292637
Bothrops leucurus	CLP195	–	–		EU867255*	EU867267*	EU867279*	EU867291*
Bothrops marajoensis		–	Brazil, Pará, Ilha de Marajó	Wüster et al. 2002			AF292605	AF292643
Bothrops moojeni	–	IB 56558	Brazil, Distrito Federal, Brasilia	Wüster et al. 2002			AF292606	AF292644
Bothrops moojeni	–	IB 55098	Brazil, São Paulo	Malhotra & Thorpe 2000			AF200222	
Bothrops moojeni	ITS 406	–	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867256*	EU867268*	EU867280*	EU867292*
Bothrops moojeni	ITS 418	–	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867257*	EU867269*	EU867281*	EU867293*

Species	Field tag	Voucher	Locality	Source	GenBank accession numbers			
					12S	16S	cyt-*b*	ND4
Bothrops moojeni	ITS 429	–	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867258*	EU867270*	EU867282*	EU867294*
Bothrops moojeni	MM OBA	released after sampling	Brazil, Sao Paulo, Itarapina, Itarapina Ecological Station		EU867259*	EU867271*	EU867283*	EU867295*
Bothrops neuwiedi	–	IB 57513	–	Wüster unpublished 2000			AF292586	AF292624
Bothrops neuwiedi	–	IB 5555	Brazil, São Paulo, Angatuba	Wüster et al. 2002			AF292585	AF292623
Bothrops osbornei	–	FHGO live 2166	Ecuador, Pichincha, Pedro Vicente Maldonado	Wüster et al. 2002			AF292595	AF292633
Bothrops pauloensis	CLP 3	–	–		EU867260*	EU867272*	EU867284*	EU867296*
Bothrops pictus	MM OP	released after sampling	Peru, Ayacucho, Pullo	Wüster et al. 2002			AF292583	AF292621
Bothrops punctatus	–	FHGO live 2452	–	Wüster unpublished 2000			AF292594	AF292632
Bothriopsis b. bilineata	–	–	French Guiana, Petit Saut	Vidal & Lecointre 1998		AF038887	AF039269	
Bothriopsis b. smaragdina	–	–	Colombia, Amazonas, Leticia	Kraus et al. 1996, Parkinson 1999, Parkinson et al. 2002	AF057214	AF057261	AY223591	U41875
Bothriopsis b. smaragdina	–	FHGO 983	Ecuador, Morona Santiago, Macuma	Wüster et al. 2002			AF292592	AF292630
Bothriopsis chloromelas	–	LSUMZ 41037	Peru, Pasco	Castoe & Parkinson 2006	DQ305430	DQ305453	DQ305471	DQ305488
Bothriopsis pulchra	–	FHGO live 2142	Ecuador, Zamora Chinchipe, Estación Científica San Francisco	Wüster et al. 2002			AF292593	AF292631

Species	Field tag	Voucher	Locality	Source	GenBank accession numbers			
					12S	16S	cyt-*b*	ND4
Bothriopsis taeniata	–	–	Suriname	Parkinson 1999, Parkinson et al. 2002	AF057215	AF057262	AY223592	AY223637
Bothriopsis taeniata	–	FHGO live 1407	Ecuador, Morona Santiago, Macuma	Wüster et al. 2002			AF292591	AF292629
Bothrocophias campbelli	–	INHMT, uncatalogued	Ecuador, Chimborazo, Pallatanga	Wüster et al. 2002			AF292584	AF292622
Bothrocophias hyoprora	–	–	Columbia, Amazonas, Leticia	Parkinson 1999, Parkinson et al. 2002	AF057206	AF057253	AY223593	
Bothrocophias hyoprora	–	FHGO live 2215	Ecuador, Morona Santiago, Macuma	Wüster et al. 2002			AF292576	AF292614
Bothrocophias hyoprora	–	–	Columbia, Amazonas, Leticia	Kraus et al. 1996				U41886
Bothrocophias microphthalmus	–	LSUMZ H-9372	Peru, Pasco	Parkinson et al. 2002	AY223657	AY223670	AY223594	AY223638
Bothrocophias microphthalmus	–	FHGO 2566	Ecuador, Zamora Chinchipe, Cuenca del Río Jamboe	Wüster et al. 2002			AF292577	AF292615

Phylogenetic Analyses

Maximum parsimony and Metropolis-Hastings coupled Markov chain Monte Carlo Bayesian methods were used to reconstruct phylogenies.

Table 8 shows all analyses. Morphological characters were analyzed separately using GFC and GW/MC methods in parsimony, only with the latter method in Bayesian methodologies. Each mitochondrial gene was also analyzed separately with both methods. In general we expect phylogenies from different mitochondrial genes to recover the same relationships because they are inherited as a single linkage unit. To verify this assumption we looked for strongly supported incongruence among gene trees and found none. As all genes appeared to support a single phylogeny, we combined them into a single analysis. Previous studies that included many of the sequences used in this study have also supported the combinability of these four gene fragments (e.g., Castoe & Parkinson, 2006; Castoe, Sasa, & Parkinson, 2005; Malhotra & Thorpe, 2004; Murphy et al., 2002; Parkinson, 1999; Parkinson, Campbell, & Chippindale, 2002). Mitochondrial analyses were followed by combined evidence analyses of morphological and molecular data. One set of combined evidence analyses included all taxa; a second included only those taxa with both phenotypic and sequence data.

Table 8. Summary of phylogenetic analyses of South American pitvipers

Analysis	Figure	Optimality criterion	Description
1	S-9	Parsimony	Morphology only, GFC
2	S-8	Parsimony	Morphology only, gap weighting and majority coding
3	S-7	Bayesian	Morphology only, gap weighting and majority coding
4	S-6	Parsimony	mtDNA only
5	S-5	Bayesian	mtDNA only
6	S-4	Parsimony	All characters included, GFC
7	2/S-3	Parsimony	All characters included, gap weighting and majority coding
8	2	Bayesian	All characters included, gap weighting and majority coding
9	S-2	Parsimony	All characters included, GFC, taxa without molecular data excluded
10	1/S-1	Parsimony	All characters included, gap weighting and majority coding, taxa without molecular data excluded
11	1	Bayesian	All characters included, gap weighting and majority coding taxa without molecular data excluded

Maximum parsimony methods were conducted with the program PAUP* version 4.0b10 (Swofford, 2002). We used heuristic searching with 200 random-taxon-addition sequences and tree bisection reconnection (TBR) branch-swapping. Support for nodes was assessed with nonparametric bootstrapping (Felsenstein, 1985) with 1,000 full heuristic pseudoreplicates and two random-taxon-addition sequence replicates per pseudoreplicate.

In Bayesian analyses, the standard Mk model was used for the morphology partition. Preliminary analyses determined that there was no increase in likelihood score with the addition of the gamma-distributed rate variation parameter; therefore we chose the simpler model. Based on the results of Castoe & Parkinson (2006), maximum partitioning of the molecular data set was done *a priori*, with all codon positions or stem and loop positions of each gene allocated independent models. Each partition was independently analyzed using MrModelTest version 2.2 (Nylander, 2004) to estimate

best-fit models of nucleotide evolution. This program only considers models that are currently available in MrBayes version 3.1.2 (Ronquist & Huelsenbeck, 2003). PAUP* was used to calculate model likelihoods for use in MrModelTest. The best-fit models were implemented as partition-specific models within partitioned-model analyses of the combined dataset as described in Castoe & Parkinson (2006). The models chosen for each partition are summarized in Table 9.

Table 9. Results of AIC model selection conducted in MrModelTest 2.2 (Nylander 2004) for partitions of the dataset.

Partition	AIC model
12S, stems	HKY + ΓI
12S, loops	GTR + Γ
16S, stems	HKY + I
16S, loops	GTR + ΓI
cyt-b, position 1	HKY + ΓI
cyt-b, position 2	GTR + Γ
cyt-b, position 3	HKY + ΓI
ND4, position 1	GTR + ΓI
ND4, position 2	HKY + Γ
ND4, position 3	HKY + Γ

Bayesian phylogenetic inference was conducted using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). All analyses were run with vague priors. Four incrementally heated chains were used in addition to the cold chain, with the temperature set at half of the program's default to facilitate chain swapping. Each analysis had two different runs beginning with random trees. Chains were run for at least 4.0×10^6 generations. All were sampled every 100 generations, with the first quarter of the runs conservatively discarded as burn-in. Tracer 1.4 (Rambaut & Drummond, 2007) was used to verify that

stationarity was reached within the burn-in period. Summary statistics and consensus phylograms with nodal posterior probability support were estimated from the combination of both runs per analysis.

We calculated genetic distance measures for cyt-*b* sequences among species groups in our dataset and among polytypic genera using sequences from Castoe & Parkinson (2006). We believe genetic distances should not be used to define taxonomic rank, but an examination of distance measures can provide a rough estimate of the amount of divergence among groups, and can allow comparisons with other groups of closely-related taxa. Cyt-*b* was chosen because its genetic distances are often reported in the literature, allowing more direct comparisons of genetic distances in these groups to those reported for other snakes (e.g., Malhotra & Thorpe, 2004; Wüster et al., 2002) We calculated genetic distance measures with the program MEGA (Kumar, Tamura & Nei, 2004), using a Kimura 2 parameter model and gamma-distributed rate variation.

Results

The final alignment of four concatenated gene fragments consisted of 2343 aligned positions: 424 from 12S, 511 from 16S, 716 from cyt-*b*, and 692 from ND4. This alignment contained 599 parsimony-informative characters. Generalized frequency coding (GFC) of morphological characters yielded 595 subcharacters, 404 of which were parsimony-informative. Gap weighting and majority coding (GW/MC) of 92 morphological characters yielded 72 that were parsimony-informative.

There were no strongly supported conflicts between parsimony and Bayesian phylogenies, although minor topology differences were found (e.g. compare Figure 9 to

Appendix D figures S-1 and S-2, Figure 10 to Appendix D figures S-3 and S-4). Additionally, support values derived from these methods were in agreement in almost all cases. Analyses with different datasets were also topologically congruent, with the highest resolution and support values in phylogenies inferred from combined evidence (Figures 1, 2, Appendix D figures S-1–S-4) followed by those from molecular evidence only (Appendix D figures S-5–S-6), and the lowest resolution and support values in phylogenies from morphological evidence only (Appendix D figures S-7–S-9). Combined evidence analyses excluding taxa with morphological data only (Figure 9, also S-1–S-2) recovered five major lineages: a *Bothrocophias* clade (labeled A, posterior probability (*Pp*) = 79, bootstrap value (*Bs*) = 57-81), a *Bothrops alternatus* clade (labeled B, *Pp* = 100, *Bs* = 71–83), a *Bothrops jararaca + B. neuwiedi* clade (labeled C, *Pp* = 100, *Bs* **=** 90–95), a *Bothriopsis* clade (labeled D, *Pp, Bs* = 100), and a *Bothrops atrox* clade (labeled E, *Pp* = 100, *Bs* = 99–100). Alternative analyses recovered the same major lineages in almost all cases but with lower support.

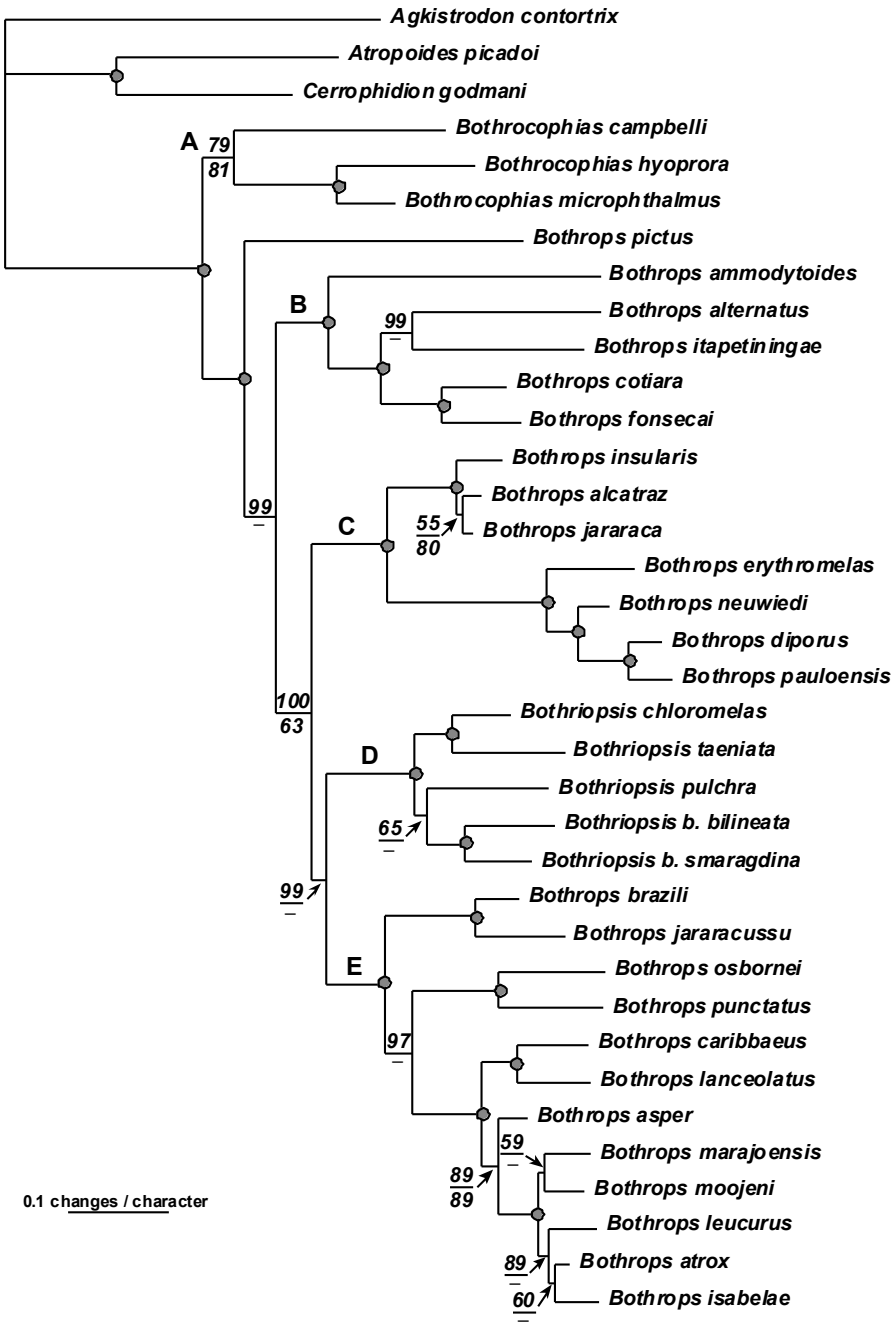

Figure 9. Bayesian MCMC 50% majority-rule consensus phylogram, excluding taxa with morphological data only (analysis 11). Phylogram derived from analysis of 2343 bp mitochondrial and 85 gap weighted or majority coded morphological characters. Posterior probabilities shown above nodes, bootstrap values from parsimony analysis of same dataset shown below nodes (analysis 10). Parsimony analysis shows minor topological differences from Bayesian analysis; refer to online figure S-1 for parsimony cladogram. Gray circles indicate posterior probabilities of 95 or greater and bootstrap values of 70 or greater. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi + B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

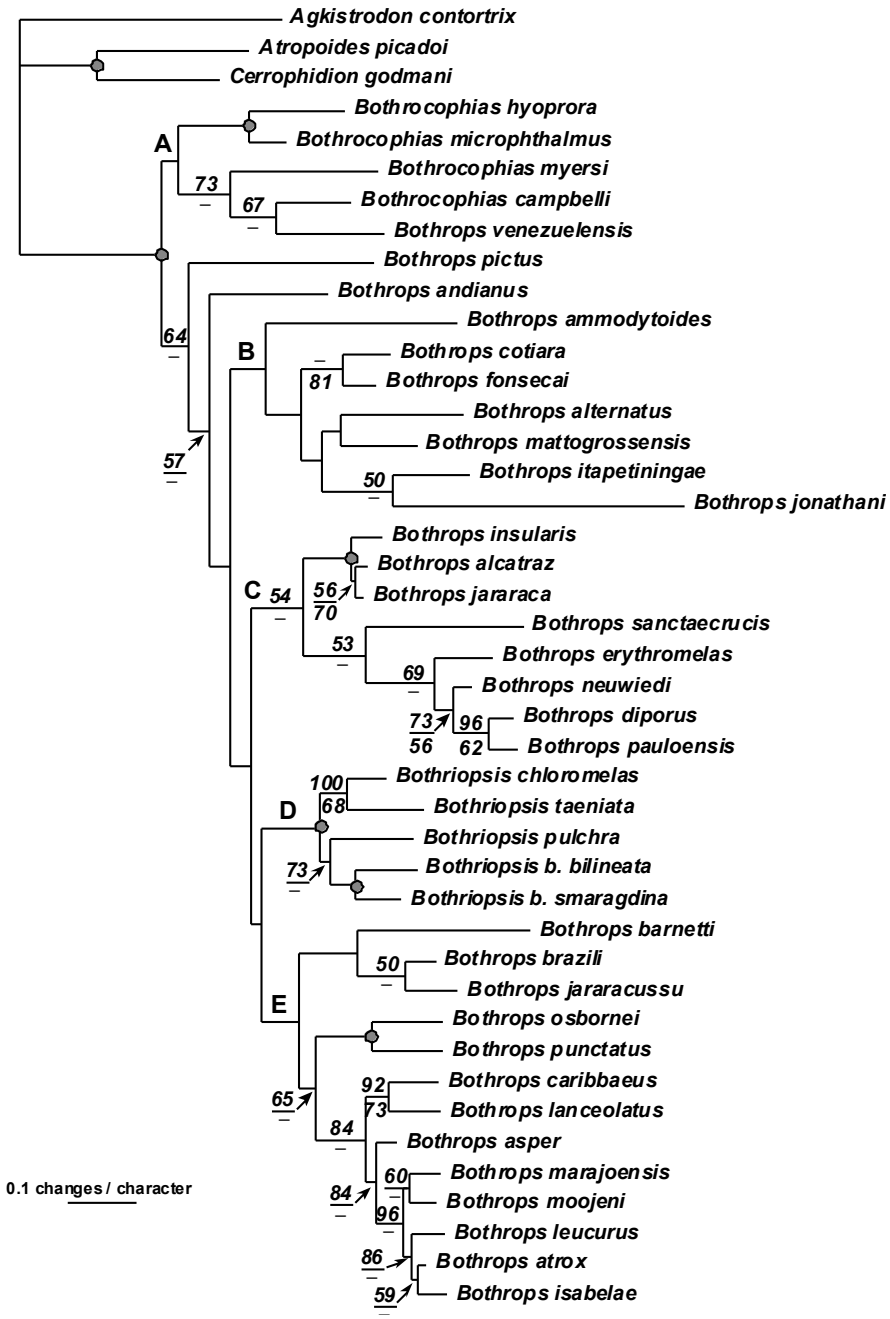

Figure 10. Bayesian MCMC 50% majority-rule consensus phylogram, including taxa with morphological data only (analysis 8). Phylogram derived from analysis of 2343 bp mitochondrial and 85 gap weighted or majority coded morphological characters. Posterior probabilities shown above nodes, bootstrap values from parsimony analysis of same dataset shown below nodes (analysis 7) Parsimony analysis shows minor topological differences from Bayesian analysis; refer to online figure S-3 for parsimony cladogram. Gray circles indicate posterior probabilities of 95 or greater and bootstrap values of 70 or greater. Dashes indicate support values less than 50. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi + B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

Analysis 11, a Bayesian combined evidence analysis excluding taxa with morphological data only, is our preferred hypothesis for delineating species groups, as it had the highest support values overall and was based on the largest dataset while avoiding possible complications of adding taxa with 90% or more missing data to the analysis (Wiens, 2003, 2006). Analysis 8 is our preferred taxon-comprehensive hypothesis and is also a Bayesian combined evidence analysis. Like analysis 11, it has the benefits of evolutionary models for DNA data that may be more biologically realistic than parsimony and a method known to outperform other types of analysis under a range of conditions (Holder & Lewis, 2003; Huelsenbeck et al., 2002). Analysis 8 recovered the same species groups as analysis 11, although with lower support values. We attribute this to the inclusion of taxa based on morphology only (i.e., taxa with extensive missing data), and so we prefer to use this analysis for the placement of taxa in species groups defined by analysis 11.

In our preferred phylogenetic hypotheses, the *Bothrocophias* clade (labeled A) consisted of *Bothrocophias campbelli, B. hyoprora,* and *B. microphthalmus* and included *B. myersi* on the basis of morphological data (*Pp* = 73). The *Bothrops alternatus* clade (labeled B) consisted of that species, *B. ammodytoides, B. itapetiningae, B. cotiara,* and *B. fonsecai*. Analysis 8 (*Pp* = 79) also included *B. jonathani*. The *Bothrops jararaca + B. neuwiedi* clade (labeled C) consisted of those species, *B. diporus*, *B. erythromelas, B. pauloensis, B. insularis,* and *B. alcatraz*. The *Bothriopsis* clade (labeled D) consisted of *B. chloromelas, B. taeniata, B. pulchra,* and both subspecies of *B. bilineata*. Sister to the *Bothriopsis* clade was a *Bothrops atrox* clade (labeled E) consisting of that species, *B.*

leucurus, B. isabelae, B. moojeni, B. marajoensis, B. asper, B. lanceolatus, B. caribbaeus, B. punctatus, B. osbornei, B. jararacussu, and *B. brazili*. Positions of taxa included in the phylogeny on the basis of morphological characters alone were generally poorly supported.

Certain species were recovered in different positions in different analyses. *Bothrops pictus* was the only species not recovered in a species group in analysis 11; it was sister to the remainder of the *Bothrops + Bothriopsis* clade (*Pp* = 97). In parsimony analysis 10, however, a sister relationship of *B. pictus* to the *B. alternatus* clade was supported by a bootstrap value of 56; that relationship was not recovered in majority-rule consensus of the shortest trees. In all other cases of alternative placements the species relationships were supported with posterior probability and bootstrap values less than 65. Species with alternative placements were *Bothrops andianus, B. barnetti, B. mattogrossensis, B. sanctaecrucis, and B. venezuelensis*.

Genetic distance measures within South American species groups ranged from 6.5–11.3%, and distances between species groups within South American pitvipers ranged from 11.1–16.7% (Table 10). Overall, within-genus distance measures ranged from 8.5–21.9%.

Table 10. Cytochrome *b* distances within and among selected genera recovered with the Kimura 2-parameter model with gamma-distributed rate variation. Sequences for *Bothrocophias, Rhinocerophis, Bothropoides, Bothriopsis*, and *Bothrops* taken from this study, all other sequences from Castoe & Parkinson (2006). Thick black line denotes South American bothropoid clade.

	Gloydius	*Cryptelytrops*	*Parias*	*Viridovipera*	*Trimeresurus*	*Protobothrops*	*Agkistrodon*	*Crotalus*	*Sistrurus*	*Ophryacus*	*Lachesis*
Gloydius	**0.117**										
Cryptelytrops	0.233	**0.082**									
Parias	0.251	0.187	**0.121**								
Viridovipera	0.228	0.169	0.169	**0.088**							
Trimeresurus	0.250	0.202	0.215	0.199	**0.170**						
Protobothrops	0.227	0.222	0.216	0.200	0.234	**0.139**					
Agkistrodon	0.223	0.210	0.216	0.208	0.229	0.202	**0.065**				
Crotalus	0.256	0.236	0.251	0.233	0.259	0.238	0.211	**0.153**			
Sistrurus	0.251	0.255	0.234	0.234	0.255	0.228	0.201	0.182	**0.187**		
Ophryacus	0.225	0.235	0.227	0.227	0.241	0.207	0.193	0.233	0.213	**0.148**	
Lachesis	0.245	0.233	0.243	0.227	0.260	0.220	0.203	0.224	0.226	0.193	**0.111**
Bothriechis	0.244	0.225	0.235	0.210	0.249	0.222	0.201	0.213	0.229	0.200	0.216
Cerrophidion	0.235	0.239	0.199	0.199	0.242	0.193	0.179	0.209	0.201	0.182	0.197
Porthidium	0.239	0.241	0.225	0.218	0.243	0.224	0.205	0.249	0.243	0.215	0.233
Atropoides	0.242	0.225	0.212	0.193	0.234	0.199	0.180	0.207	0.207	0.189	0.198
Bothrocophias	0.280	0.234	0.244	0.229	0.255	0.243	0.233	0.244	0.263	0.228	0.245
Rhinocerophis	0.274	0.217	0.218	0.206	0.240	0.231	0.223	0.232	0.251	0.232	0.241
Bothropoides	0.261	0.234	0.230	0.200	0.261	0.249	0.220	0.229	0.248	0.230	0.260
Bothriopsis	0.278	0.224	0.242	0.222	0.257	0.245	0.233	0.253	0.268	0.225	0.244
Bothrops	0.257	0.226	0.238	0.217	0.259	0.230	0.224	0.236	0.259	0.213	0.233

	Bothriechis	*Cerrophidion*	*Porthidium*	*Atropoides*	*Bothrocophias*	*Rhinocerophis*	*Bothropoides*	*Bothriopsis*	*Bothrops*
Bothriechis	**0.141**								
Cerrophidion	0.192	**0.083**							
Porthidium	0.211	0.166	**0.127**						
Atropoides	0.181	0.121	0.166	**0.095**					
Bothrocophias	0.220	0.206	0.234	0.195	**0.138**				
Rhinocerophis	0.197	0.191	0.227	0.180	0.150	**0.071**			
Bothropoides	0.227	0.217	0.247	0.201	0.171	0.151	**0.073**		
Bothriopsis	0.217	0.203	0.241	0.190	0.132	0.131	0.144	**0.067**	
Bothrops	0.204	0.198	0.223	0.197	0.153	0.149	0.152	0.123	**0.069**

Discussion

Resolution of Major Lineages

Numerous studies have included species of *Bothrops, Bothriopsis,* and *Bothrocophias* in phylogenetic estimates, but until this study no taxon-comprehensive combined dataset was available. We have recovered four major lineages in the *Bothrops + Bothriopsis* clade (labeled B–E, respectively): 1) *Bothrops alternatus* clade, 2) *B. neuwiedi* clade *+ B. jararaca* clade*,* 3) *Bothriopsis* clade, and 4) *Bothrops atrox* clade. The resolution of these lineages is supported by several lines of evidence. In analysis 11, the species groups were supported with posterior probabilities of 100. In the corresponding parsimony analyses 9 and 10 these groups were supported with bootstrap values of 71–100. More taxon-comprehensive and more data-poor analyses in this study had lower support, but the same groups were recovered in all phylogenies. The *Bothrops alternatus* group was supported by 27 mitochondrial and one unique morphological character, the *B. neuwiedi + B. jararaca* group by 38 mitochondrial and no unique morphological characters, *Bothriopsis* by 48 mitochondrial and four unique morphological characters, and *Bothrops atrox* group by 50 mitochondrial and one unique morphological character (Table 11). The results have been corroborated by morphological and molecular studies, including Castoe & Parkinson (2006), Gutberlet & Harvey (2002), Wüster et al. (2002), and Salomão et al. (1999, 1997).

Table 11. Phenotypic synapomorphies and shared natural history traits among species within major lineages of South American pitvipers. Diet data from Martins et al. (2002), habitat data from Martins et al. (2001) and Campbell & Lamar (2004), range data from Campbell & Lamar (2004).

Proposed genus	Number of DNA synapomorphies	Phenotypic synapomorphies	Diet	Habitat	Geographic range
Bothrocophias	12S: 4, 16S: 5, cyt-*b*: 11, ND4: 14	Keel on dorsal scales tuberculate on caudal part of body, Meckellian foramen completely or partially divided into two foramina, distinct white spots on posterior infralabials and gulars present	Diet generalists, including a high proportion of lizards (41.7% in *B. hyoprora*), anurans and mammals (25% each in *B. hyoprora*)	Terrestrial in rainforest, montane wet forest, and cloud forest	Andean South America: Ecuador, Colombia, Peru, Bolivia, western Brazil
Rhinocerophis	cyt-*b*: 10, ND4: 17	One to two palatine teeth	Diet generalists including a high proportion of mammal prey (42.8–60% in *B. ammodytoides* and *B. itapetiningae*) or mammal specialists	Terrestrial in open areas or edges of moderate to montane broadleaf and/or *Araucaria* forests, swamps, or cerrados	southern South America: southeastern Brazil, Paraguay, Uruguay, Argentina; one species found in central and southern Bolivia
Bothropoides	12S: 6, 16S: 1, cyt-*b*: 19, ND4: 12	No unique phenotypic synapomorphies, intermediate width of lateral margin of head of ectopterygoid shared with *Bothrocophias*	Diet generalists, some mammal specialists (*B. pubescens*), some including a high proportion of birds (*B. insularis*), or centipedes (66.7% in *B. alcatraz*) in diet; ontogenetic shift in prey types in the larger species	Terrestrial in dry to wet habitats in caatinga vegetation, cerrados, rock outcrops, grassy areas, or broadleaf forests (*B. erythromelas* and *B. neuwiedi* complex) or semiarboreal in Atlantic forests (*B. jararaca* complex)	eastern South America: Brazil including continental islands, Bolivia, southeastern Peru, Paraguay, Uruguay, northern to central Argentina

Proposed genus	Number of DNA synapomorphies	Phenotypic synapomorphies	Diet	Habitat	Geographic range
Bothriopsis	12S: 11, 16S: 4, cyt-*b*: 21, ND4: 12	Pleurapophyses of midcaudal vertebrae in contact distally, choanal process of palatine positioned posteriorly, prehensile tail, green ground color	Diet generalists with a high proportion of mammal (40.9–50.0%) and anuran (35.7–40.9%) prey	Semiarboreal in lowland rainforests, Atlantic forests, wet montane forest or cloud forests	Amazonian South America: Colombia, Ecuador, Peru, Bolivia, Brazil, Venezuela, Guyana, French Guiana, Suriname
Bothrops	12S: 9, 16S: 4, cyt-*b*: 14, ND4: 23	Four palatine teeth (five in *B. moojeni* and *B. jararacussu*, three in *B. brazili* and *B. sanctaecrucis*)	Diet generalists with a high proportion of mammal (42.1–70.1%) and anuran (12.8–33.6%) prey	Terrestrial to semiarboreal in lowland rainforests to gallery forests and swamps in cerrados to Atlantic forests	northern South America: Pacific versant of Andes and coastal lowlands in Colombia, Ecuador, and northwestern Peru, Atlantic versant of Andes in Peru and Bolivia, Venezuelan Andes, and equatorial forests east of Andes exclusive of Uruguay, southern Paraguay, and Argentina south of Misiones; Central America: southern Mexico to Panama; Lesser Antilles: St. Lucia and Martinique

We also recovered a monophyletic *Bothrocophias* lineage (labeled A in figures) with strong support in mitochondrial and combined evidence phylogenies, and with lower support in other analyses. *Bothrocophias* is supported by 34 mitochondrial and three morphological synapomorphies (Table 11). Monophyly of this genus is in agreement with the morphological dataset of Gutberlet & Harvey (2002) and the molecular dataset of Castoe & Parkinson (2006).

Placement of Species within Lineages

In most cases, species were recovered in the same clades in multiple analyses and their phylogenetic placement was supported by prior evidence (e.g., Table 5 and references therein, Campbell & Lamar, 2004; Silva, 2000, 2004). In the case of *Bothrocophias campbelli*, two prior studies recovered alternative placements of the species: Gutberlet & Harvey's (2002) morphological analysis found it within *Bothrocophias*, supporting the content of the genus as defined by Gutberlet & Campbell (2001), while Wüster et al.'s (2002) mitochondrial analysis found *B. campbelli* sister to *Bothrops + Bothriopsis*. Combined evidence analysis 11 provided strong support for the monophyly of *Bothrocophias* including *B. campbelli* (*Pp* = 96). In only two cases, *B. campbelli* did not fall within a *Bothrocophias* clade. Analysis 2 (Appendix D figure S-8) recovered it sister to the rest of the ingroup excluding *Bothrops erythromelas*, and analysis 5 (Figure S-5) recovered it sister to *Bothrops + Bothriopsis*. The majority of our results and most prior work strongly suggest that *B. campbelli* is part of the *Bothrocophias* lineage.

A few species were recovered in uncertain phylogenetic positions or were unavailable to this study, but other sources of evidence allow us to make recommendations on their group placement; further phylogenetic testing of these recommendations is warranted. First, *Bothrocophias myersi* was included in analysis on the basis of morphological data only; in Bayesian analysis 8 (Figure 10), the species was part of *Bothrocophias,* but in parsimony analyses 1, 6, and 7 and Bayesian morphological analysis 3 (Figures S-3, S-4, S-7, S-9) it was found within *Bothrops* (*Bs* < 50). Gutberlet & Campbell (2001) recovered *B. myersi* within *Bothrocophias* in their analysis and description of the species and genus. Based on this evidence and results presented here, we suggest that the current generic allocation is appropriate. Second, *Bothrocophias colombianus* was included in that genus by Campbell & Lamar (2004) on the basis of external morphology. Too few specimens were available to include this species in phylogenetic analysis, but scale data from two specimens (FMNH 55898 and UTA R25949) support the inclusion of *B. colombianus* in *Bothrocophias*. In addition, canthorostrals were observed on FMNH 55898, a character state previously observed only in *Bothrocophias hyoprora* and *B. microphthalmus*.

Bothriopsis oligolepis and *B. medusa* could not be included in final analyses because too few specimens were available (Table 12). Preliminary analyses placed *B. oligolepis* within *Bothriopsis*, and its green coloration, prehensile tail, and arboreal lifestyle suggest that the current designation is correct. The semiarboreal lifestyle of *B. medusa* in addition to its Venezuelan distribution (Campbell & Lamar, 2004) places its affinities with either *Bothriopsis* or the *Bothrops atrox* group (Table 11). The tan to

brown, gray or olive coloration is unlike most *Bothriopsis* species, but the pattern of transverse bands on the dorsum is similar to *Bothriopsis* species and unlike the spade-shaped dorsal markings on most *B. atrox* group specimens. We suggest retaining the current designation until more data are available.

Bothrops mattogrossensis and *B. pubescens* were elevated from subspecies of *B. neuwiedi* by Silva (2000, 2004). *Bothrops pubescens* was not included in final analyses due to a lack of specimens, but preliminary analyses recovered it in a clade with *B. neuwiedi* and *B. diporus*. Based on this and on its membership in the *B. neuwiedi* complex, we suggest that it belongs to the *B. neuwiedi* lineage. *Bothrops mattogrossensis* was recovered in *B. alternatus* and *B. jararaca + B. neuwiedi + B. alternatus* clades in alternative analyses (Figure 10, also S-3–S-4, S-7–S-9), but the similar morphology that originally classified this species as *B. neuwiedi* suggests that it also belongs in the *B. neuwiedi* clade.

Table 12. Habitat, distribution and proposed genera for all species of *Bothrops* (*sensu* Campbell & Lamar, 2004), including those not represented in the present analysis. Distribution and habitat data from Campbell & Lamar (2004).

Proposed genus	Species	Original Describer	Distribution	Habitat
Rhinocerophis	*alternatus*	Duméril, Bibron, & Duméril, 1854	southeastern Brazil, Paraguay, Uruguay, northern Argentina	Humid habitats in tropical, subtropical and temperate deciduous forests
Rhinocerophis	*ammodytoides*	Leybold, 1873	along eastern versant of Andes in Argentina	Temperate to subtropical savannas and steppes; arid, sandy, rocky areas
Rhinocerophis	*cotiara*	Gomes, 1913	southeastern Brazil and northern Argentina	Humid temperate *Araucaria* forest and associated savannas
Rhinocerophis	*fonsecai*	Hoge & Belluomini, 1959	southeastern Brazil	Mixed forest dominated by *Araucaria*, *Podocarpus*, and broad-leaved trees
Rhinocerophis	*itapetiningae*	Boulenger, 1907	southeastern Brazil	Open fields and bushy areas
Rhinocerophis	*jonathani*	Harvey, 1994	eastern slopes of Altiplano, central and southern Bolivia	Dry, rocky grassland
Bothropoides	*alcatraz*	Marques, Martins, & Sazima, 2002	Ilha Alcatrazes, Brazil	Low Atlantic Forest vegetation
Bothropoides	*diporus*	Cope, 1862	Argentina, Paraguay, southwestern Brazil	Chaco, wet palm-grasslands, semitropical deciduous forest, *Araucaria* forest, pampas
Bothropoides	*erythromelas*	Amaral, 1923	northeastern Brazil	Xeric and semiarid thornforest, dry tropical deciduous forest, open rocky areas
Bothropoides	*insularis*	Amaral, 1922	Ilha Queimada Grande, Brazil	Dry, rocky island habitat with scrubby forest, clearings and shrubs

Proposed genus	Species	Original Describer	Distribution	Habitat
Bothropoides	*jararaca*	Wied-Neuwied, 1824	southern Brazil, northeastern Paraguay, northern Argentina	Tropical deciduous forests and savanna, semitropical upland forests
Bothropoides	*lutzi*	Miranda-Ribero, 1915	northwestern Brazil	Savanna (cerrado) and thornscrub
Bothropoides	*mattogrossensis*	Amaral, 1925	southern Peru, Bolivia, Paraguay, northern Argentina, southern to central Brazil	Savanna (cerrado), Pantanal, Chaco, wet palm-grasslands
Bothropoides	*neuwiedi*	Wagler, 1824	eastern Brazil	Tropical and semitropical deciduous forest, temperate forest, Atlantic coast sand ridges
Bothropoides	*pauloensis*	Amaral, 1925	southern Brazil	Seasonally dry savanna (cerrado) and Atlantic forest associated with open areas
Bothropoides	*pubescens*	Cope, 1870	Uruguay and extreme southern Brazil	Pampas and grasslands
Bothrops	*andianus*	Amaral, 1923	central Andes in Peru and Bolivia	Montane and lower montane wet forests
Bothrops	*asper*	Garman, 1884	Atlantic versant of Mexico from Tamaulipas southward, northern Guatemala and Honduras, Atlantic lowlands of Nicaragua, Costa Rica and Panama, Pacific versant of Colombian and Ecuadorian Andes, northern Venezuela	Principally tropical rainforest and tropical evergreen forest, or edges of savannas
Bothrops	*atrox*	Linnaeus, 1758	tropical lowlands east of Andes, exclusive of Paraguay, Uruguay, and Argentina	Lower montane wet forest, savanna/gallery forest, tropical deciduous forest, rainforest

Proposed genus	Species	Original Describer	Distribution	Habitat
Bothrops	*brazili*	Hoge, 1954	east of Andes in equatorial forests of Colombia, Ecuador, Peru, Bolivia, southern and eastern Venezuela, Guyana, Suriname, French Guiana, and northwestern Brazil	Elevated Amazonian primary forest
Bothrops	*caribbaeus*	Garman, 1887	Saint Lucia Island, Lesser Antilles	Lowland tropical forest, including coastal plains with low humidity
Bothrops	*isabelae*	Sandner-Montilla, 1979		
Bothrops	*jararacussu*	Lacerda, 1884	Brazil, Paraguay, southern Bolivia, northeastern Argentina	Tropical rainforest, tropical semideciduous forest, broad-leaved evergreen forest, paraná pine forest
Bothrops	*lanceolatus*	Bonnaterre, 1790	Martinique, Lesser Antilles	Humid upland regions and wetter portions of northern windward coast
Bothrops	*leucurus*	Wagler, 1824	eastern Brazil	Atlantic forest remnants, tropical deciduous forest
Bothrops	*marajoensis*	Hoge, 1966	northern Brazil	Lowland savanna
Bothrops	*moojeni*	Hoge, 1966	central and southeastern Brazil, eastern Paraguay, northern Argentina, eastern Bolivia	Semiarid or seasonally dry tropical savannas
Bothrops	*muriciencis*	Ferrarezzi & Freire, 2001	eastern Brazil	Mesic Murici Forest, in Atlantic Forest
Bothrops	*osbornei*	Freire-Lascano, 1991	western slopes of Andes in Ecuador and extreme northwestern Peru	Subtropical moist and wet forest and montane wet forest
Bothrops	*pirajai*	Amaral, 1923	eastern Brazil	Atlantic lowland wet forest and lower montane wet forest

Proposed genus	Species	Original Describer	Distribution	Habitat
Bothrops	*punctatus*	García, 1896	Pacific foothills and coastal plain in Panama, Colombia, Ecuador	Subtropical and tropical moist and wet forest and montane wet forest
Bothrops	*sanctaecrucis*	Hoge, 1966	Amazonian lowlands of Bolivia	Lower montane wet forest
Bothrops	*venezuelensis*	Sandner-Montilla, 1952	northern and central Venezuela	Lower montane wet forest and cloud forest, including temperate areas
—	*barnetti*	Parker, 1938	Pacific coast of Peru	Arid desert scrub
—	*lojanus*	Parker, 1930	southern Ecuador	Arid temperate regions, primarily montane dry forest
—	*pictus*	Tschudi, 1845	Peru	Arid to semiarid coastal foothills, river valleys, and lower Andean slopes; dry rocky regions
—	*roedingeri*	Mertens, 1942	Peru, on Pacific coastal plain and foothills	Desert, low deciduous thickets, lower montane dry forest

Bothrops sanctaecrucis was not included in prior phylogenies; it was recovered in the *B. atrox* lineage in parsimony analyses (1, 2, 6, and 7) but was found in alternative placements in Bayesian analyses. Its range in Bolivia and terrestrial lifestyle in lower montane wet forest, as well as its strong resemblance to *Bothrops moojeni* (Campbell & Lamar, 2004) make it a likely member of the *Bothrops atrox* group (see Table 11). Likewise, *Bothrops andianus* was included in analysis on the basis of morphological data only, and in analysis 8 was sister to *Bothrops + Bothriopsis* excluding *Bothrops pictus* and *B. venezuelensis* (Figure 10). *Bothrops andianus* was also recovered as sister to *Bothrocophias myersi* within the *Bothrops+Bothriopsis* clade in three parsimony analyses (1, 6, and 7, Appendix D figures S-3, S-4, S-9). Its range in Peru and Bolivia and terrestrial habitat in montane wet forests make affinities with either *Bothrocophias* or the

Bothrops atrox group likely (Table 11). *Bothrops andianus* has a lacunolabial like the *Bothrops atrox* group and unlike *Bothrocophias* species that have the second supralabial separate from the prelacunal scale (Campbell & Lamar, 2004). In addition, *B. andianus* lacks tuberculate dorsal scales found on *Bothrocophias* individuals. We suggest a *Bothrops atrox* group placement is supported by outside evidence. Finally, *B. venezuelensis* was found in or near *Bothrops, Bothriopsis,* and *Bothrocophias* clades in alternative analyses. Its Venezuelan range places its affinities with either the *Bothrops atrox* group or with *Bothriopsis*, but its primarily terrestrial habits, brownish coloration and lack of a prehensile tail make it more similar to the *B. atrox* group than to *Bothriopsis*. This is supported by combined evidence analyses 6 and 7 (figures S-3 and S-4).

In contrast to the species above, additional evidence cannot help to place four species in recovered species groups. *Bothrops barnetti* was included in analyses on the basis of morphology only, and combined evidence analyses placed it near *B. pictus* although morphology-only analyses yielded different relationships. Similarly, evolutionary relationships of *Bothrops lojanus* are uncertain based on scale data from six specimens (Appendix E), although it was typically recovered sister to most *Bothrops + Bothriopsis* species in pilot analyses. Based on their habitats in arid regions of Peru and southern Ecuador, respectively (Campbell & Lamar, 2004), their affinities may be with the arid Peruvian species *Bothrops pictus.* All three species may be sister to *Bothrops* as currently defined. Until more comprehensive morphological or sequence data are available, *B. barnetti, B. lojanus* and *B. pictus* cannot be definitively placed in the

phylogeny. *Bothrops roedingeri* has sometimes been regarded as a synonym of *B. pictus* (see Campbell & Lamar, 2004), and due to this fact as well as its desert habitat and range near *B. pictus*, these two species would likely be congeners. Because of the uncertain position of *B. pictus*, we do not have a strong hypothesis for the phylogenetic placement of *B. roedingeri*.

Beta Taxonomy and Genetic Distance

Based on evidence for the paraphyly of *Bothrops* in this and previous studies cited above, and based on the monophyly and distinctness of species groups found in this study as well as earlier work, we suggest recognition of major lineages of *Bothrops* as distinct genera. As *Bothrops lanceolatus* is the type-species of the genus, the generic name *Bothrops* is assigned to the *B. atrox* group. The generic name *Rhinocerophis*, with type species *R. ammodytoides*, is available for the *alternatus* group. We propose the new name *Bothropoides* for the *neuwiedi-jararaca* group. As required, we define these three genera below. No taxonomic changes are necessary for *Bothriopsis* or *Bothrocophias*, as this study has found support for their monophyly.

In an overview of genetic distances among pitviper genera, cyt-*b* distances of South American pitviper species groups were similar to those in other genera, ranging from 6.7–13.8% within-group divergence and 12.3–17.1% between-group divergence (Table 10). In comparison, the clade of Central American pitviper genera *Cerrophidion, Porthidium,* and *Atropoides,* closely related to the South American clade, had within-group distances of 8.3–12.7% and between-group distances of 12.1–23.4%. In Malhotra & Thorpe (2004), within-group distances ranged from 4.4–14.2% and between-group

distances ranged from 10.3–26.5%. In our opinion, genetic distances alone do not provide a metric for delimiting genera or species, but similarity of genetic distance measures may be taken as additional support for the distinctiveness of the South American groups.

Basis for Systematic Revision

Our taxonomy agrees with several authors who recommend dividing *Bothrops* into less speciose and more ecologically and phenotypically cohesive monophyletic genera (Castoe & Parkinson, 2006; Gutberlet & Campbell, 2001; Harvey et al., 2005; Parkinson, 1999). We share their motivations for these changes. First, in agreement with many other studies we find *Bothrops* paraphyletic with respect to *Bothriopsis* and recommend changing the taxonomy of *Bothrops* to recognize only monophyletic groups (Campbell & Lamar, 1992; Castoe & Parkinson, 2006; Gutberlet & Harvey, 2002; Parkinson, 1999; Parkinson et al., 2002). Second, we recovered evolutionarily distinct lineages in *Bothrops* formerly recognized as distinct species groups (see Table 5, Araújo & Martins, 2006; Martins et al., 2001, 2002), and believe that these lineages should be named (Parkinson et al., 2002). Third, we recognize the distinctiveness of *Bothriopsis* and consider continued recognition of that genus to be valuable (Gutberlet & Campbell, 2001). Fourth, we recognize that the major lineages not only have morphological and DNA-based synapomorphies but they have distinct ranges and habitats (Table 11), and these differences would be more clearly recognized through naming lineages as genera. Naming the major lineages as genera is in keeping with recent practice in pitviper

taxonomy of dividing speciose groups into smaller monophyletic genera (Burger, 1971; Campbell & Lamar, 1989, 1992; Malhotra & Thorpe, 2004).

Some authors have recommended synonymizing *Bothriopsis* with *Bothrops* and also mention the possibility of synonymizing the small, cohesive sister-genus *Bothrocophias* with *Bothrops* (Salomão et al., 1997; Vidal et al., 1997; Wüster et al., 2002). Part of this motivation has been to avoid the problems inherent in changing the names of medically important species. Taxonomic changes will likely result in temporary communication difficulties in the research and health care fields (Pook & McEwing, 2005; Wüster, 1996; Wüster et al., 1997; Wüster, Golay & Warrell, 1998, 1999a; Wüster & Harvey, 1996). This is a concern, but these changes will include more information on the relationships among South American pitvipers and so are likely to be important to toxinologists and clinicians dealing with venoms and envenomations. We feel that the long-term good of a stable and evolutionarily informative taxonomy will outweigh the short-term drawbacks of proposing changes to the scientific names of venomous snake species.

Another proposed reason for synonymizing *Bothriopsis* (and possibly *Bothrocophias*) with *Bothrops* is that the clade is derived from a single invasion of South America, and splitting it could obscure this biogeographic pattern (Wüster et al., 2002). This is true, but we also recognize the biogeographic pattern of South American colonization seen in the divergence of major lineages and think it would be clarified through naming them as genera. It is likely that those studying South American

biogeography using pitvipers would be familiar with their phylogeny and therefore taxonomic changes should not greatly affect biogeographic understanding.

Wüster et al. (2002) also suggest that although *Bothrops + Bothriopsis* contains greater morphological and natural history diversity than other genera, it appears no older based on cyt-*b* divergence levels. Our cyt-*b* genetic distance results suggest that although the major lineages certainly contain less genetic divergence than *Bothrops + Bothriopsis* their divergence levels are similar to those of other recognized genera.

A further motivation for synonymizing *Bothriopsis* with *Bothrops* is that since arboreal species *Bothrops punctatus* and *B. osbornei* are more closely related to the terrestrial or semiarboreal *Bothrops atrox* group than to the arboreal genus *Bothriopsis* (Table 5), there is little reason to recognize *Bothriopsis* as a separate genus (Wüster et al., 2002). Arboreality has evolved multiple times within the Crotalinae (Castoe & Parkinson, 2006; Gutberlet & Harvey, 2004; Malhotra & Thorpe, 2004), and it can be argued that continued recognition of *Bothriopsis* serves to cast taxonomic light on an additional instance of this phenomenon.

In addition to naming new genera or synonymizing *Bothriopsis* with *Bothrops*, other taxonomic options would be A) to delay taxonomic recommendations until complete data are available, B) to name the major lineages and *Bothriopsis* as subgenera of *Bothrops* under the rules of the ICZN, or C) to recognize *Bothriopsis* as a clade and name remaining clades without categorical ranks under the precepts of the PhyloCode (de Queiroz & Gauthier, 1990, 1992, 1994). First, the paraphyly of *Bothrops* with respect to *Bothriopsis* is an ongoing taxonomic problem that will be resolved with

the adoption of our proposed taxonomy. We anticipate the four species currently *incertae sedis* will be assigned to genera without requiring name changes to our proposed generic arrangement. Evidence strongly indicates that with additional data these genera will stand, therefore we do not consider the unassigned species a hindrance to adoption of our proposed taxonomy. Second, our concerns with naming subgenera are the same as the drawbacks of simply synonymizing *Bothriopsis* with *Bothrops*. Continuing to recognize the large and variable *Bothrops* requires disregarding a morphologically and ecologically distinct genus (*Bothriopsis*) as well as other evolutionarily distinct lineages. Within pitvipers subgenera are rarely recognized and so naming subgenera would not be materially different from including *Bothriopsis* within *Bothrops*. Third, as most concerns about taxonomic changes are in relation to changing species names, and as the current PhyloCode (Cantino & de Queiroz, 2007) specifies that species names are to be governed under the rank-based codes such as the ICZN, we choose to make taxonomic recommendations under the ICZN to avoid confusion about the correct names of species.

It is our responsibility as systematists to analyze and describe biodiversity and to utilize nomenclature to recognize distinct evolutionary lineages. The best way to recognize the evolutionary patterns recovered in this study is to recognize the major lineages as genera. Although future biodiversity research may result in minor changes to the content of these genera, we infer – on the basis of thorough taxon and character sampling and robust analytical methods – that the lineages themselves will continue to be supported.

Systematic Account

See McDiarmid et al. (1999) and Campbell & Lamar (2004) for synonyms. See Gutberlet & Campbell (2001) for a description of *Bothrocophias* and Campbell & Lamar (2004) for a description of *Bothriopsis* and for the inclusion of *Bothrocophias colombianus* in *Bothrocophias*, as the content of these genera has not changed.

Bothropoides gen. nov.

Type species: Bothrops neuwiedi Wagler 1824

Etymology: The generic name is derived from the Greek *bothros*, referring to the facial pit, and also referring to the currently named genus *Bothrops*. The term *oides* means "similar to" or "having the nature of", recognizing the affinity of these species to other terrestrial South American pitvipers. Names ending in this suffix are masculine.

Content: Bothropoides alcatraz, B. diporus, B. erythromelas, B. insularis, B. jararaca, B. lutzi, B. mattogrossensis, B. neuwiedi, B. pauloensis, B. pubescens

Definition: Members are of moderate length and girth, and terrestrial, lacking a prehensile tail. Dorsal color gold (*B. insularis*) to brown or black with dorsal markings spade-shaped, some lacking spots between spades (*B. alcatraz, B. insularis, B. jararaca, B. pauloensis*; *B. diporus*), others showing them (*B. erythromelas, B. lutzi, B. mattogrossensis, B. neuwiedi, B. pubescens*). A postorbital stripe is present (pale in most *B. insularis* specimens); dorsal head patterning is variable among species and they share no other distinctive head markings.

There are 3–5 interoculabials, 7–11 supralabials, 5–12 keeled intersupraoculars (smooth in *B. erythromelas* and one specimen each of *B. insularis* and *B. alcatraz*), 4–10

scales between the first pair of postcanthals, 21–34 interrictals, 144–206 ventrals, 21–30 dorsal scale rows at midbody, 31–66 divided or divided and entire subcaudals. Prelacunal and second supralabial fused (in *B. jararaca, B. alcatraz* and *B. insularis*) or separate with 0–1 rows of subfoveals. Supralacunal separate from middle preocular (one *B. mattogrossensis* had scales fused). Loreal wider than high or square (one *B. neuwiedi* had loreal higher than wide), loreal pit ventral to naso-orbital line. Postnasal in contact with first supralabial in some individuals. Dorsal scales keeled with typical thin ridge.

From examination of hemipenes of *B. diporus, B. alcatraz,* and *B. insularis*: many lateral spines on hemipenes with lateral calyces distal to crotch in most members of the genus, few spines with lateral calyces reaching crotch in *B. insularis*. Mesial spines present on hemipenes except for half of the *B. insularis* specimens. Calyces spinulate except in one *B. insularis* with smooth calyces.

From examination of osteological samples of *B. neuwiedi* and *B. jararaca*: 3–5 palatine teeth, 10–16 pterygoid teeth, 11–15 dentary teeth. Maxillary fang longer than height of maxilla, medial wall of maxillary pit cavity well-developed, pit in anterolateral wall of maxillary pit cavity simple or with a small rounded projection. Foramen absent from ventral surface of lateral process of prootic. Lateral margin of head of ectopterygoid of intermediate width, ectopterygoid shaft flat and tapering to narrow and not tapering, ectopterygoid base with a long overlapping projection. Choanal process of palatine positioned medially and greatly reduced (*B. neuwiedi*) or attenuate (*B. jararaca*) in shape. Meckellian foramen single, angular and splenial partially fused.

Diagnosis: Bothropoides differ from other South American pitvipers in 38 mitochondrial characters (Table 11). External characters overlap with other South American genera, with no unique synapomorphies in scalation. Distribution in eastern South America combined with terrestrial habitat in grasslands or broadleaf forests (*Bothropoides neuwiedi* group) or semiarboreal habitat in Atlantic forests (*B. jararaca* group) distinguishes this genus from others (see Table 11). *Bothropoides* has fewer interrictals (21–34) than the other South American genera (24–40), and some individuals have high numbers of supralabials (7–11, also seen in *Rhinocerophis*; all other South American genera have 7–8 supralabials). *Bothropoides* differs from *Bothrops* and *Bothriopsis* in having most species with the prelacunal separate from the second supralabial (*B. jararaca, B. alcatraz,* and *B. insularis* have the prelacunal fused to the second supralabial). Some specimens have both divided and entire subcaudals, a state seen also in *Bothriopsis*. *Bothropoides* differs from *Bothriopsis* in the lack of a prehensile tail and lack of green coloration. It differs from *Bothrocophias* in the lack of white spots on the gular scales, and the lack of tuberculate keels on posterior dorsal scales. *Bothropoides* differs from some *Rhinocerophis* (*R. alternatus, R. cotiara, R. fonsecai, R. jonathani*) in the absence of distinctive back bars on the underside of the head.

Distribution: Eastern South America: in Brazil and associated islands, Bolivia, southeastern Peru, Paraguay, Uruguay, and northern to central Argentina (Campbell & Lamar, 2004). See Campbell & Lamar (2004) for range maps of individual species.

Remarks: We did not examine individuals of *Bothrops lutzi*, but based on prior work by Silva that elevated this species out of the *Bothrops neuwiedi* complex (Silva, 2000, 2004), we include it in the genus *Bothropoides*.

Rhinocerophis Garman, 1881

Type species: Rhinocerophis nasus (Garman, 1881), a junior synonym of *Bothrops ammodytoides* (Leybold, 1873)

Etymology: The generic name is derived from the Latin *Rhinoceros*, meaning "nose-horn", referring to the strongly upturned snout of *R. ammodytoides*, and *ophis*, meaning "snake". Names ending in this suffix are masculine.

Content: Rhinocerophis alternatus, R. ammodytoides, R. cotiara, R. fonsecai, R. itapetiningae, R. jonathani

Definition: Members are short to elongate, of moderate girth to stout, and terrestrial, lacking a prehensile tail. Dorsal color brown to black with dorsal markings either spade-shaped, generally with spots between spades (*R. alternatus, R. fonsecai*; no spots between spades in *R. jonathani*, sometimes missing in *R. cotiara*), trapezoidal with spots between trapezoids (*R. itapetiningae*), or spotted (*R. ammodytoides)*. On head are spade-shaped dorsal markings and a postorbital stripe, with distinctive black bars on gulars of *R. alternatus, R. cotiara, R. fonsecai,* and *R. jonathani*.

There are 3–4 interoculabials, 7–10 supralabials, 5–16 keeled intersupraoculars, 5–12 scales between the first postcanthals, 25–40 interrictals, 145–181 ventrals, 23–35 dorsal scale rows at midbody, 25–55 divided subcaudals. Prelacunal and second supralabial separate with 0–1 subfoveal scale rows, supralacunal separate from middle

preocular (fused in *R. jonathani* and one specimen of *R. alternatus*). Loreal wider than high to higher than wide, loreal pit ventral to naso-orbital line. Postnasal not in contact with first supralabial. Dorsal scales keeled with typical thin ridge.

From examination of hemipenes of *R. alternatus*: mesial spines on hemipenes present, spinulate calyces distal to crotch, many (>12) lateral spines.

From examination of osteological samples of *R. cotiara, R. fonsecai,* and *R. itapetiningae*: 1–2 palatine teeth, 10–14 pterygoid teeth, 11–13 dentary teeth. Maxillary fang shorter than height of maxilla, medial wall of pit cavity in maxilla well developed. Lateral margin of head of ectopterygoid narrow, single pit on posterior surface of anterior end of ectopterygoid, ectopterygoid shaft narrow and not tapered, base with a long overlapping projection. Choanal process of palatine positioned anteriorly to medially, moderately high to attenuate. Supratemporal thick and rounded with a small projection. Meckellian foramen single; angular and splenial partially to completely fused.

Diagnosis: Rhinocerophis differs from other South American pitvipers in 27 mitochondrial characters and in having few (1–2) palatine teeth (versus 3–6 teeth), a morphological synapomorphy (Table 11). Distribution in southern South America combined with terrestrial habitat in open areas, grasslands, swamps, or broadleaf and *Araucaria* forests distinguishes this genus from others (see Table 11). *Rhinocerophis* individuals have the maxillary fang shorter than the height of the maxilla, and show black bars on the gular scales of some species (*R. alternatus, R. cotiara, R. fonsecai*, and *R. jonathani*). *Rhinocerophis* have fewer subcaudals (25–55) than the other genera (31–

86), and some specimens have high numbers of supralabials (7–10, also seen in *Bothropoides*; other South American genera have 7–8). *Rhinocerophis* differs from *Bothrops* and *Bothriopsis* in having the prelacunal scale separated from the second supralabial. It differs from *Bothriopsis* in the lack of green coloration and the lack of a prehensile tail. It differs from *Bothrocophias* in the lack of tuberculate keels on posterior dorsal scales. Almost all species differ from *Bothrocophias* in color pattern: while *Bothrocophias* species have spade-shaped dorsal markings lacking spots between the spades, *Rhinocerophis* species have spots between the spades (*R. alternatus, R. cotiara, R. fonsecai*), have trapezoidal markings with spots between them (*R. itapetiningae*), or have a checkered pattern (*R. ammodytoides*). Only *R. jonathani* lacks spots between spades but it can be distinguished by the presence of black bars on the gular scales, as mentioned above.

Distribution: Southern South America: in southeastern Brazil, central and southern Bolivia, Paraguay, Uruguay, and Argentina (Campbell & Lamar, 2004). See Campbell & Lamar (2004) for range maps of individual species.

Bothrops Wagler, 1824

Type species: Bothrops lanceolatus Lacépède 1789

Etymology: The generic name is derived from the Greek *bothros*, referring to the facial pit, and *ops*, meaning either “eye” or “face”. It refers to the loreal pits between the nostril and eye, and names ending in this suffix are masculine.

Content: Bothrops andianus, B. asper, B. atrox, B. brazili, B. caribbaeus, B. isabelae, B. jararacussu, B. lanceolatus, B. leucurus, B. marajoensis, B. moojeni, B. muriciencis, B. osbornei, B. pirajai, B. punctatus, B. sanctaecrucis, B. venezuelensis

Definition: Members are of moderate length to elongate, are thin to moderately stout, and are terrestrial, lacking a prehensile tail. Dorsal color brown to black, with trapezoidal to spade-shaped markings on most species (*B. lanceolatus* with spots, *B. osbornei* and *B. punctatus* with vertical bands). Head pattern variable from patternless to speckled to paired spots to spade-shaped pattern, as well as a postorbital stripe in most species (faint to absent in *B. brazili* and *B. sanctaecrucis,* absent in some *B. moojeni*); no other distinctive head markings.

There are 3–4 interoculabials, 7–8 supralabials, 3–13 smooth or keeled intersupraoculars, 3–11 scales between the first pair of postcanthals, 24–36 interrictals, 153–227 ventrals, 22–33 dorsal scale rows at midbody, 38–72 divided subcaudals (one *B. atrox* and two *B. jararacussu* specimens with both divided and entire subcaudals). Prelacunal and second supralabial fused (one *B. brazili* specimen with scales divided), supralacunal separate from middle preocular (one *B. asper* and one *B. atrox* with scales fused). Sublacunal entire, loreal pit ventral to nasoorbital line (one *B. caribbaeus* and one *B. venezuelensis* with pit crossed by line). Dorsal scales keeled with typical thin ridge.

From examination of hemipenes of *B. atrox, B. asper, B. brazili, B. jararacussu, B. leucurus, B. moojeni, B. punctatus* and *B. venezuelensis*: many lateral spines, lateral

calyces distal to crotch (one quarter of *B. brazili* specimens with lateral calyces reaching crotch).

From examination of osteological samples of *B. asper, B. atrox, B. brazili, B. jararacussu, B. moojeni,* and *B. punctatus*: pleurapophyses of midcaudal vertebrae long and slender (one-quarter of *B. brazili* specimens with short and slender pleurapophyses), 3–5 palatine teeth, 12–21 pterygoid teeth, 8–18 dentary teeth. Maxillary fang longer than height of maxilla, medial wall of pit cavity in maxilla well-developed, pit in anterolateral wall of maxillary pit cavity simple or with a small rounded projection. Lateral margin of head of ectopterygoid intermediate to narrow, shaft of ectopterygoid flat and tapering to narrow without tapering, pits on posterior surface of anterior end of ectopterygoid single or paired, ectopterygoid base long and overlapping, base of ectopterygoid longer than base of pterygoid. Choanal process of palatine positioned medially, moderate to attenuate in shape. Medial margin of dorsal portion of prefrontal moderately to weakly concave, dorsal surface of frontals with elevated margins (one specimen of *B. asper* and one of *B. atrox* with flat dorsal surface). Supratemporal with a small projection (one *B. asper* with expanded supratemporals lacking projections); supratemporal thick and rounded. Meckellian foramen single.

Diagnosis: Bothrops differs from other South American pitvipers in 50 mitochondrial characters (Table 11). In addition, *Bothrops* species generally have four palatine teeth, a morphological synapomorphy of the genus (*B. moojeni* and *B. jararacussu* have five; *B. brazili* and *B. sanctaecrucis* have three). *Bothriopsis* and *Bothrops* are distinguished from other South American genera by having higher

numbers of ventrals (157–236 and 153–227 respectively, compared to 125–206) and having the prelacunal fused to the second supralabial (also seen in *Bothropoides jararaca, B. alcatraz, B. insularis,* and some *Bothrocophias*). *Bothrops* is distinguished from *Bothriopsis* in its brown to black coloration and lack of a prehensile tail, except for *Bothrops osbornei* and *B. punctatus* with prehensile tails. These two *Bothrops* species occur west of the Andes as opposed to *Bothriopsis* species that all range east of the Andes.

Distribution: Most species found in South America east of the Andes, exclusive of Uruguay, southern Paraguay, and central to southern Argentina (Campbell & Lamar, 2004). *Bothrops caribbaeus* and *B. lanceolatus* are found on the Caribbean islands of Saint Lucia and Martinique. *Bothrops osbornei, B. punctatus,* and *B. asper* range through Peru, Ecuador and Colombia west of the Andes, and *B. asper* ranges northward in Middle America through the countries of Panama, Costa Rica, Nicaragua, Honduras, Guatemala, Belize and Mexico. See Campbell & Lamar (2004) for range maps of individual species.

Remarks: According to Ferrarezzi & Freire (2001, in Campbell & Lamar, 2004), *Bothrops muriciencis* is most similar in overall appearance to *Bothrops pirajai*, *B. brazili, B. jararacussu,* and *B. sanctaecrucis*, with *B. pirajai* suggested as the closest relative. *Bothrops pirajai* is poorly known and specimens were unavailable, but it is very similar to some specimens of *B. brazili* and *B. jararacussu* (Campbell & Lamar, 2004). As the aforementioned species included in the study all are found in *Bothrops* as described in this paper, we assign *B. muriciencis* and *B. pirajai* to the genus as well.

Key to South American Bothropoid Genera

1. Dorsal ground color green, gray, or brown, dorsal head color black or matching dorsum, tail prehensile, prelacunal and second supralabial fused 2

   Dorsal ground color and dorsal head color gold or brown to black, tail not prehensile, prelacunal and second supralabial fused or separate with 0–1 rows of subfoveals 3

2. Found east of the Andes, dorsal color usually green (lavender gray to green in *B. taeniata*, tan to brown, gray, or olive in *B. medusa*).....*Bothriopsis*

   Found west of the Andes, dorsal color brown to greenish tan .....*Bothrops*

3. Keel on dorsal scales tuberculate on caudal part of body, rostral higher than broad or square, distinct white spots on posterior infralabials and gulars may be present, canthorostrals may be present, 125–169 ventral scales (one specimen with 192 scales),.....*Bothrocophias*

   Keel on dorsal scales typical thin ridge, rostral broader than high to square or higher than broad in species lacking tuberculate dorsal scales, distinct white spots and canthorostrals absent, 145–227 ventral scales 4

4. Black bars on gular scales may be present; if absent, species has dorsal pattern of spots or parallel bands and nonprehensile tail. Dark patterning on head generally spade-shaped; head has a pattern of paired spots in species that have black bars on gular scales, have a dorsal pattern of parallel bands, or lack a nasal pore. Prelacunal and second supralabial separate with 0–1 subfoveals, loreal scale longer than high to higher than long, 25–40 interrictals, 25–55 subcaudals.....*Rhinocerophis*

Black bars on gular scales absent, markings on dorsum trapezoidal to spade-shaped except in species with prehensile tails. Dark patterning on head absent, speckled, as paired spots, or spade-shaped. Prelacunal and second supralabial fused or separate with 0–1 subfoveals, loreal scale longer than high to square, 21–34 interrictals, 31–72 subcaudals.....5

5. Prelacunal and second supralabial separate with 0–1 subfoveal scales; if fused, species is a Brazilian island endemic (*B. alcatraz* or *B. insularis*) or a coastal mainland species in southern Brazil, northeastern Paraguay and northern Argentina, generally having 8 supralabials and 170–216 ventrals (*B. jararaca*). Subcaudals both divided and entire or all divided, 7–11 supralabial scales, 144–206 ventral scales, mesial spines on hemipenes present.....*Bothropoides*
   Prelacunal and second supralabial fused. Species sympatric with *B. jararaca* either have fewer supralabials or fewer ventrals, or both. In all species, subcaudal scales divided, 7–8 supralabial scales, 153–227 ventral scales, mesial spines on hemipenes absent or present.....*Bothrops*

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CHAPTER 4: THE SERPENT AND THE EGG: UNIDIRECTIONAL EVOLUTION OF REPRODUCTIVE MODE IN VIPERS?

Introduction

The original formulation of Dollo's Law states that an organism cannot return, even partially, to an identical condition expressed by an ancestor (Dollo 1893, 1905, see also Simpson 1953, Collin and Miglietta 2008). This pattern of unidirectional evolution has been rejected by a number of recent phylogenetic studies (e.g. Collin and Cipriani 2003, Whiting et al. 2003, Chippindale et al. 2004, Kohlsdorf and Wagner 2006, Domes et al. 2007, Wiens et al. 2007, Brandley et al. 2008, Kohlsdorf et al. 2010), but several of these have been criticized for methodological flaws (Goldberg and Igić 2008, Galis et al. 2010). Unidirectional evolution remains the assumed pattern for a number of life history characteristics, therefore we evaluate the evidence for this pattern for a key trait in vertebrate life history, reproductive mode (see also Lynch and Wagner, 2009).

In vertebrates, reproductive mode is commonly understood to mean laying eggs (oviparity) or producing free-living offspring (viviparity), and is a prominent yet perplexing variable in life history evolution. Oviparity is primitive and often exclusively characterizes entire animal lineages, whereas viviparity has arisen multiple times (Blackburn 1982). Within the two basal amniote clades, mammals and reptiles, we see a major difference in the number of reproductive mode changes. In mammals, monotremes retain oviparity and viviparity probably arose only once, in the stem

leading to marsupials and placental mammals. Among living and fossil reptiles there are no known viviparous turtles, archosaurs (including birds), or rhyncocephalians, yet livebearing has arisen almost a hundred times among living squamates (Fitch 1970, Blackburn 1985). Here we capitalize on reproductive diversity within one subclade of squamate reptiles, the vipers, to rigorously appraise the possibilities and conceptual implications of evolutionary reversals in reproductive mode.

In Viperidae, an estimated 80% of species bear live young (Appendix F), and viviparity has arisen multiple times over tens of millions of years (Wüster et al. 2008; this study). This allows preliminary evaluation of the timing of transitions. Interestingly, recent phylogenetic hypotheses (Lenk et al. 2001, Castoe and Parkinson 2006, Wüster et al. 2008, Pyron and Burbrink 2009) place oviparous taxa within groups containing viviparous taxa, suggesting potential reversals from viviparity to oviparity.

The transition from oviparity to viviparity involves multiple complex changes: endocrine modifications to postpone parturition, suppression of nesting behavior, reduction or loss of organs and pathways needed in eggshell formation, and gain of adaptations for fetal respiration and nutrition (Blackburn 1995, Lee and Doughty 1997; but see de Fraipont et al. 1999). Because of the modifications required for a transition to viviparity in animals, a reversal to oviparity is considered unlikely on theoretical grounds (Neill 1964, Fitch 1970, Tinkle and Gibbons 1977), although the literature lacks strong empirical evidence or detailed justification for unidirectional evolution of reproductive mode (Lee and Doughty 1997).

Evolutionary reversals from viviparity to oviparity in squamate reptiles have been addressed in the past, but there is little evidence to definitively support reproductive mode reversal (but see Lynch and Wagner, 2009). Benabib et al. (1997) suggested a possible reversal to oviparity with a lizard species, but the inference had little support. De Fraipont et al. (1996) inferred multiple apparent reversals from viviparity to oviparity throughout squamate evolution. Criticisms of de Fraipont et al. (1996) highlighted multiple uncertainties in the phylogenies, counting particular transitions more than once, and other errors (Blackburn 1999, Shine and Lee 1999, Surget-Groba et al. 2001). Reanalysis of the 1996 dataset by de Fraipont et al. (1999) found equivocal evidence for reversibility of viviparity. Blackburn (1999) argued that reversals to oviparity cannot be ruled out theoretically, but no convincing empirical evidence has yet been found. Lynch and Wagner (2009) subsequently found strong evidence for reversal to oviparity in a sand boa, and Lynch (2009) concluded that among vipers a model that included apparent reversals was best supported by likelihood methods, albeit at a much lower rate than transitions from oviparity to viviparity. Lynch thus provided the first strong cases against Dollo's Law for reproductive mode in snakes, but as we will show below, additional model tests refine that conclusion for vipers. In particular, we use character mapping to investigate where and when reversals may have occurred. Because transitions to ancestral states should be long separated from origins of derived states to qualify as violations of Dollo's Law (Marshall et al. 1994), their timing should be evaluated with explicit phylogenetic methodology as we do in this study.

Most studies described above were primarily based on parsimony analysis of character evolution (but see Lynch, 2009; Lynch and Wagner, 2009). Maximum likelihood and Bayesian methods are now often used because they provide probabilistic estimates of character states at a node, and they can be used to statistically treat hypotheses about character evolution (Huelsenbeck and Bollback 2001, Collin and Miglietta 2008). Additionally, reverse-jump Markov Chain Monte Carlo Bayesian methods (RJ-MCMC) include models of evolution in the analysis and provide a means to determine which models are best supported by posterior probability (Pagel et al. 2004). RJ-MCMC has been used for character state reconstruction in only a few papers (see Ekman et al. 2008, Xiang and Thomas 2008, Montgomery et al. 2010, Rasmussen and Cameron 2010), and it has not yet been applied to tests of unidirectional evolution.

The goal of the present study is to re-examine the evolution of reproductive mode in vipers, incorporating multiple analyses and methods to best assess whether this character follows Dollo's Law of unidirectional evolution. We hypothesize that, contrary to this law, reversals are possible. This possibility of reversal may be due to conservation of developmental pathways over long periods of time, making phenotypic change easily reversible (Collin and Miglietta, 2008). The selective force driving the conservation of these pathways would be constraints on pleiotropic effects of pathway members. In accordance with this hypothesis we predict that vipers have experienced at least one evolutionary reversal from viviparity to oviparity. We test our hypothesis using multiple model comparison and ancestral character state reconstruction approaches,

summarize our results identifying reversals and discuss these in the context of Dollo's Law.

Methods

Phylogenetic estimation

To avoid circularity the dataset for phylogeny reconstruction was independent of the character of interest (Lee and Doughty 1997). As several character reconstruction methods assume that the phylogeny includes all extant taxa, we included representatives of all of the approximately 270 species of Viperidae that had DNA sequences available (Appendix F). This sampling included data for over 65 percent of the approximately 70 species of true vipers (Viperinae) and almost 80 percent of the approximately 200 species of pitvipers (Crotalinae), as well as *Azemiops feae*, the single species of Azemiopinae. Recent work (FitzJohn et al. 2009) suggests that accuracy and precision of BiSSE inference is essentially unaffected for phylogenies 75–100% complete. Published sequences constituted the majority of the dataset, and we added new information for 17 species. Four of these species had no published sequence data in GenBank prior to this study.

The mitochondrial sequences used in this study consisted of rRNA genes 12S and 16S and protein coding genes cytochrome *b* (cyt-*b*) and NADH dehydrogenase subunit 4 (ND4). These genes are commonly used to infer interspecific and intergeneric relationships in snakes (e.g. Parkinson 1999, Austin 2000, Parkinson et al. 2002, Malhotra and Thorpe 2004, Castoe et al. 2007, Wüster et al. 2007, Pyron and Burbrink

2009). Sequences were aligned with the Muscle algorithm (Edgar 2004) in MEGA 5.05 (Tamura et al.) using default parameters. Internal gaps in the alignment represented by <50% of taxa were deleted; all other gaps were treated as missing data. We chose *Acrochordus granulatus* as the far outgroup for comparison with recent family-level phylogeny (Wiens et al., 2008); Wüster et al. 2008), with 22 other colubroid species also included as outgroups (Appendix F). We partitioned the dataset into eight segments: one for each rRNA gene (two total) and one for each codon position in protein-coding genes (six total). We calculated model likelihoods for each partition in PAUP*, and estimated best-fit models of nucleotide evolution with MrModelTest 2.2 (Nylander 2004) using the Akaike Information Criterion (AIC). We conducted partitioned-model phylogenetic inference with BEAST 1.5.3 (Drummond and Rambaut 2007) using a Yule speciation process and a relaxed uncorrelated lognormal clock. We constrained lognormal priors for the time to most recent common ancestor (tMRCA) for certain groups based on fossil data: (1) the genus *Sistrurus* first appears in the late Miocene (Clarendonian; Parmley and Holman, 2007) and (2) *Agkistrodon contortrix* first appears in the late Miocene (Late Hemphillian; Holman, 2000). The constraint for *Sistrurus* was set for the stem of the group, with a mean of 4.7 Ma ± 0.4 SD and no offset. *A. contortrix* is the earliest-diverging member of its genus and therefore the constraint was placed at the MRCA of the genus, with a mean of 4.7 Ma ± 0.4 SD and no offset. Based on phylogeographic information on vicariance between mainland and Baja California desert regions (Castoe et al., 2009; Castoe et al., 2007) we set a normal prior on the tMRCA of *Crotalus atrox* and *C. ruber* to be 3.29 Ma ± 0.2 SD. We ran two independent

Markov chains for $4x10^7$ iterations, sampling every 1×10^5 iterations. We used Tracer 1.5 (Rambaut and Drummond 2007) to verify stationarity of the Markov chain and ensure that ESS values exceeded 200, and conservatively discarded the first 1×10^7 generations as burnin, resulting in a sample of 600 independent topologies with associated ultrameric branch length estimates. We also generated a phylogeny with oviparous and viviparous species constrained to separate clades and compared the likelihoods using Bayes Factors in Tracer 1.5 (Rambaut and Drummond 2007).

Character evolution estimates

Information on reproductive mode for each species was taken from the literature (Appendix F). Two species (*Garthius chaseni* and *Trimeresurus malabaricus*) do not have reproductive modes reported; in analyses that do not allow unknown states we treated these as having either mode, similar to species that show both reproductive modes (*Echis carinatus* and *Protobothrops jerdonii*). In addition, we treated *Atheris barbouri* as having unknown reproductive mode due to weak evidence for oviparity; Rasmussen and Howell (1998) mentioned *A. barbouri* was "apparently oviparous like the species of *Atheris*," but all other species of *Atheris* are viviparous.

Parsimony

We compared character state changes across the sample of 600 trees under reversible, irreversible, and Dollo models using MacClade 4.08 (Maddison and Maddison 2005). We estimated character history at all nodes across all trees using the Trace Character History module in Mesquite followed by the Step Through Trees command

(Maddison et al. 2007). Character values for nodes were calculated as the number of nodes reconstructed with the character state over the total tree sample in order to incorporate node confidence into character estimates.

Likelihood

Models of character evolution were tested with likelihood methods using the program Multistate in the package BayesTraits (Pagel et al. 2004, available at www.evolution.rdg.ac.uk). Using our posterior sample of 600 topologies and the character states for extant taxa, we tested three competing models of character transitions: 1) a Dollo model in which the transition probability for the change from viviparity to oviparity was constrained to be 0, 2) an equal rates model that constrained changes in both directions to have equal probability, and 3) a variable rates model that estimated transition probabilities for both directions independently. For all models, outgroups were eliminated to better conform to assumptions of complete taxon sampling. Additionally, the root node representing the ancestor of viperids was constrained to oviparity based on prior work asserting that this is the ancestral state for this group (e.g. Blackburn 1985) and that constraining the root is necessary for an appropriate test of Dollo's Law (Nosil and Mooers 2005). This was done using the "fossil" command. By constraining the root node instead of allowing the root state frequency to be determined by the tip frequencies, we avoid overestimating the frequency of viviparity at the root node and provide a conservative test of unidirectional evolution

Additionally, we used an evolutionary model that allows speciation and extinction rates to vary based on different states of a given character, using the BiSSE module in Mesquite (Maddison et al. 2007). The BiSSE model has six parameters: speciation rates when lineages are in (1) state 0 and (2) state 1, extinction rates for lineages in each character state (3-4), and rates of character transitions (5) from state 0 to state 1 and (6) from state 1 to state 0. State-dependent speciation (λ) and extinction (μ) rates either were constrained to be equal or varied independently; state transition rates were constrained to be equal, varied independently, or only allowed transitions from oviparity to viviparity (Dollo model). We constrained the root node representing the ancestor of viperids to oviparity using a revised BiSSE module designed by FitzJohn (FitzJohn and Goldberg, pers. comm.). We increased the number of optimizations for each tree from the default of 2 to 5 to increase the probability of convergence.

For all maximum likelihood analyses harmonic mean likelihoods across all 600 trees were compared using AIC, calculated as -2 * ln(likelihood) + 2K, and K being the number of parameters estimated from the data. Subtracting a model of interest from the model with the minimum AIC score produces a ΔAIC score, allowing comparisons among non-nested models. Models with ΔAIC of two or less have substantial support; models with ΔAIC of ten or more are considered to have no support (Burnham and Anderson, 2002).

Bayesian

Our fourth model comparison used RJ-MCMC to simultaneously determine the model and parameters with the highest posterior probability given the reproductive

mode data (Pagel and Meade 2006). We again used the program Multistate in the package BayesTraits (Pagel et al. 2004, available at www.evolution.rdg.ac.uk). As the distribution of character transition rates was not known *a priori,* we tested uniform, exponential, and gamma distributions for the rate parameters. As recommended by the authors of BayesTraits (Pagel and Meade 2006), we did not specify the parameters of the chosen distribution but rather seeded them from a uniform (0–10) hyperprior distribution. We ran each Markov chain for $1.0x10^8$ generations, sampling every 500 generations after a $1.0x10^7$ generation burnin. We ran three chains each for the chosen distribution to ensure convergence on the same parameters, and also used this analysis to reconstruct ancestral character states at generic-level nodes. Nodal character state estimates were determined by defining a clade with the AddNode command, which estimates support over the subset of trees that contain that clade. This value was then multiplied by the posterior probability estimate for that node in the phylogeny.

Results

Phylogeny

The final alignment consisted of 2289 characters, of which 1233 were parsimony-informative (12S 411, 216 informative; 16S 494, 189 informative; cyt-*b* 716, 416 informative; ND4 668, 412 informative). The consensus phylogeny was congruent with recent phylogenies (e.g. Wüster et al. 2008), and most nodes were resolved with strong support (Figure 11–Figure 12).

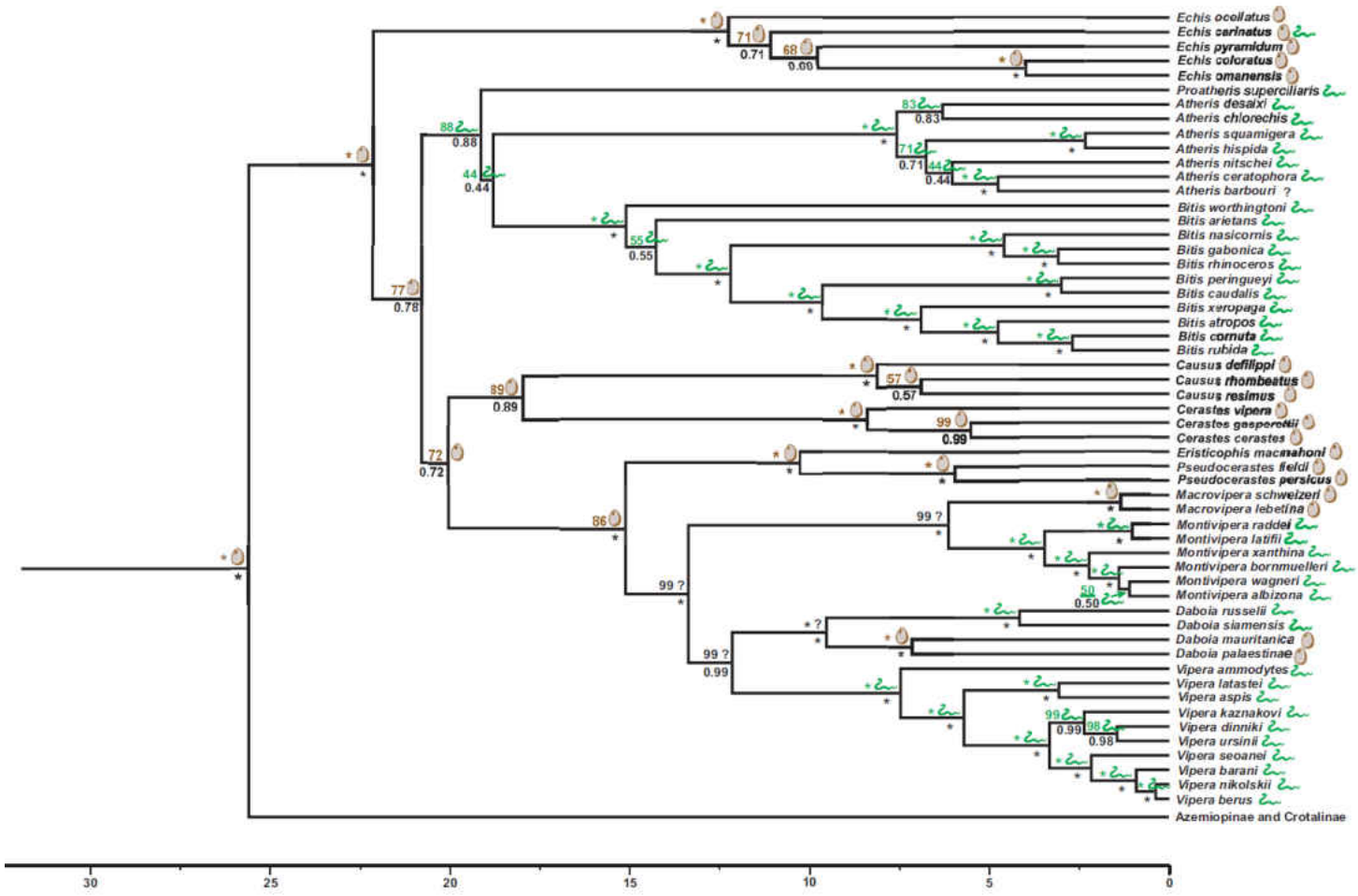


Figure 11. Ultrameric phylogram of viper relationships with nodes showing the evolution of reproductive mode inferred via parsimony. Brown eggs denote oviparity, green snakes denote viviparity, question marks denote equivocal character states. Percent of trees reconstructed with character state shown above nodes; phylogeny reconstruction shown below nodes. Asterisk denotes 100% or 1.0 Pp. Branch lengths scaled to millions of years

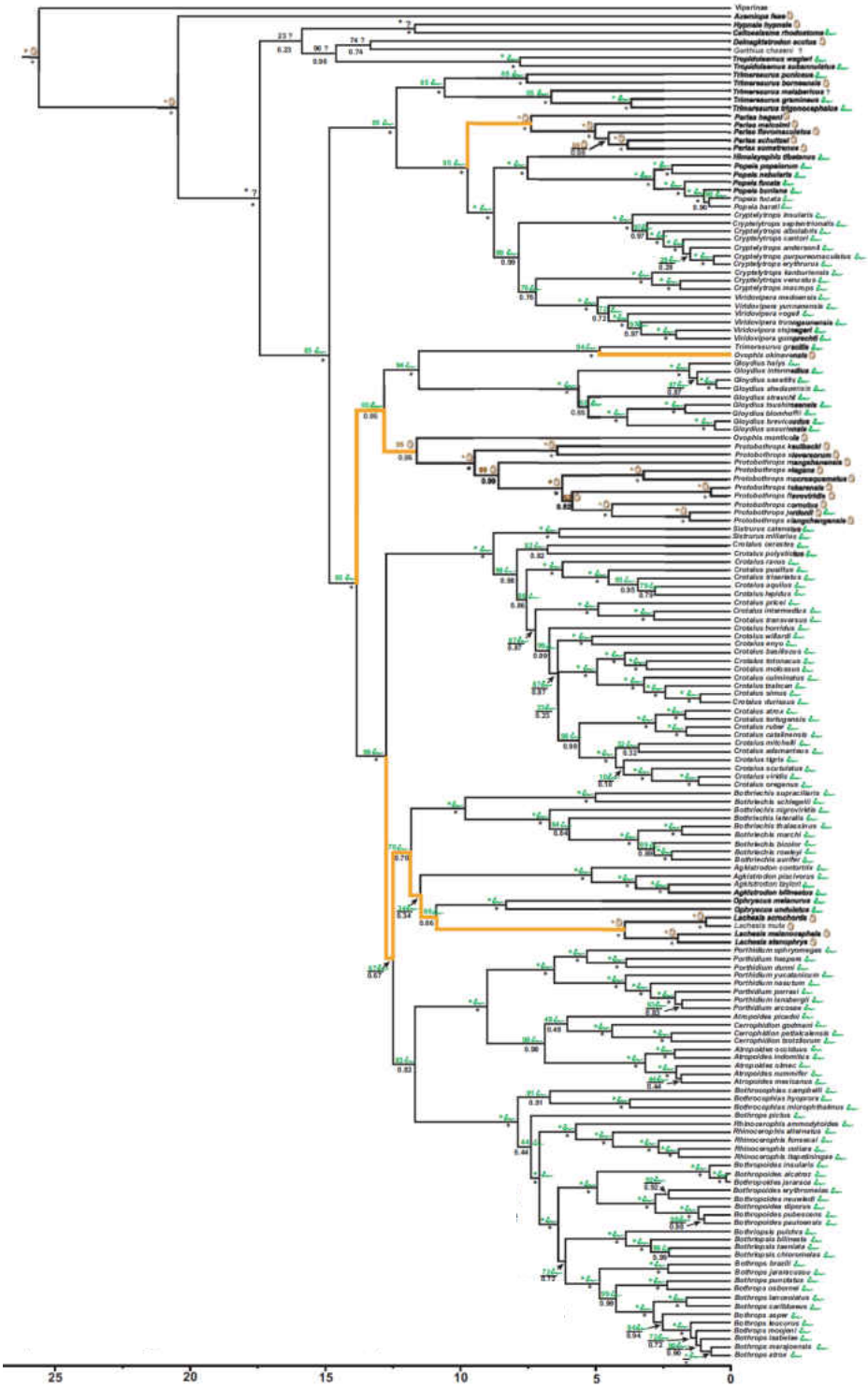


Figure 11 continued

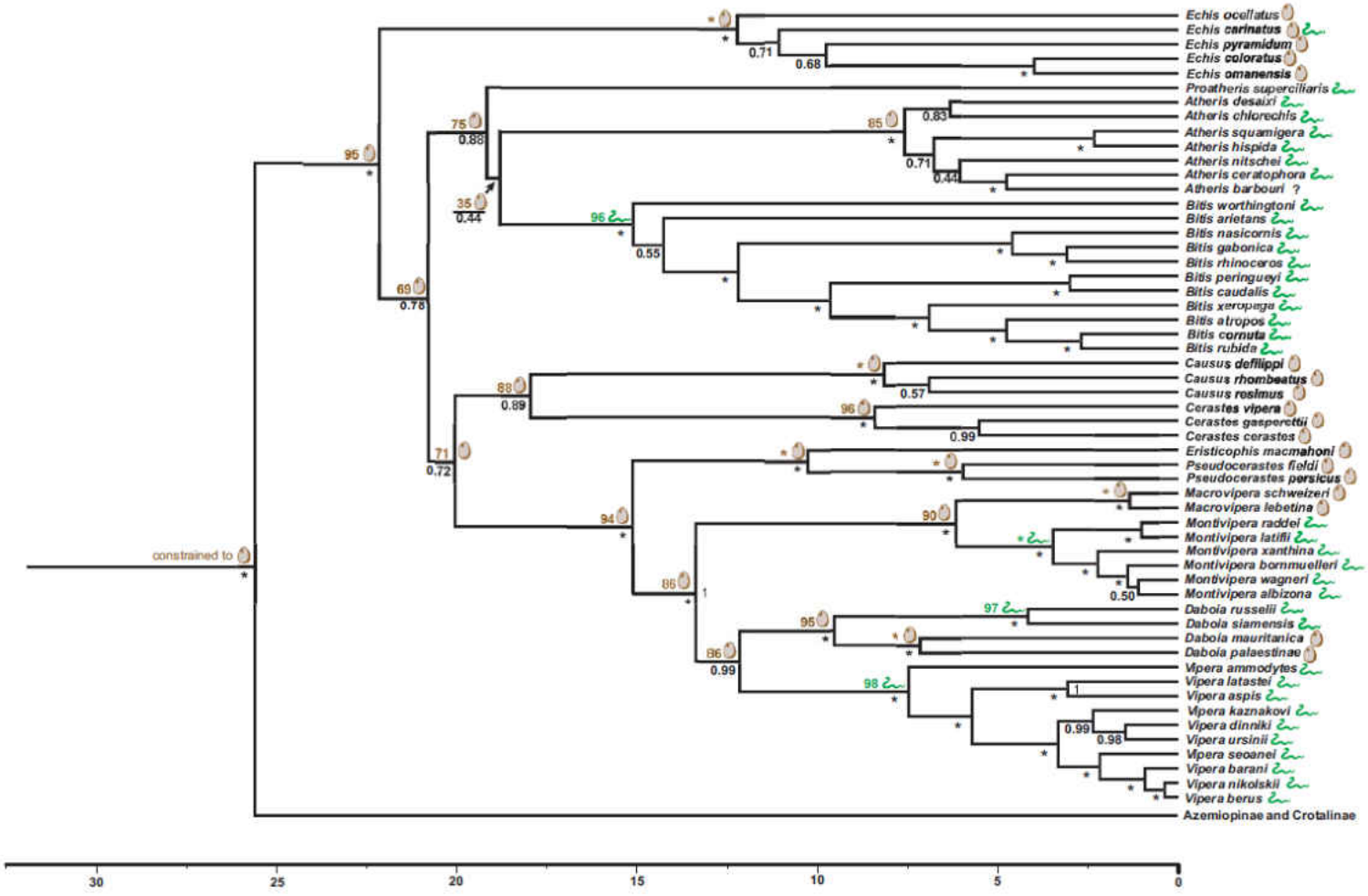


Figure 12. Ultrameric phylogram of viper relationships with nodes showing the evolution of reproductive mode inferred via Bayesian RJMCMC. Brown eggs denote oviparity, green snakes denote viviparity, question marks denote equivocal character states. Percent of trees reconstructed with character state shown above nodes, posterior probability (Pp) for phylogeny reconstruction shown below nodes. Asterisk denotes 100% or 1.0 Pp. Branch lengths scaled to millions of years.

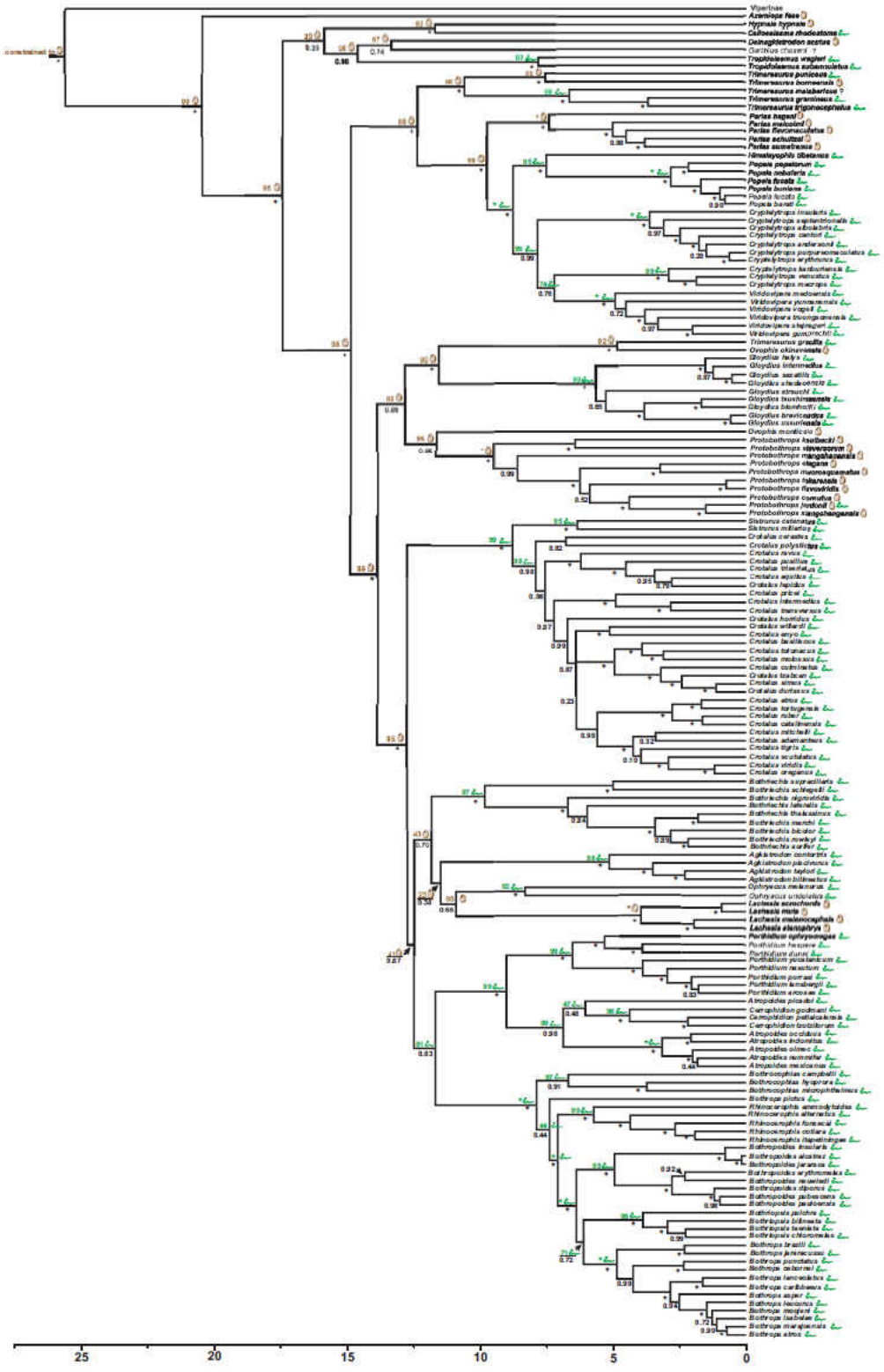


Figure 12 continued

A notable area of low support in this phylogeny is intergeneric relationships within Viperinae, which were also resolved with low support in previous work (e.g. Lenk et al. 2001, Wüster et al. 2008). We used the phylogeny that did not constrain oviparous and viviparous species to separate clades because it fit the data significantly better, with harmonic mean log likelihood of -105100 ± 1.776 SE compared to -106000 ± 4.329 for the constrained phylogeny (ΔBIC -413.9 for constrained model).

Character evolution

The reversible model of character evolution was most parsimonious, with an average of 17.16 and a range of 17–19 steps across all trees. Irreversible evolution resulted in an average of 24.45 and range of 20–27 steps; Dollo parsimony had an average of 24.94 and range of 23–27 steps. Parsimony character mapping showed similar patterns to character maps from other methods, but with higher node confidences (Figure 11,Figure 13). One well-supported reversal from viviparous ancestors to oviparous descendants was recovered: *Lachesis* was oviparous in 100% of trees, with the common ancestor of New World pitvipers viviparous in 99% of trees (Figure 11, Figure 13). Three other reversals were recovered with low support: oviparous *Parias* (100%) had three viviparous ancestors with 85% support, oviparous *Protobothrops* (95%) had two viviparous ancestors with 85% support, and oviparous *Ovophis okinavensis* had a viviparous direct ancestor (94%).

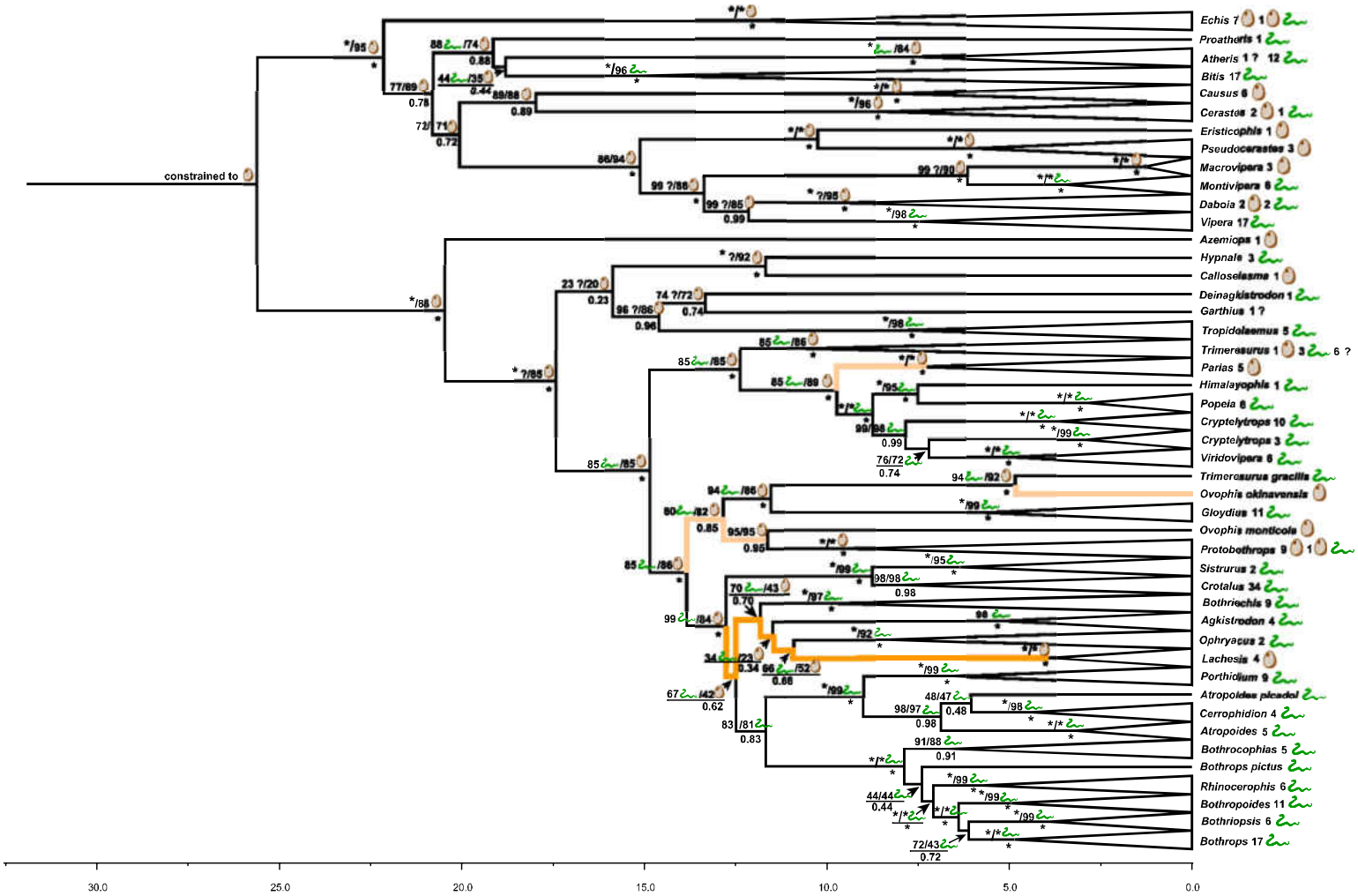
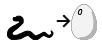


Figure 13. Phylogram of viperid relationships showing the evolution of reproductive mode. Eggs denote oviparity; snakes denote viviparity, question marks denote species with unknown character states. Percentage of nodes recovered by parsimony/posterior probability for character reconstruction shown above node; posterior probability for phylogeny reconstruction shown below node.

In Multistate maximum likelihood comparison, the character evolution model that best fit the data was variable rates, with average ln(likelihood) (lnL) of -49.30 ± 0.830 SD (Table 13). Higher lnL scores represent more optimal models. Equal rates and Dollo models had lower likelihoods with ΔAIC values of 6.2 and 7.8 compared to the optimal model; these values suggest some support for the nonoptimal models. The preferred model estimated the rate of transitions from oviparity to viviparity at 0.03405 ± 0.00374 SD, approximately ten times higher than the rate of apparent reversals (0.003227 ± 0 SD).

Table 13. Maximum likelihood models tested. All models have some support under AIC, optimal model is in italics. Parameter values are averages taken over the sample of 600 trees including standard deviations. Eggs symbolize rates under oviparity; snakes symbolize viviparity.

			Character state transition rate (q)			
Model	Parameters	LnL			AIC	ΔAIC
Variable rates	*2: $q_{ovip\ to\ vivip} \neq q_{vivip\ to\ ovip}$*	*-49.30 ± 0.83*	*0.0340 ± 0.0037*	*0.00323 ± 0.000*	*102.6*	*0*
Equal rates	1: $q_{ovip\ to\ vivip} = q_{vivip\ to\ ovip}$	-53.42 ± 0.84	0.0136 ± 0.0014		108.8	6.244
Dollo	1: $q_{vivip\ to\ ovip} = 0$	-54.21 ± 1.45	0.0487 ± 0.0057	0	110.4	7.824

BiSSE estimates found no significant effect of character state on speciation or extinction rates, with the optimal model constraining speciation and extinction rates to be equal for oviparous and viviparous lineages, and constraining reversals from viviparity to oviparity to minimum rates (Table 14). The only other model with ΔAIC support was the Dollo model allowing speciation and extinction rates to vary with character state. Models allowing reversals were significantly less likely, with ΔAIC values of 14.65 to 19.13.

Table 14. BiSSE models tested. Model name includes number of parameters for that model. Model 5d has some support under AIC, optimal model is bold. Parameters not mentioned in models were allowed to vary independently of each other. Parameter values are harmonic means taken over the sample of 600 trees. Eggs symbolize rates under oviparity; snakes symbolize viviparity.

			Speciation rate (λ)		Extinction rate (μ)		Character state transition rate (q)			
Model	Parameters	LnL	🥚	🐍	🥚	🐍	🥚→🐍	🐍→🥚	AIC	ΔAIC
6	All rates variable	646.7	0.113	0.196	2.33e-6	3.62e-7	0.0282	0.0031	-1283	19.13
5a	Speciation rates equal ($\lambda_{ovip}=\lambda_{vivip}$)	647.8	0.193		3.874e-6	6.350e-6	6.770e-7	0.0102	-1286	16.39
5b	Extinction rates equal ($\mu_{ovip}=\mu_{vivip}$)	647.8	0.093	0.193	4.925e-6		1.355e-6	0.0104	-1286	16.45
5c	Character state transition rates equal ($q_{ovip\ to\ vivip}=q_{vivip\ to\ ovip}$)	646.7	0.113	0.197	2.635e-6	1.350e-6	0.0031		-1283	18.65
5d	Dollo transition rates ($q_{vivip\ to\ ovip}=0$)	654.0	0.122	0.196	1.039e-6	1.042e-6	0.0416	1.000e-7	-1298	4.000
4a	$\lambda_{ovip}=\lambda_{vivip}$, $\mu_{ovip}=\mu_{vivip}$	646.7	0.196		2.493e-6		0.0282	0.0031	-1285	16.65
3a	$\lambda_{ovip}=\lambda_{vivip}$, $\mu_{ovip}=\mu_{vivip}$, $q_{ovip\ to\ vivip}=q_{vivip\ to\ ovip}$	646.7	0.197		1.159e-6		0.003		-1287	14.65
3b	**$\lambda_{ovip}=\lambda_{vivip}$, $\mu_{ovip}=\mu_{vivip}$, $q_{vivip\ to\ ovip}=0$**	**654.0**	**0.196**		**1.328e-6**		**0.042**	**1.000e-7**	**-1302**	**0**

RJ-MCMC analysis with exponential and gamma-distributed hyperpriors had the highest harmonic mean likelihoods, and the exponential prior was used in further analysis to reflect the philosophical preference for explanations requiring fewer events (Occam's razor, FitzJohn et al. 2009). RJ-MCMC sampled the Dollo model most often, with that model used in 84.62% of the posterior probability sample. The next model with support was the equal rates model, found in 14.82% of the posterior probability sample. Character state transition rates were estimated from all post-burnin samples, with average $q_{ovip\ to\ vivip} = 0.0407 \pm 0.0002$ SD and $q_{10} = 0.0181 \pm 0.0002$ SD. Ancestral states reconstructed under RJ-MCMC generally had strong support for shallow, genus-level nodes, with low support for deeper nodes (Figure 12–Figure 13). This finding led to a lack of support for apparent reversals in this analysis. Constraint of backbone nodes to oviparity or viviparity led to support for different models of character evolution: oviparity constraints supported Dollo models and viviparity constraints supported equal transition rate models. Oviparity constraints (-50.54 to -50.30) had greater log likelihoods than viviparity constraints (-53.38 to -53.24), but viviparity models had some support under AIC (Table 15). Nodal support for backbone nodes generally showed support for the character state of the additional node constraint.

Table 15. Bayesian RJ-MCMC models tested based on node constraints (above), and estimated character states across nodes involved in potential reversals using backbone node constraints (below). Character evolution model support measured as proportion of posterior probability; optimal model is bold. Parameter values are averages taken over the sample of 600 trees and including standard deviations. Eggs symbolize oviparity; snakes symbolize viviparity. Bolded values denote optimal models of character state change or optimal character states for node constraints. All analyses after the first have the root node fossilized to oviparity. Values below are posterior probabilities for the labeled character state at that node.

			Character state transition rate (q)		Models of character state change						
Constrained nodes	Constraint	LnL	🥚 → 🐍	🐍 → 🥚	Equal rates	Higher rate of 🐍 → 🥚	Higher rate of 🥚 → 🐍	Dollo: Zero 🐍 → 🥚	Zero 🥚 → 🐍	AIC	ΔAIC
None	–	-50.92 ± 1.60	0.0248 ± 0.015	0.0160 ± 0.011	0.1258	0.0010	0.0011	0.2807	**0.5914**	–	–
Root only	oviparity	-50.77 ± 2.41	0.0407 ± 0.016	0.0181 ± 0.013	0.1482	0.0028	0.0028	**0.8462**	0	–	–
Crotalinae	oviparity	-50.54 ± 2.43	0.0436 ± 0.014	0.0179 ± 0.013	0.0547	0.0031	0.0032	**0.9390**	0	**103.1**	**0**
	viviparity	-53.71 ± 1.02	0.0146 ± 0.004	0.0146 ± 0.010	**0.9986**	0.0007	0.0007	0	0	109.4	6.354
Trimeresurus sensu lato (*s.l.) + Protobothrops/ Gloydius* group + New World pitvipers	oviparity	-50.37 ± 2.35	0.0450 ± 0.012	0.0186 ± 0.014	0.0068	0.0026	0.0026	**0.9880**	0	**102.7**	**0**
	viviparity	-53.38 ± 1.03	0.014 ± 0.004	0.014 ± 0.010	**0.9979**	0.0009	0.0011	0	0	108.8	6.015
Trimeresurus s.l.	oviparity	-50.35 ± 2.33	0.0452 ± 0.012	0.0166 ± 0.013	0.0048	0.0027	0.0029	**0.9897**	0	**102.7**	**0**
	viviparity	-53.36 ± 1.02	0.0145 ± 0.004	0.0145 ± 0.010	**0.9967**	0.0018	0.0016	0	0	108.7	6.032
Trimeresurus s.l. excluding *Trimeresurus sensu stricto*(*s.s.*)	oviparity	-50.35 ± 2.33	0.0451 ± 0.012	0.0171 ± 0.013	0.0060	0.0024	0.0024	**0.9892**	0	**102.7**	**0**
	viviparity	-53.37 ± 1.03	0.0145 ± 0.004	0.0144 ± 0.010	**0.9959**	0.0021	0.0020	0	0	108.7	6.053
Protobothrops/Gloydius group + New World pitvipers	oviparity	-50.38 ± 2.35	0.0451 ± 0.012	0.0176 ± 0.014	0.0064	0.0023	0.0027	**0.9886**	0	**102.8**	**0**
	viviparity	-53.37 ± 1.02	0.0145 ± 0.004	0.0145 ± 0.010	**0.9973**	0.0014	0.0013	0	0	108.7	5.989
New World pitvipers	oviparity	-50.31 ± 2.30	0.0454 ± 0.012	0.0109 ± 0.012	0.0002	0.0002	0.0002	**0.9993**	0	**102.6**	**0**
	viviparity	-53.24 ± 1.18	0.0147 ± 0.005	0.0145 ± 0.010	**0.9695**	0.0151	0.0154	0	0	108.5	5.856

RJ-MCMC, reverse jump Markov chain Monte Carlo. AIC, Akaike information criterion. ΔAIC, change in AIC from minimum value to value of other model.

Constrained nodes →	Crotalinae		*Trimeresurus s.l. + Protobothrops/Gloydius* group + New World pitvipers		*Trimeresurus s.l.*		*Trimeresurus s.l.* excluding *Trimeresurus s.s.*		*Protobothrops/Gloydius* group + New World pitvipers		New World pitvipers	
Estimated nodes ↓	oviparity	viviparity	oviparity	viviparity	oviparity	viviparity	oviparity	viviparity	oviparity	viviparity	oviparity	viviparity
AIC	**103.1**	109.4	**102.7**	108.8	**102.7**	108.7	**102.7**	108.7	**102.8**	108.7	**102.6**	108.5
Trimeresurus s.l. + Protobothrops/ Gloydius group + New World pitvipers	94 O	99 V	–	–	–	–	–	–	–	–	–	–
Trimeresurus s.l.	95 O	95 V	99 O	95 V	–	–	–	–	–	–	–	–
Trimeresurus s.l. excluding *Trimeresurus s.s.*	96 O	73 V	99 O	73 V	100 O	73 V	–	–	–	–	–	–
Parias	100 O	100 O	100 O	100 O	100 O	100 O	100 O	100 O	–	–	–	–
Protobothrops/ Gloydius group + New World pitvipers	95 O	93 V	99 O	93 V	–	–	–	–	–	–	–	–
Protobothrops/ Gloydius group	99 O	80 O	100 O	80 O	–	–	–	–	100 O	80 O	–	–
Protobothrops + Ovophis	100 O	99 O	100 O	99 O	–	–	–	–	100 O	99 O	–	–
New World pitvipers	95 O	100 V	99 O	100 V	–	–	–	–	–	–	–	–
New World pitvipers excluding rattlesnakes	83 O	100 V	96 O	100 V	–	–	–	–	–	–	100 O	100 V
Agkistrodon + Bothriechis + Ophryacus + Lachesis	82 O	100 V	96 O	100 V	–	–	–	–	–	–	100 O	99 V
Ophryacus + Lachesis	91 O	66 V	99 O	66 V	–	–	–	–	–	–	100 O	65 V
Lachesis	100 O	100 O	100 O	100 O	–	–	–	–	–	–	100 O	100 O

O, oviparity. V, viviparity.

Discussion

Evolution of reproductive mode in vipers

We postulate multiple gains of viviparity in vipers (Figure 11Figure 13), but find equivocal support for reversals. Parsimony results showed apparent reversals in the ancestor of *Lachesis* with low support for reversals in the ancestors of *Parias, Ovophis okinavensis,* and *Protobothrops + Ovophis monticola* (Figure 11,Figure 13). Parsimony can take phylogenetic uncertainty into account but generally ignores uncertainty in character reconstruction; therefore we expect the support for these reversals to be overestimates. The *Lachesis* parsimony result, however, continues to provide an avenue for further study.

Maximum likelihood analyses found models allowing apparent reversals to be optimal (Table 13), but BiSSE likelihood and RJ-MCMC analysis found the Dollo model optimal; the latter did not infer strongly supported reversals from oviparity to viviparity in the phylogeny (Table 14, Figure 12Figure 13). BiSSE models found no significant effect of reproductive mode on speciation or extinction rates, supporting the validity of results from all model tests.

The model testing and character mapping results seem to be due to low support for intergeneric phylogenetic relationships and for the character reconstructions at backbone nodes. This is additionally supported by the results from RJ-MCMC analyses constraining backbone nodes to oviparity or viviparity (Table 15). Phylogenetic and character information in the backbone of the phylogeny does not appear to be strong

enough to overcome the influence of prior values on backbone nodes. An increase in phylogenetic resolution may help accept or reject unidirectional evolution for reproductive mode in vipers, but current results emphasize the importance of looking for congruence in multiple analyses in order to confidently detect violations of a well-established pattern.

Our parsimony and maximum likelihood results are in agreement with de Fraipont et al. (1996, 1999) in their detection of apparent reversals, and show that a focus on species- or genus-level variation in character states can provide perspective on evolutionary patterns that are not apparent from analysis of higher taxonomic levels (Shine and Lee 1999). Our inferred patterns also contribute to the findings of Lynch and Wagner (2009), who used parsimony and likelihood methods to support an apparent reversal from viviparity to oviparity in the boid *Eryx jayakari*. Their work finding an apparent reversal in a terminal taxon is enlightening, but inference of apparent reversals at deeper nodes would better suggest violations of Dollo's Law. Deeper inferred reversals are preferred because these nodes should be less affected if, through natural history research, an oviparous terminal is found to contain viviparous members. Our work points toward those possibilities, but better resolution is necessary.

Our results contrast with the viper work of Lynch (2009) in that we find the model constraining speciation, extinction and character state transition rates to be equal is not significantly different from models allowing those parameters to vary. Lynch found higher speciation rates in viviparous lineages. However our results agree with Lynch that transitions to viviparity were at least ninefold higher than transitions to

oviparity (Table 14).Our most optimal BiSSE model and the most optimal RJ-MCMC model inferred Dollo transition rates, which suggests an even more extreme difference in character state transition rates. The major difference between these studies appears to be taxon sampling, as this phylogeny contains more comprehensive sampling of pitvipers. Sampling differences can certainly contribute to differences in phylogeny estimation, and character reconstruction methods often assume complete taxon sampling. Because of the equivocal nature of the combined results from Lynch's (2009) and our study, we find no definitive support for a particular model of reproductive mode evolution in vipers.

Lee and Shine (1998) suggest that since neither viviparity nor oviparity is evolutionarily "superior", there is no compelling reason to expect evolution to act unidirectionally. They suggested the presence of five potential reversals in squamate reptiles, two of those occurring in viperid genera *Lachesis* and *Cerastes*. The apparent reversal in *Lachesis* is supported by parsimony, but apparent reversals in *Cerastes* were not found in any of our analyses, possibly due to low phylogenetic resolution among viperines. Lee and Shine's argument is supported by our viper results and should certainly be evaluated in other squamate reptiles, as well as expanded to other groups containing oviparous and viviparous lineages.

Implications for studies of character evolution

Our results support the importance of addressing current criticisms of phylogenetic tests of Dollo's Law and other patterns of character evolution (Goldberg and Igić 2008): taking phylogenetic uncertainty into account in character state

reconstruction, fulfilling the assumptions of the analyses used, correctly assigning character state frequencies to the root node, and accounting for character-state-specific rates of lineage diversification. In some cases, preliminary analyses that ignored one or more of these criticisms inferred different patterns of character evolution, which would have led to very different conclusions.

The number of nodes in which character states are not strongly supported (Figure 11Figure 13) suggests the importance of using models of character evolution that take all sources of uncertainty into account in character state reconstruction. In some cases a character state was inferred with >95% confidence, but low support for the existence of the node lowered the confidence in that reconstruction.

Additionally, we ran MCMC analyses that tested the effect of stem length on character state reconstruction, and found it had minimal impact. Replacing the stem estimated by outgroup rooting with one of minimal length resulted in estimates that were well within one standard deviation of the estimate using the outgroup root (e.g. $q_{ovip\ to\ vivip}$ = 1.03 ± 0.32 with outgroup rooting, 1.09 ± 0.33 without). Character state assignment was similarly unaffected with node estimates changing no more than 4% posterior probability. In no case did the length of the stem affect conclusions. This suggests that the differences between our outgroup sampling and that of Lynch (2009) should have no impact on results.

Incomplete sampling violates the assumptions of most character reconstruction methods (e.g. Maddison et al. 2007), although most phylogenies at this scale do not include all species. Our sampling included >75% of viperids, and work by FitzJohn et al.

(2009) suggests BiSSE inference should be little affected by this amount of missing data. Work by Lynch (2009) in vipers found little effect on model estimates for phylogenies over 70% complete, and our ingroup sampling is more complete. Although character mapping may be affected by incomplete sampling, missing potential reversals, it appears that reproductive mode is generally conserved at the generic level. We sampled >95% of genera, making future work unlikely to change our conclusions.

Including outgroups in character analysis strongly violates the assumption of complete taxon sampling, and preliminary analysis including outgroups found all model tests strongly rejecting the Dollo model in favor of models including apparent reversals. In light of our results finding only marginal evidence of reversals, it seems that the inclusion of outgroups can have a strong influence and lead researchers to potentially incorrect conclusions.

One of the most strongly criticized aspects of phylogenetic tests of character evolution is incorrect assignment of character state frequencies to the root node of the phylogeny. Preliminary analyses that did not constrain the ancestor of viperids to oviparity resulted in reconstructions with higher likelihoods, but tended to reconstruct that root node as viviparous, which is incorrect based on prior work and the character states of extant taxa (Blackburn 1985). This error is predicted because the high frequency of viviparity in vipers can lead to incorrect estimation of character state frequencies at the root node (Goldberg and Igić 2008). Therefore we consider our constrained analysis (Figure 11Figure 13) to be the most biologically realistic reconstructions.

Although character-dependent variation in speciation and extinction rates may lead to false inferences of apparent reversal, in vipers we found no significant effect of character state on either speciation or extinction rates. Lynch (2009) found speciation rates to be significantly different for oviparous and viviparous vipers, which would suggest BiSSE to be the most appropriate analysis in this group. Our BiSSE results are somewhat different than those of Lynch as they support Dollo models while the prior work allows a low rate of reversals. Overall, we find no definitive evidence supporting or rejecting Dollo's Law.

In contrast to methodological criticisms of studies finding character reversals, Wiens (2011) suggested in certain cases methodological biases may favor Dollo's Law. He cites a few situations where the law may be incorrectly supported or give ambiguous results, including if species with reversals have higher diversification rates, if they go extinct and are undetected among extant taxa. The most relevant situation to this study is if a trait is regained multiple times within a clade, a clear pattern of loss and regain may be replaced by a mosaic of trait presence and absence. As multiple oviparous and viviparous groups are spread throughout the tree of vipers causing a mixture of states to be recovered in ancestral nodes, this could certainly lead to the ambiguity recovered by our analyses. We agree with Wiens that a detailed simulation study should provide insight into the difficulties in rejecting Dollo's Law when it is false as well as the difficulties in supporting it when it is correct.

Future work on reproductive mode evolution

Our study found equivocal support for unidirectional evolution of viviparity from oviparity. Some methods suggested reversals are possible, particularly in *Lachesis*. Below we discuss additional considerations for inferring reversals: timing of changes and identification of developmental pathways.

The assumption underlying unidirectional evolution is that genes in the pathway leading to the ancestral character accumulate mutations once the derived character is fixed in the population. This means that transitions from derived to ancestral states occurring shortly after the origin of the derived state may be permitted by Dollo's Law. The reversals which are most interesting are those separated from origins of a derived state by greater than ten million years (Marshall et al. 1994). A review of recent Dollo's Law studies (Wiens 2011) finds several examples of apparent reversals occurring 15–60 million years after a complex character was lost. Timing of potential character state change in *Lachesis* supports continued research on this group. The estimated origin of viviparity was in New World pitvipers, occurring 13.8 mya (95% CI 11.0–16.5; 20.1–29.1 per Wüster et al. 2008), with the estimated reversal in *Lachesis* occurring 3.9 mya (95% CI 2.9–5.2; 3.5–9.8 per Wüster, also see Figs. 1, S2). This suggests the potential reversal occurred 10 million years or more after the origin of viviparity in the group. Although Sanders et al. (2010) suggest Wüster's dates may be older than predicted by certain fossils, our relative results are generally congruent with Wüster et al.

The second requirement to discover true bidirectional evolution is to investigate developmental mechanisms that give rise to a complex character, to distinguish

between convergence and true reversal (Collin and Miglietta 2008). If a character state arises through different pathways in ancestral lineages compared to lineages with phylogenetic patterns of reversal, the apparent reversals are actually convergent and unidirectional evolution may still stand. Mechanistic examination suggests that oviparity in sand boas may in fact be an independent evolution of that character state and not a true reversal (Lynch and Wagner 2009). A separate consideration is that selection on pleiotropic effects of the genes underlying a character state may conserve the possibility for that state to re-evolve through one or few mutational changes. Conservation of genes with pleiotropic effects is likely the mechanism underlying the re-evolution of metamorphic development in salamanders after 20–42 million years (Chippindale et al. 2004) and the re-evolution of shell coiling in slipper limpets after more than ten million years (Collin and Cipriani 2003). We consider selection on pleiotropic effects to be a mechanism driving true reversals to ancestral states. Comparison of reproductive mechanisms in the viperid groups mentioned above is beyond the scope of our study, but our results suggest that detailed comparisons of these genera with their closest viviparous relatives should prove enlightening.

Conclusions

When challenging an accepted explanation of biological patterns, one must find strong inferences of a competing pattern and be confident in the accuracy of those inferences. For example, the growing number of reported exceptions to the pattern of Dollo's Law (reviewed in Collin and Miglietta 2008) are accompanied by a growing number of criticisms of the methods used, citing overconfidence in the results (Lee and

Shine 1998, Blackburn 1999, Goldberg and Igić 2008). Our methods provide a conservative test of Dollo's Law and find equivocal support for violations of that law, illustrating the validity of current criticisms. These methods are easily replicated and should provide a strong test for any examination of patterns of character evolution.

In the case of transitions between oviparity and viviparity, the difficulty of these changes has simply been asserted and not empirically demonstrated (Lee and Doughty 1997). Costs of oviparity such as lowered ability to keep eggs at the proper temperature have been discussed often (Shine 1985, Shine and Lee 1999, Shine 2004), but the benefits of oviparity and the costs of viviparity are rarely considered (but see Lynch and Wagner 2009). Pregnant females are burdened and must thermoregulate, making them more vulnerable to predation and less able to capture prey. Viviparous females may require appropriate energy sources throughout gestation, while oviparous females are freed from reproductive constraints on energy intake after laying. These and other reasons suggest selection may favor bidirectional evolution. We suggest further study on the patterns and processes of reproductive mode changes, but place the burden of proof on adherents of the view that oviparity has not reversed within squamates.

Reproductive mode variation is a dramatic macroevolutionary pattern in amniotes, and as such reversals from viviparity to oviparity are interesting from a variety of developmental and evolutionarily ecological perspectives. Our analysis provides potentially rewarding avenues of research in this area. Detailed comparative studies of embryo-maternal relationships across potential transitions in viperid reproductive modes, as well as investigation into potential selective factors driving the retention of or

reversal to oviparity, are clearly called for. Moreover, within vipers the putative pattern of origins and reversals in reproductive mode warrant further analysis in the context of an equally complex pattern for the presence and absence of parental care in these snakes (Greene et al. 2002).

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CHAPTER 5: EVALUATING SOUTH AMERICAN DIVERSIFICATION HYPOTHESES IN PITVIPERS (SERPENTES: CROTALINAE)

Introduction

Historical biogeographic analysis can be divided into three phases: examining geographic ranges of one or a few focal taxa, inductively proposing processes causing observed patterns, and testing those proposals for generalizability (Ball, 1975; Crisp et al., 2010). In the Neotropics, many hypotheses have been generated to explain the great number of species found there but few comprehensive tests have been conducted. Although biogeography deals with past events that are not directly observed, those events have predictable effects on the landscape and its component species that lead to testable expectations for the evolution of lineages. Hypotheses generated by past work on independent datasets can be tested in new empirical systems that can support some alternative explanations and reject others in order to identify the processes with greatest effects on biodiversity in a focal region.

Traditional biogeographic hypotheses often relied solely on area cladograms, which combine the evolutionary relationships of multiple organisms to compile relationships among geographic areas (reviewed in Donoghue and Moore, 2003). These methods rely solely on the branching patterns of phylogenetic trees, but ignore the information contained in branch lengths: relative amounts of evolution from common ancestors. More recent studies have taken advantage of analyses that connect fossil

data to these branch lengths and include estimations of divergence dates along with the relationships among taxa (e.g. Chacón et al., 2012; Ruiz et al., 2012). This allows estimates of temporal relationships as well as spatial relationships, and greatly expands the power of phylogenetics to test biogeographic predictions.

Neotropical historical biogeography has mostly focused on the late Tertiary (Neogene) and Quaternary periods, which hosted a number of geological and climatic changes that should have affected speciation (Hoorn and Wesselingh, 2010a). In the Miocene, the Andes mountains rose, which redirected watersheds to the east: water from the northern-flowing proto-Orinoco basin shifted course to flow east as the new Amazon River (Figure 14). During periods of high sea levels in the Miocene and Pliocene, inland brackish seas filled in the Amazonian tributaries (Pebas basin), lowlands east of the southern Andes (Paraná basin), and the area between the Guyana and Brazilian shields (Pirabas basin, Figure 14–Figure 15). Finally, in the Pliocene and Pleistocene, climate cycles associated with glaciation towards the poles may have changed habitats in the Amazon basin (e.g. Figure 16).

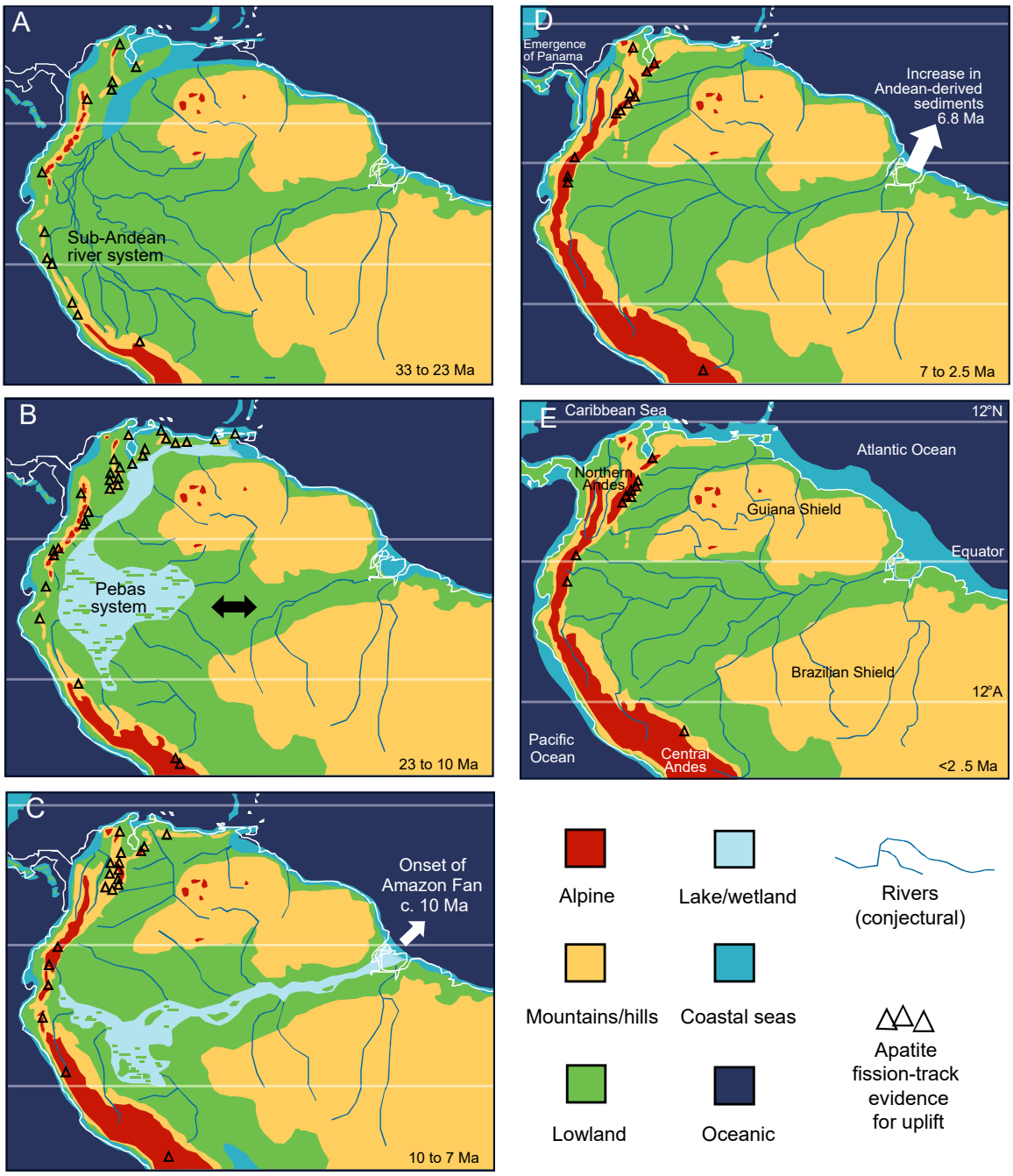

Figure 14. Paleogeographic maps of South America from Hoorn et al. (2010), representing geological barriers to pitviper expansion. Before entrance of pitvipers, the Andean range began to rise (A), with a peak of mountain building approximately 12Ma and inland seas forming (B). Uplift continued and restricted biotic dispersal (C). The Amazon River began its current flow pattern, *terre firme* rainforests expanded, and the Isthmus of Panama closed allowing the Great American Biotic Interchange (D). By the Quaternary Period geologic change had completed (E). Note that South America migrated north during the Paleogene period.

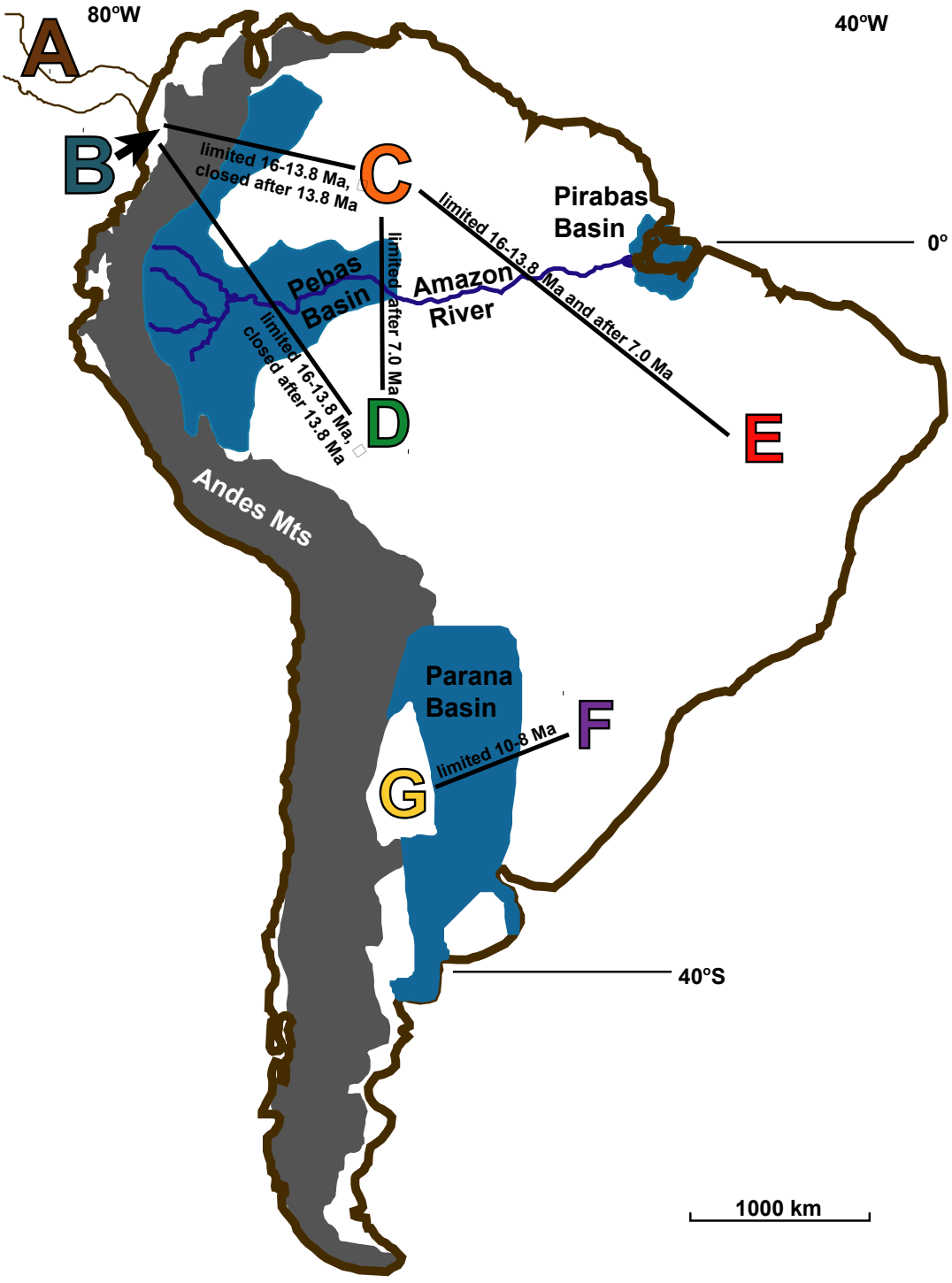

Figure 15. Map of South America modified from Rebata-H et al. (2006), showing potential barriers to organismal dispersal: areas of marine incursion, the Andes mountain range and the Amazon River. Letters represent the regions used in this study, with A also representing outgroups with ranges north of the study area. Times where dispersal is limited or closed between adjacent areas noted on lines (dispersal constraints 0.001 and 0.0001, respectively, in Lagrange).

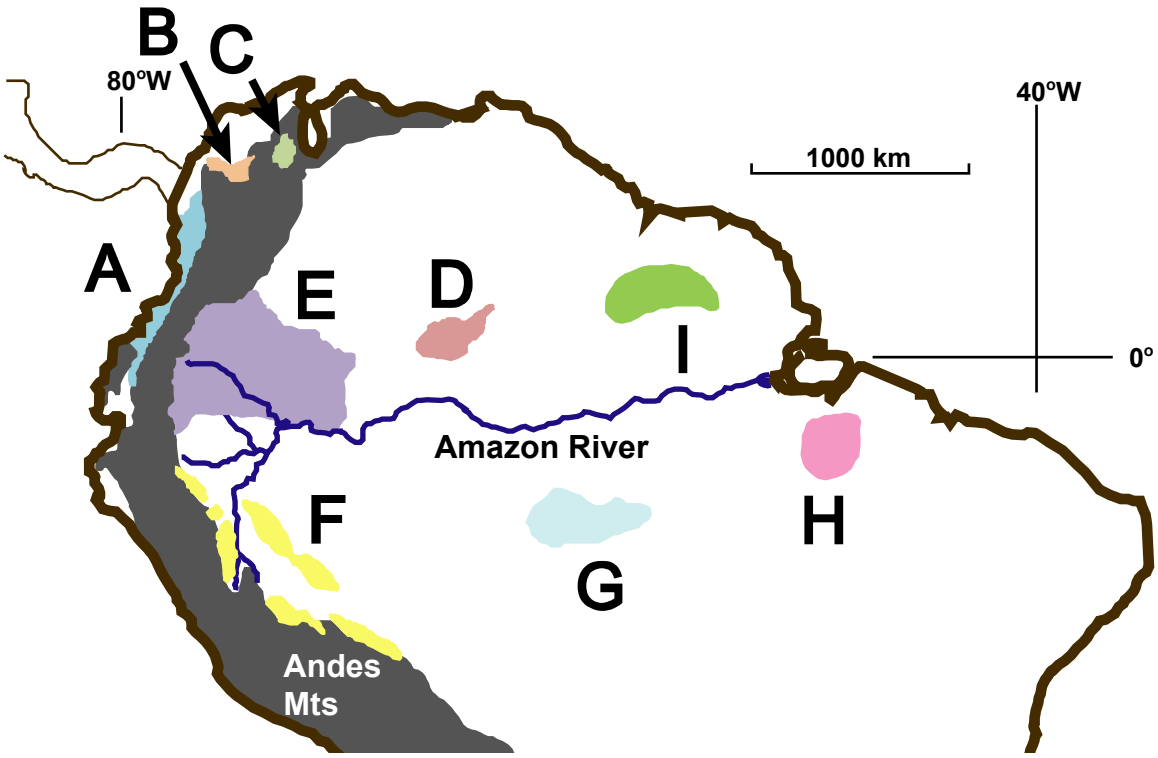

Figure 16. Map of South America modified from Rebata-H et al. (2006) showing refugial areas predicted by Haffer (1959): A) Chocó, B) Nechí, C) Catatumbo, D) Imerí, E) Napo, F) East Peruvian, G) Madeira-Tapajós, H) Belém, and I) Guiana. After 10 Ma dispersal from mid-Andean and Pacific versant sites (A-C) to Amazonian sites (D-I) is constrained (set to 0.0001 in Lagrange).

South America is a popular site for biogeographic work, partially because the Neotropics inform hypotheses on why the tropics contain more species than temperate areas, and also because of the amazing diversity of Amazonia. For example, the Neotropics contain the world's greatest plant diversity (Myers et al., 2000). Multiple hypotheses have been put forth to explain Neotropical diversity, including long-term climatic stability (Raven and Axelrod, 1974), Pleistocene climatic instability (Haffer, 1969), and interactions among geological and climatic processes occurring across the last 25 million years (Bush, 1994). Unfortunately, many of these explanations were based on incomplete knowledge – Nelson et al. (1990) showed that proposed biodiversity hotspots in Amazonia coincided with locations of biological field stations and field expeditions, suggesting that hypotheses were based on sampling artifacts instead of biological processes. Only in the 1990s did the approximate timing of the origin of modern Amazonia and its biota begin to be known (Wesselingh et al., 2010). In recent decades progress in geological knowledge, molecular phylogeny, climate modeling, and biodiversity documentation and modeling have shed light on diversification timing in South America (Hoorn and Wesselingh, 2010b; Wesselingh et al., 2010).

Because of molecular evidence, hypotheses for tropical diversification shifted from those relying on Quaternary climate changes to those citing primarily Neogene geographical and topographical reorganization, and most recently to those focusing on both types of drivers (Table 16, Rull, 2011).

Table 16. South American diversification hypotheses (Hyp.) and predictions tested in this study. Letter codes in spatial predictions correspond to areas defined in text and Figure 15, Figure 16, and Figure 19.

Name	Description	Spatial Prediction	Temporal Prediction
Allopatry			
1. Andean allopatry	Rising of the Andes split populations	Sister lineages east (A–B) and west (C–G) of mountain range	10 million years ago (Ma)
2. Marine incursion	Inundation of inland seas split populations	Sister lineages across basins:	Marine highstands:
		Pebas: slopes of Andes (B) vs. central Amazon region (C or D), or between northern and southern areas of central Amazon (C vs. D)	Pebas: 3.6–5, 8–10 and 13.8–16 Ma
		Pirabas: Guyana shield (C) vs. Brazilian shield (E)	Pirabas: 3.6–5 and 13.8–16 Ma
		Paraná: southeastern region (F) vs. southern Andes (G)	Paraná: 8–10 Ma
3. River barrier	Origin of Amazon River split populations	Sister lineages north (C) and south (D–E) of Amazon River	6.8 Ma or 2.4 Ma
Parapatry and climate			
4. Andean altitude	Rising of the Andes generated new climatic niches	Sister or ancestor-descendant lineages across Andean climate zones (CAC vs. CAT vs. CAF, SAC vs. SAT)	CAC vs. CAT 12 Ma, CAT vs. CAF 10 Ma
5. Museum	Middle altitude slopes with stable climate generated diversity during Quaternary; species preserved in lowlands	Sister or ancestor-descendant lineages across caliente and templada climate zones in Andes, Guyana and Brazilian highlands (e.g. CAC vs. CAT)	0.01–2.6 Ma
6. Divergence-vicariance	Middle altitude slopes with changing climate generated diversity during Quaternary	Sister or ancestor-descendant lineages across all climate zones in Andes, Guyana and Brazilian highlands (e.g. CAC vs. CAT vs. CAF)	0.01–2.6 Ma
7. Refugia	Climatically stable pockets of lowland forest isolated populations and drove divergence between refugia	Sister lineages across adjacent and nonoverlapping refugial areas (e.g. D vs. E)	0.01–2.6 Ma

These hypotheses can be generally classified as allopatric due to geologic change, parapatric due to geologic change, or based on climate changes.

Researchers have long assumed that the rising of the Andes led to allopatric speciation between Pacific and Amazonian lowland taxa (Hyp. 1, e.g. Brumfield and Edwards, 2007; Chapman, 1917). However, the importance of this event to diversification is mostly untested. The age of Andean uplift has not been settled (Rull, 2011), but recent research suggests the Central Andes rose in the Paleogene, 65–34 million years ago (Ma, Hoorn et al., 2010). Mountain formation in the Northern Andes first peaked approximately 23 Ma, with the most intense peaks of uplift approximately 12 Ma and 4.5 Ma. The mountain range was predicted to be low in Ecuador 20 Ma, leaving a possible connection between the Pacific and Amazonian versants through which terrestrial animals could pass (Hoorn, 1993; Hulka et al., 2006). That passage is expected to have closed by 9 Ma (Hulka et al., 2006). The Eastern Cordillera, which would have closed off dispersal from Panama to the Amazonian basin, started developing between 12.9 and 11.8 Ma (Hoorn et al., 1995) and is thought to have reached 50% of its current elevation, approximately 2000m, by 10 Ma (Gregory-Wodzicki, 2000; Hartley, 2003). This hypothesis predicts that species on either side of the Andes should form separate clades as a result of genetic isolation, and speciation should occur approximately 10 Ma.

A related hypothesis is that Andean uplift led to speciation via the opening of new climatic niches (Hyp. 4, Chapman, 1917; Chapman et al., 1926). Mountain rise led to the generation of new environments with colder climates, which would have been

populated by extensions of species ranges from lower altitudes. Local adaptation to these new habitats would have led to speciation via parapatry. This hypothesis predicts that sister species should have adjacent ranges, species at higher altitudes should be younger, and speciation should occur during or soon after the time of uplift. As the Guyana and Brazilian highlands predate the predicted entrance of vipers into South America (de Almeida et al., 1981), the rising of these areas would not affect viper diversification and is therefore not considered here.

Gutberlet and Campbell (2001) attributed the evolution of toadheaded pitvipers (*Bothrocophias*) to a combination of Andean allopatry and altitudinal uplift. They expected allopatry to cause divergence of Amazonian versant species *B. hyoprora* and *B. microphthalmus* from Pacific versant species *B. myersi, B. colombianus,* and *B. campbelli*. They expected that divergence within these groups was the result of altitudinal uplift. On the Amazonian side, uplift would drive divergence of lowland *B. hyoprora* from highland *B. microphthalmus*. On the Pacific side, *B. myersi* is the lowland form and would have diverged from *B. colombianus*, found in intermediate to high elevations, via parapatry. Highland inhabitant *B. campbelli* would have diverged from the group most recently via parapatry.

Altitudinal shift is also proposed to drive speciation in forest-pitvipers (*Bothriopsis*), separating cloud forest species *B. medusa, B. chloromelas, B. oligolepis*, and *B. pulchra* from lowland forms *B. bilineata* and *B. taeniata* (Werman, 2005). The phylogenetic affinities of *Bothrops andianus* are poorly characterized (see discussion in Fenwick et al., 2009), but its divergence is also attributed to Andean uplift (Werman,

2005). Zamudio and Greene (1997) suggested Andean allopatry drove the separation of Central American bushmasters *Lachesis melanocephala* and *L. stenophrys* from South American bushmasters *L. acrochorda* and *L. muta.*

A second allopatric hypothesis was proposed by Nores (1999) for avian speciation: diversification was driven by inland seas which filled during late Tertiary and Quaternary periods of sea-level rise (Hyp. 2, Figure 15). Haq et al. (1987) proposed a period of sea level rise about 100 m above present levels occurred in the Zanclean (5–3.6 Ma, Walker and Geissman, 2009) and a period of rise up to 150 m above present levels in the Langhian through early Serravallian (16–13.8 Ma). Incursions of saltwater into inland areas were predicted at these times between the Guiana and Brazilian Shields (Pirabas-Barreiras basin, Rossetti, 2001; Rossetti et al., 2005). Incursions were predicted to the south (Paraná basin) just after the Miocene drop in sea level at 10–8 Ma (Marshall et al., 1993).

In addition, the rising of the Eastern Cordillera of the Andes gave rise to a wetland basin to the east, Lake Pebas, which was sometimes inundated with saltwater from the Caribbean and/or Pacific (Rebata-H et al., 2006). One inundation was predicted to occur during the 16–13.8 Ma marine highstand, and an ebb to a more restricted basin occurred 10–8 Ma (Rebata-H et al., 2006). Werman (2005) suggested the divergence of Central American from South American bushmasters may have been due to isolation by the Pebas basin, an alternative to the Andean allopatry explanation favored by Zamudio and Greene (1997). The occurrence and extent of all of these inland seas is still controversial (Hoorn et al., 2010; Rull, 2011).

An additional effect of the rising of the Andes is the changing of river flow from the northern-flowing proto-Orinoco river to the northeast-flowing Amazon River, with entrenchment of the river in its current direction of flow 6.8 Ma (Figueiredo et al., 2009, 2010). Figueiredo et al. (2009, 2010) mentioned that the modern Amazon River was fully established 2.4 Ma, and this date was argued to be the correct date of river establishment by Campbell (2010). The river barrier hypothesis proposes that these changes in drainage patterns in the Miocene split populations to the north and south of the new barrier (Hyp. 3). This proposal is a modification of the original riverine barrier hypothesis proposed by Wallace to explain the distribution of monkeys in Amazonia (Wallace, 1852). Critics question whether the barrier effect of Amazonian rivers in the past was strong enough to cause speciation (Haffer, 2008). They cite the lack of spatial separation of animals in headwater regions, the transfer of land from one side of the river to the other as flow patterns change, and that the barrier effect may have been considerably weakened during dry periods of Quaternary climate cycles when rivers were contained within narrow, deep canyons (Haffer, 2008).

The refugia hypothesis, originally described by Haffer (1969), suggests that Pleistocene climate cycles iteratively separated tropical populations into separate areas of suitable habitat at the edges of the Amazon basin during glacial maxima and then connected them as forests expanded during glacial minima (Hyp. 7). He based the hypothesis on distributions of Amazonian endemic birds, and identified refugia based on range overlap in conjunction with areas of high rainfall (Bush, 1994; Haffer, 1969). This hypothesis dominated explanations of Neotropical diversity until recent decades (Hoorn

et al., 2011). Other work found support for refugia in some plants, butterflies, bees, scorpions, amphibians and lizards (reviewed in Bush, 1994), leading researchers to redraw refugial boundaries. The proliferation of proposed refugial areas (Bush, 1994), and the extension of proposed times of speciation across the Cenozoic (Haffer, 1997; Haffer, 2008) have frustrated attempts to test this hypothesis, but Pleistocene dating of speciation is still commonly assumed. Critics contend that interpretations of high endemism in certain areas are an artifact of disproportionate collecting intensity, not a result of environmental conditions driving speciation (Nelson et al., 1990). Others dismiss the assumed glacial aridity in the Neotropics (Colinvaux, 1997; Colinvaux et al., 1996; but see Simpson, 1997), and this view is presently widespread (Rull, 2011). As tested in this study, the refugia hypothesis predicts that sister species should be found in adjacent areas of endemism, and that speciation occurred in the Quaternary.

The refugia hypothesis is proposed to drive divergence between forest-pitviper species *Bothriopsis bilineata* and *B. taeniata* (Werman, 2005). Relationships within Amazonian lanceheads (*Bothrops*) and among populations within lancehead species may also be driven by isolation in refugial areas (Werman, 2005; Wüster et al., 1999). Climate change was also implicated in the evolution of southern lanceheads (*Rhinocerophis*) and Brazilian lanceheads (*Bothropoides*), although this was attributed to earlier Cenozoic cooling and drying trends and rain shadow effects of the rising Andes (Werman, 2005).

The museum hypothesis (Hyp. 5) also relies on climatic fluctuations driving speciation. In this case new species originate in climatically stable habitat pockets in highlands surrounding the Amazon during Pleistocene climate change. Those species

then expand their ranges into the Amazonian lowlands, which preserve them as a museum preserves specimens. The expectation is that the stable climate of Amazonian lowlands during climate fluctuations kept lineages from going extinct, and allowed those lineages to persist until the present. This preservation leads to the present great diversity of organisms in northern South America. The museum hypothesis does not require the major floral changes expected by the refugia hypothesis (Fjeldså et al., 1999; Haffer, 2008), and therefore avoids those criticisms of the refugia hypothesis that dismiss Amazonian aridity (Colinvaux, 1997; Colinvaux et al., 1996). This hypothesis predicts Pleistocene speciation and sister species occurring between lowlands and highland slopes.

The disturbance-vicariance hypothesis (Hyp. 6) suggests that Quaternary climate change led to species migration up and down highland slopes, a stressor that could have led to fragmentation of the geographic range and allopatric speciation of lineages (Bush, 1994; Haffer, 2008). This explanation is related to the intermediate disturbance hypothesis in ecology. Under this model the areas of greatest movement, the upland slopes, should be the areas of greatest endemic diversity. Sister species should occur across slopes with most speciation occurring in the Pleistocene. Because this hypothesis relies on existing highland areas at the time of speciation, Andean, Guyanan and Brazilian highlands could all contribute to biodiversity.

In general, molecular phylogenetic evidence does not appear to show a chronological trend for speciation of extant lineages, with timing varying among different types of organisms (Rull, 2008). Evidence suggests many extant clades

originated in the Neogene and continued to speciate through the Quaternary, with others constrained to only one of those periods (Rull, 2011).

Methods of biogeographic reconstruction that take advantage of the temporal information in branch lengths have been introduced recently (Goldberg et al., 2011; Ree and Sanmartín, 2009), and offer more rigorous tests of biogeographic hypotheses than cladistic analyses that relied only on branching patterns (e.g. Maciel et al., 2010; Nylander et al., 2008; Passoni et al., 2008). Dispersal-Extinction-Cladogenesis (DEC) methods model dispersal and local extinction along branches of a phylogeny, then estimate the ranges of descendant branches at each node (Ree et al., 2005; Ree and Smith, 2008). This method takes its origin from ancestral character state reconstruction and is therefore subject to the benefits and concerns of character estimation methods. For example, these methods assume complete taxonomic sampling, which is a concern that should be addressed in current and future work (Rull, 2011).

South American pitvipers are an ideal group for testing Neogene and Quaternary diversification hypotheses. Bothropoid vipers (genera *Bothrops, Bothriopsis, Bothropoides, Rhinocerophis,* and *Bothrocophias*) entered South America from Central America approximately 15–10 Ma (Castoe et al., 2009), and South American bushmasters (*Lachesis*) diverged 18–6 Ma (Zamudio and Greene, 1997); these groups therefore existed in the area during the time when many of the geological changes explained above occurred. In addition, the South American rattlesnake (*Crotalus durissus*) entered the continent near the time of the closure of the Isthmus of Panama at 3Ma (Wüster et al., 2005). Pitvipers greatly diversified in South America, generating

51 species in the six genera and great population-level diversity in the rattlesnake (Campbell and Lamar, 2004; Wüster et al., 2005). Bushmasters originated in Central America, with *Lachesis melanocephala* and *L. stenophrys* located there and *Lachesis acrochorda* and *L. muta* expanding into northern South America (Campbell and Lamar, 2004). A single bothropoid invasion gave rise to toadheaded pitvipers (*Bothrocophias*) in the Andes, Amazonian lanceheads (*Bothrops*) and forest-pitvipers (*Bothriopsis*) in Amazonia, Brazilian lanceheads (*Bothropoides*) on the Brazilian Shield, and southern lanceheads (*Rhinocerophis*) in the southeast (Fenwick et al., 2009). The extensive range and overlap in generic distributions provides multiple groups for testing any given hypothesis.

We reconstruct the biogeographic history of South American pitvipers using sequence data to test the specific spatial and temporal predictions of the hypotheses described above. We expect to find a select set of hypotheses that have empirical support from pitviper speciation events, which represent promising avenues for testing in other biological systems. We expect to find another set of hypotheses with low or no support from pitviper speciation, which should be viewed with caution by researchers working with other Neotropical terrestrial animals.

Methods

Input data

In order to infer accurate branch lengths and divergence times from Miocene to present, we used a large mitochondrial DNA dataset including 99 terminals, extensively

sampling all major New World lineages (Table 17). Outgroup species are mainly taken from Castoe & Parkinson (2006) and sources therein; ingroup species are mainly from Fenwick et al. (2009). Taxonomic references in this study follow Fenwick et al. (2009) for ingroup and Campbell and Lamar (2004) and Malhotra and Thorpe (2004) for outgroup.

We used four mitochondrial fragments common to pitviper studies: 12S and 16S ribosomal RNA genes and protein coding genes NADH dehydrogenase subunit four (ND4) and cytochrome b (cyt-*b*). We added new sequences for 33 samples following the methods of Castoe and Parkinson (2006). Alignments were done with the MUSCLE algorithm (Edgar, 2004) in MEGA 5.05 (Tamura et al., 2011) using default parameters. Internal gaps in the alignment represented by <50% of taxa were deleted; all other gaps were treated as missing data in analysis. We used separate partitions for each rRNA gene and for codon positions of protein-coding fragments. We determined partition-specific models with MrModelTest 2.2 (Nylander, 2004) using the Akaike Information Criterion (AIC).

Table 17. Species used, voucher data, collecting locality, and GenBank accession numbers for each species analyzed in pitviper phylogeny. Accession numbers labeled TBD are sequences original to this study. Institutional abbreviations are listed in Leviton, Gibbs, Heal & Dawson (1985).

Species	Field ID	Museum ID	Locality	12S	16S	cyt-*b*	ND4
South American ingroup							
Lachesis acrochorda	CLP 319		Colombia	JN870187	JN870197	JN870197	JN870212
Lachesis melanocephala	–		Costa Rica: Peninsula de Oro			U96018	U96028
Lachesis muta	Cadle 135		Peru	AF057221	AF057268	AY223604	AY223644
Lachesis stenophrys	–		Costa Rica: Limón Prov.	AF057220	AF057267	AY223603	U41885
Bothrocophias campbelli	INHMT uncataloged		Ecuador: Chimborazo Prov.			AF292584	AF292622
Bothrocophias hyoprora	–		Colombia: Dept. Amazonas	AF057206	AF057253	AY223593	U41886
Bothrocophias microphthalmus		LSUMZ H9372	Peru: Pasco Region	AY223657	AY223670	AY223594	AY223638
Rhinocerophis alternatus	DPL 2879		–	AY223660	AY223673	AY223601	AY223642
Rhinocerophis ammodytoides		MVZ 223514	Argentina: Neuquén Prov.	AY223658	AY223671	AY223595	AY223639
Rhinocerophis cotiara	WW		Brazil	AF057217	AF057264	AY223597	AY223640
Rhinocerophis fonsecai	IB 55543		Brazil: São Paulo			AF292580	AF292618
Rhinocerophis itapetiningae	ITS 427		Brazil: São Paulo	EU867253	EU867265	EU867277	EU867289
Bothropoides alcatraz	CBGM baz001		Brazil: São Paulo: Ilha de Alcatrazes			AY865820	
Bothropoides diporus	PT 3404		Argentina: La Rioja Prov.	DQ305431	DQ305454	DQ305472	DQ305489
Bothropoides erythromelas	RG 829		Brazil: Algoas	AF057219	AF057266	AY223600	U41877
Bothropoides insularis	WW		Brazil: São Paulo: Ilha Queimada Grande	AF057216	AF057263	AY223596	AF188705, AY223641
Bothropoides jararaca	(19)6		Brazil: São Paulo	EU867254	EU867266	EU867278	EU867290
Bothropoides neuwiedi		IB 5555	Brazil: São Paulo			AF292585	AF292623
Bothropoides pauloensis	CLP 3		–	EU867260	EU867272	EU867284	EU867296

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4
Bothropoides pubescens	SC N132		Uruguay: Dept. Rocha	JN870180	JN870192	JN870200	TBD
Bothriopsis bilineata	S.2		Brazil: São Paulo	TBD	TBD	TBD	TBD
Bothriopsis chloromelas		LSUMZ 41037	Peru: Pasco Region	DQ305430	DQ305453	DQ305471	DQ305488
Bothriopsis oligolepis	WW 2957		Peru: Cuzco Region			TBD	TBD
Bothriopsis pulchra	JM 78		Ecuador	JN870179		TBD	TBD
Bothriopsis taeniata	–		Suriname	AF057215	AF057262	AY233592	AY223637
Bothrops andianus		CORBIDI 8355	–	TBD	TBD	TBD	TBD
Bothrops asper	CLP50	MZUCR 11152	Costa Rica: Puntarenas Prov.	AF057218	AF057265	AY223599	U41876
Bothrops atrox	WW 743		–	AY223659	AY223672	AY223598	AY223641
Bothrops barnetti	WW 2060		Peru	TBD	TBD	TBD	TBD
Bothrops brazili		RWM 17831 (from USNM)	Venezuela: Amazonas	EU867252	EU867264	EU867276	EU867288
Bothrops caribbaeus	–		Saint Lucia			AF292598	AF292636
Bothrops jararacussu	DPL 104		–	AY223661	AY223674	AY223602	AY223643
Bothrops lanceolatus	–		Martinique			AF292599	AF292637
Bothrops leucurus	CLP 195		–	EU867255	EU867267	EU867279	EU867291
Bothrops marajoensis	–		–			AF292605	AF292643
Bothrops moojeni	ITS 418		Brazil: São Paulo	EU867257	EU867269	EU867281	EU867293
Bothrops osbornei	FHGO live 2166		Ecuador: Pichincha Prov.			AF292595	AF292633
Bothrops pictus	WW 2471	CORBIDI 2066	–		TBD	TBD	TBD
Bothrops punctatus	FHGO live 2452		–			AF292594	AF292632
Bothrops roedingeri	WW 2479		–				TBD
Outgroups							
Agkistrodon bilineatus	WWL 2		Costa Rica: Guanacaste Prov.	AF156593	AF156572	AY223613	AY156585
Agkistrodon contortrix	M 338		USA: Ohio	AF057229	AF057276	AY223612	AF156576

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4
Agkistrodon piscivorous	CLP 30		USA: South Carolina	AF057231	AF057278	AY223615	AF156578
Agkistrodon taylori	CLP 140		Mexico: Tamaulipas	AF057230	AF057230	AY223614	AF156580
Atropoides indomitus	ENS 10630		Honduras: Dept. Olancho	TBD		DQ061194	DQ061219
Atropoides mexicanus	CLP 168		Costa Rica: San José Prov.	AF057207	AF057254	AY223584	U41871
Atropoides occiduus		UTA R-29680	Guatemala: Dept. Escuintla	DQ305423	DQ305446	AY220315	AY220338
Atropoides olmec	JAC 16021	UTA R-25113	Mexico: Veracruz	AY223656	AY223669	AY223585	AY223632
Atropoides picadoi	CLP 45 (12S, 16S, cyt-b)	MZUCR 11156 (12S, 16S, cyt-b), UMMZ 177000 (ND4)	Costa Rica: Alajuela Prov. (12S, 16S, cyt-b), Costa Rica: Heredia Prov. (ND4)	AF057208	AF057255	AY223593	U41872
Bothriechis aurifer	DPL 2984	UTA R-35031	Guatemala	DQ305425	DQ305448	DQ305466	DQ305483
Bothriechis bicolor	ENS 10507	UTA R-34156	Mexico: Chiapas	DQ305426	DQ305449	DQ305467	DQ305484
Bothriechis lateralis	CLP 48	MZUCR 11155	Costa Rica: San José Prov.	AF057211	AF057258	AY223588	U41873
Bothriechis marchi		UTA R-52959	Guatemala: Dept. Zacapa	DQ305428	DQ305451	DQ305469	DQ305486
Bothriechis nigroviridis	CLP 49	MZUCR 11151	Costa Rica: San José Prov.	AF057212	AF057259	AY223589	AY223635
Bothriechis rowleyi	JAC 13295	UTA R-22243	Mexico: Oaxaca	DQ305427	DQ305450	DQ305468	DQ305485
Bothriechis schlegelii	CLP 51	MZUCR 11149	Costa Rica: Cariblanco de Sarapiqui	AF0572113	AF057260	AY223590	AY223636
Bothriechis supraciliaris	–		Costa Rica: Puntarenas Prov.	DQ305429	DQ305452	DQ305470	DQ305487
Bothriechis thalassinus		UTA R-52958	Guatemala: Dept. Zacapa	DQ305424	DQ305447	DQ305465	DQ305482
Calloselasma rhodostoma		UTA R-22247	–	AF057190	AF057237	AY223562	U1878
Cerrophidion godmani	ENS 5857	UTA R-40008	Guatemala: Dept. Baja Verapaz	DQ305419	DQ305442	AY220325	AY220348
Cerrophidion petlalcalensis	ENS 10528		Mexico: Veracruz	DQ305420	DQ305443	DQ061202	DQ061227
Cerrophidion sasai	CLP 46	MZUCR 11153	Costa Rica: San José Prov.	AF057203	AF057250	AY223578	U41879
Cerrophidion tzotzilorum	ENS10529		Mexico: Chiapas	JN870182	JN870193	DQ061203	DQ061228

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4
Cerrophidion wilsoni	ENS10632		Honduras: Dept. Francisco Morazán			EU684286	EU684301
Crotalus adamanteus	CLP4		USA: Florida	AF057222	AF057269	AY223605	U41880
Crotalus aquilus		ROM 18114 (12S, 16S, cyt-b), ROM 42394 (ND4)	Mexico: Distrito Federal (12S, 16S, cyt-b), Mexico: Aguascalientes (ND4)	AF259231	AF259124	AF259161	HQ257762
Crotalus atrox	CLP 64		USA: Texas	AF0572225	AF057272	AY223608	AY223646
Crotalus basiliscus		ROM 18188 (12S, 16S, cyt-b), unknown (ND4)	Mexico: Nayarit	AF259244	AF259136	AF259174	AY704894
Crotalus catalinensis		ROM18250, BYU34641-42	Mexico: Baja California Sur: Santa Catalina Isl.	AF259259	AF259151	AF259189	
Crotalus durissus		ROM 18261	Venezuela	AF259247	AF259139	AF259177	TBD
Crotalus horridus		UTA R-14697 (12S, 16S, cyt-b), TNHC 65471 (ND4)	USA: Arkansas (12S, 16S, cyt-b), USA: Texas (ND4)	AF259252	AF259144	AF259182	JN870207
Crotalus intermedius	JAC8881	TNHC	Mexico: Oaxaca	TBD	TBD	TBD	JN870208
Crotalus lepidus		ROM 18128 (12S, 16S, cyt-b), unknown (ND4),	Mexico: Chihuahua (12S, 16S, cyt-b), USA: New Mexico (ND4)	AF259230	AF259123	AF259160	U41881
Crotalus mitchelli		ROM18178	USA: California	AF259250	AF259142	AF259180	
Crotalus molossus	CLP66		USA: Texas	AF057224	AF057271	AY223607	AY223645
Crotalus oreganus	CP 014 (ND4)	ROM 19656 (12S, 16S, cyt-b)	USA: California	AF259253	AF259145	AF259183	AF194149
Crotalus polystictus		ROM FC-263 or ROM 18139	Mexico: Distrito Federal	AF259236	AF259129	AF259166	
Crotalus pricei		ROM FC-2144 or ROM 18158	Mexico: Nuevo León	AF259237	AF259130	AF259167	

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4
Crotalus pusillus		ROM FC-271 (12S, 16S, cyt-b), ROM 47056 (ND4	Mexico: Michoacán	AF259229	AF259122	AF259159	HQ257880
Crotalus ravus		UTA-live	Mexico: Puebla	AF057226	AF057273	AY223609	AY223647
Crotalus ruber		ROM 18197-98 or ROM 18207 (12S, 16S, cyt-b), RWV 2001-08 (ND4)	USA: California	AF259261	AF259153	AF259191	DQ679838
Crotalus scutulatus		ROM 18210 or ROM 18218 (12S, 16S, cyt-b), UTEP CRH-153 (ND4)	USA: Arizona (12S, 16S, cyt-b), USA: New Mexico (ND4)	AF259254	AF259146	AF259184	AF194167
Crotalus simus	WW-1321 (12S, 16S), 1097 (cyt-b, ND4), MSM 192 (Rag1)		Costa Rica: Guanacaste Prov. (12S, 16S), Costa Rica: Puntarenas Prov. (cyt-b, ND4), Guatemala: Dept. Zacapa (Rag1)	EU624240	EU624274	EU624302	AY704885
Crotalus tigris	CLP 169		USA: Arizona	AF057223	AF057270	AY223606	AF156574
Crotalus triseriatus		ROM 18121	Mexico: Distrito Federal	AF259233	AF259126	AF259163	
Crotalus viridis	CP 048	UTEP 17625	USA: Colorado	DQ020027		AF147866	AF194157
Crotalus willardi	HWG 2575 (12S, 16S, cyt-*b*), W9306 (ND4)	TNHC (ND4)	USA: Arizona	AF259242	AF259134	AF259172	JN870209
Cryptelytrops macrops	AM B27		Thailand: Bangkok	AF517163	AF517176	AF517184	AF517219
Cryptelytrops pupureomaculatus	AM B418	CAS 212246	Myanmar: Ayeyarwade Region	AY352807	AY352746	AY352772	AY352841
Deinagkistrodon acutus	CLP 28		China	AF057188	AF057235	AY223560	U41883
Gloydius halys	–		Kazakhstan	AF057191	AF057238	AY223564	AY223621
Gloydius strauchi		ROM 20473	China: Sichuan Prov.	AF057192	AF057239	AY223563	AY223620
Himalayophis tibetanus	AM B258	ZMB 65641	Nepal: Helambu	AY352776	AY352715	AY352749	AY352810

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4
Mixcoatlus melanurus	RLG 1086	UTA R-34605	Mexico	AF057210	AF057257	AY223587	AY223634
Ophryacus undulatus	CLP 73		Mexico	AF057209	AF057256	AY223586	AY223633
Ovophis monticola	JBS 16330	CAS 215050	China: Yunnan Prov.	DQ305416	DQ305439	DQ305462	DQ305480
Parias flavomaculatus	AM B3		Philippines: Luzon	AY059535	AY059551	AF171916	AY059584
Popeia popeiorum	AM B34		Thailand: Phetchaburi Prov.	AY059542	AY059558	AY059572	AY059591
Porthidium arcosae	WW 750		Ecuador	AY223655	AY223668	AY223582	AY223631
Porthidium dunni	ENS 9705		Mexico: Oaxaca	AY223654	AY223667	AY223581	AY223630
Porthidium lansbergii	WW 787		Venezuela: Falcón	EU624242	EU624276	AY713375	AF393623
Porthidium nasutum	CLP 52	MZUCR 11150	Costa Rica: Limón Prov.	AF057204	AF057251	AY223579	U41887
Porthidium ophryomegas		UMMZ 210276	Costa Rica: Guanacaste Prov.	AF057205	AF057252	AY223580	U41888
Porthidium porrasi	MSM		Costa Rica: Puntarenas Prov.	DQ305421	DQ305444	DQ061214	DQ061239
Porthidium yucatanicum	JAC 24438		Mexico: Yucatán	JN870189	JN870198	DQ061215	DQ061244
Protobothrops flavoviridis		UMMZ 199973	Japan: Ryukyu Isls.: Tokunoshima Isl.	AF057200	AF057247	AY223574	U41894
Protobothrops jerdonii		CAS 215051	China: Yunnan Prov.	AY294278	AY294269	AY294274	AY294264
Sinovipera sichuanensis	GP7	YBU 030116	China: Sichuan Prov.	HQ850445	HQ850446	HQ850447	HQ850449
Sistrurus catenatus	M 502		USA: Texas	AF057227	AF057274	AY223610	AY223648
Sistrurus miliarius		UTA live	USA: Florida	AF057228	AF057275	AY223611	U41889
Trimeresurus borneensis	AM B301		Malaysia: Sabah	AY352783	AY352722	AY352754	AY352817
Trimeresurus wiroti	–		Thailand: Nakhon Si Thammarat Prov.			DQ646788	
Tropidolaemus subannulatus	CLP 141		Indonesia: Borneo: West Kalimantan Prov.	AF057198	AF057245	AY223571	AY223625
Viridovipera gumprechti	AM A164		Thailand: Loei Prov.	AF517168	AF517181	AY352766	AF157224

Phylogenetic estimation and divergence dating

We used the package BEAST v.1.6.1 (Drummond and Rambaut, 2007) to simultaneously infer the relationships and divergence times among taxa. We followed Bayesian relaxed molecular clock methods, with uncorrelated lognormal rates among branches (Drummond et al., 2006) and a Yule speciation model. We constrained lognormal priors for the time to most recent common ancestor (tMRCA) for certain groups based on fossil data: (1) the root of the tree corresponds to the first appearance of the subfamily Crotalinae, in the early Miocene (Hemingfordian; Holman, 2000), (2) the genus *Sistrurus* first appears in the late Miocene (Clarendonian; Parmley and Holman, 2007) and (3) *Agkistrodon contortrix* first appears in the late Miocene (Late Hemphillian; Holman, 2000). The first two constraints were placed at the stems of the origins of Crotalinae and *Sistrurus*, respectively. *A. contortrix* is the earliest-diverging member of its genus and therefore the constraint was placed at the MRCA of the genus. Offsets were set as the most recent ages of the strata in which the fossils were found, means were set to 5 Ma and standard deviations were set to 1 Ma. This resulted in an offset of 15.97 Ma and a prior credible interval (PCI) of 16.56–31.68 for Crotalinae, an offset of 10.3 Ma and a PCI of10.89–26.01 for *Sistrurus*, and an offset of 4.9 Ma and a PCI of 5.48–20.61 for *Agkistrodon.* Based on phylogeographic information on vicariance between mainland and Baja California desert regions (Castoe et al., 2009; Castoe et al., 2007) we set a normal prior on the tMRCA of *Crotalus atrox* and *C. ruber* to be 3.29 Ma ± 0.2 SD.

All calibrations are independent of the geological data used to define biogeographic hypotheses (Crisp et al., 2010). We ran two independent Markov chains for $5x10^7$ iterations, with chains sampled every 5000 iterations. We used Tracer 1.5 (Rambaut and Drummond 2007) to verify stationarity of the Markov chain and to determine that the posterior sample and almost all parameters had ESS>200, suggesting that the posterior distribution was adequately sampled. We discarded the first 1×10^7 generations of final runs as burnin. We combined the posterior samples from both runs using LogCombiner in BEAST, and report the results of the combined posterior sample.

Geographic range evolution

In order to estimate the geographic distributions of ancestral nodes across the sample of phylogenetic trees, we assigned each extant species to its appropriate geographic ranges based on published data collected in Campbell and Lamar (2004, data available from authors).

For the Andean allopatry, river barrier and marine incursion hypotheses, species were assigned to one or more of seven regions: A) Panama and regions north, B) Pacific versant of Andes, C) northwest region north of the Amazon, east of the Andes and west of the Guyana Shield, D) central region south of the Amazon, east of the Andes, and west of the Brazilian Shield, E) northwest region including the Brazilian Shield, F) southwest region south of the Brazilian Shield and east of the Paraguay and southern portion of the Paraná Rivers, and G) southeast region east of the Andes and west of the Paraná River (Figure 15). Maximum range size for inferred ancestors was based on the maximum range of extant species, which was four regions and resulted in 49 ranges.

The algorithm used allows dispersal constraints to be set as proportions of a maximum rate of 1.0, to incorporate the prior assumption that some areas are more difficult to reach than others. We set dispersal to adjacent regions as 1 but restricted dispersal to nonadjacent regions as 0.1*(number of regions crossed). The minimum dispersal rate was 0.01 for a step from outgroup region A to regions E, F, or G.

For the Andean parapatry and altitudinal shift hypotheses, species were assigned to the Central (CA) or Southern Andes (SA), the Guyana Highlands (G), and/or the Brazilian Shield (B). Species were also assigned to altitudinal zones: tierra caliente (0-762 m), tierra templada (763-1828 m), or tierra fría (1829-3658 m) (Salter et al., 2005). No snake ranges have been reported from higher elevations. Maximum range size was based on the maximum range of extant species, which was five regions. Ancestral ranges were constrained to span adjacent regions: 1) regions of tierra caliente, 2) from tierra caliente to tierra templada within a region, or 3) from tierra templada to tierra fría within the Central Andes. This resulted in a set of 103 ranges. Similar to allopatry, dispersal to adjacent regions was 1 but dispersal to nonadjacent regions was set as 0.1*(number of regions crossed). In addition, dispersal across tierra templada from the Central to the Southern Andes was treated as adjacent ancestral ranges could not include these two regions and no others. The minimum dispersal rate was 0.001 for a step from Central Andean tierra fría to tierra templada of another region. Based on geological data (Gregory-Wodzicki, 2000; Hartley, 2003) the Andes did not reach the elevation of tierra fría until 10 Ma and therefore dispersal to this region was set to 0 from the origin of the phylogeny until 10 Ma.

For the refugia hypothesis, species were assigned to the refuges described by Haffer (1969, Figure 16): 1) Chocó, 2) Nechí, 3) Catatumbo, 4) Imerí, 5) Napo, 6) East Peruvian, 7) Madeira-Tapajós, 8) Belém, and 9) Guiana. More recent maps denoting 40 or more refugial areas (e.g. Brown, 1987) are beyond the capabilities of our analytical methods, and therefore we focus more on timing of speciation events rather than on geographic patterns. The maximum range of extant species, seven regions, allowed a prohibitively large number of potential ancestral ranges (236 possible ranges, preliminary analysis ran over two weeks before crashing). Therefore we constrained the maximum range of ancestral species to five regions, which is representative of all but two extant species. After elimination of ranges with disjunct areas, we had 168 possible ranges. Similar to the prior analyses, a stepping stone model was applied after 2.6 Ma: dispersal to adjacent regions was 1 but dispersal to nonadjacent regions was 0.1*(number of regions crossed). Adjacent refugial areas separated by the Andes (A and E, B and E, C and D) also had dispersal restricted to 0.1. The minimum dispersal rate was 0.0001 for a step from the outgroup region to that south or east of the study area.

We used Lagrange (Ree et al., 2005; Ree and Smith, 2008) to estimate geographic range evolution based on the ultrameric phylogeny. The program uses maximum likelihood to optimize dispersal and extinction events in a set of discrete geographic regions over the duration of each internode in a phylogeny. It then estimates the areas inherited by each daughter lineage of a cladogenic event. This method is similar to likelihood ancestral character state analysis except that, instead of estimating a single character state for each node and therefore assuming that the two descendants

of a node inherit the same range, Lagrange assumes speciation occurs in a single region. One daughter lineage inherits the region where speciation occurs and the other lineage inherits the remainder or the entirety of the parental range. The result is an output of paired likelihoods for occupied regions for each branching event on the tree. Ree and Smith (2008) found that dispersal and local extinction tend to be underestimated but accurate estimations of ancestral ranges can be reconstructed if these events are rare relative to speciation. The input parameters were configured using a web-based tool available at http://www-reelab.net/lagrange. The output of the program is a number of potential ancestral ranges, each with a particular relative probability. We report all ranges with >10% probability and we assigned a particular node to a region or combination of regions if Lagrange reconstructed that region with >50% probability.

Results

Phylogeny and divergence dating

The final alignment consisted of 2311 characters. The consensus phylogeny was congruent with recent studies of the same taxa (e.g. Fenwick et al., 2009), and most nodes were resolved with strong support (Figure 17) The GTR+IΓ model was optimal for 12S, 16S,and some codon positions of cyt-b and ND4. As BEAST supports only a single model for all codon partitions of a gene, we used GTR+IΓ for all partitions.

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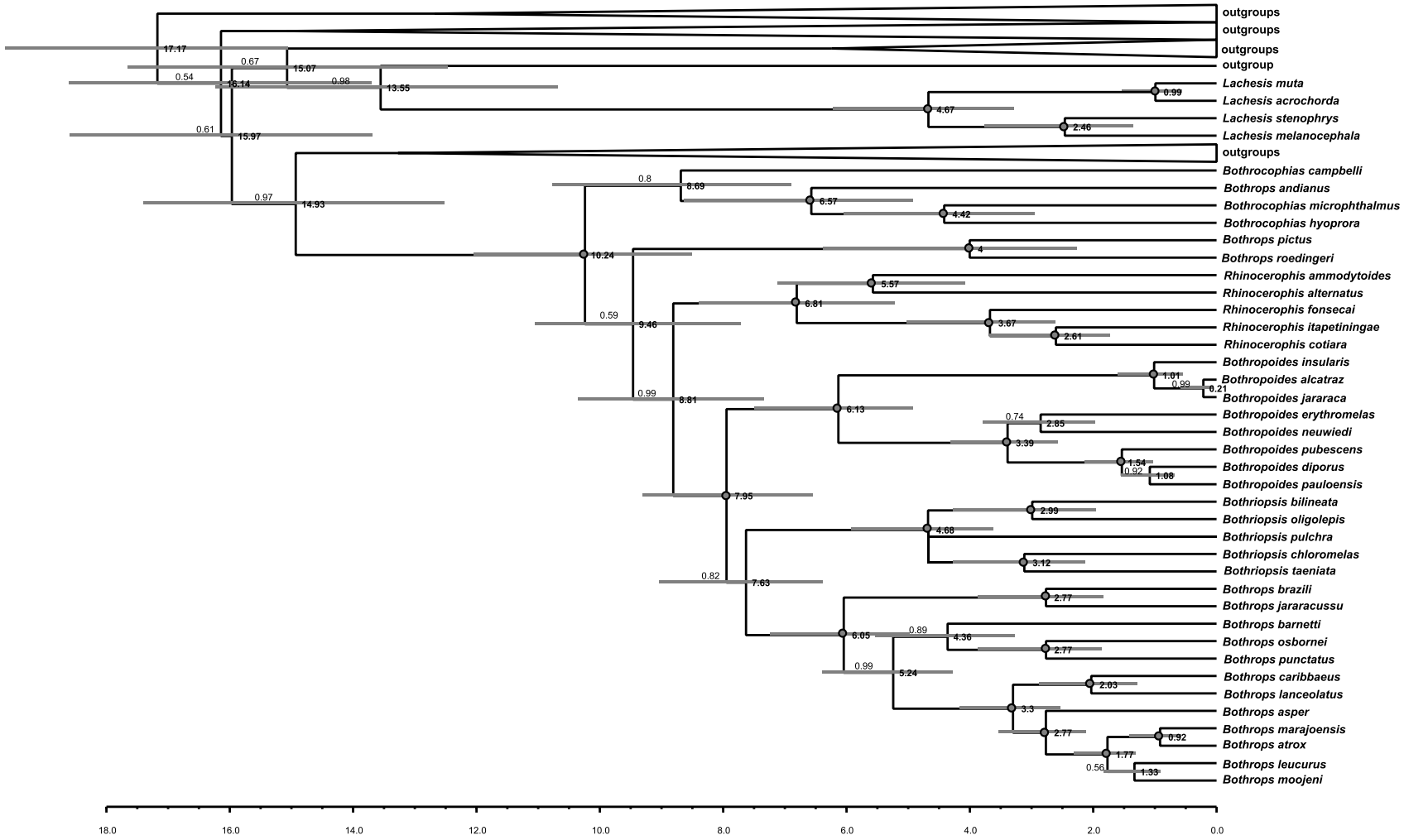

Figure 17. Ultrameric phylogram of South American pitviper relationships estimated by BEAST. Posterior probabilities shown to left of nodes, with probabilities of 1.0 represented by circles. Node ages in millions of years shown to right. Gray bars on nodes represent 95% confidence intervals of node ages.

Monophyly of each genus examined by Fenwick et al. (2009) was strongly supported by posterior probabilities (*Pp*=1.0) except for *Bothrocophias* (*Pp*=0.8). In addition, the pairing of *Bothrops pictus* and *B. roedingeri* was supported by *Pp*=1.0. Interspecies and intergeneric relationships among ingroup taxa were generally well resolved, with the notable exception of the placement of *Bothrops pictus* + *B. roedingeri* sister to all bothropoids except *Bothrocophias* (*Pp*=0.59). We estimated ancestral ranges for all nodes with posterior probability >0.5.

The divergence of bothropoids from the *Porthidium* clade at 14.93 Ma ($CI_{95\%}$ = 12.49–17.4 Ma) was similar to that estimated by Castoe et al. (2009) and Daza et al. (2010). The origin of bothropoids at 10.24 Ma ($CI_{95\%}$ = 8.49–12.05 Ma) and the origin of *Lachesis* at 4.67 Ma ($CI_{95\%}$ = 3.26–6.21 Ma) was younger than those dates estimated by Wüster et al. (2008) and Zamudio and Greene (1997). The overall depth of the tree was 17.17 Ma ($CI_{95\%}$ = 15.03–19.65 Ma), corresponding to the origin of pitvipers. Origins of genera occurred through the Miocene ($CI_{95\%}$ = 6.35–16.24 Ma) and species origins occurred from the Miocene through the Pleistocene ($CI_{95\%}$ = 0.02–10.78Ma).

Ancestral area estimation

Ancestral range estimation recovered multiple areas for most nodes (Figure 18–Figure 20). Details are discussed below.

Allopatry hypotheses

The Andean allopatry hypothesis predicts divergence between the Pacific (regions A and B) and Amazonian (regions C–G) versants of the Andes, with speciation

occurring around 10 Ma. One node in the tree was reconstructed to have divergence across the Andes with a 95% confidence interval for divergence time that spanned the temporal prediction (highlighted in Figure 18). The ancestor of *Bothrocophias campbelli*, in region B, diverged 8.69 Ma ($CI_{95\%}$ = 10.78–6.87 Ma) from the ancestor of *Bothrops andianus* and other *Bothrocophias* species, in region D. In addition, *Lachesis acrochorda*, in region B, split from *L. muta*, in D plus other regions, approximately 0.99 Ma ($CI_{95\%}$ = 1.54–0.53 Ma). This divergence does not support the temporal prediction.

Marine incursion hypotheses predict divergence across inundated areas during the times they were filled. For the Pebas basin, this predicts divergence of areas B from C, B from D, or C from D during the Miocene marine highstand of 13.8–16 Ma, the restricted inundation of 8–10 Ma, and the Pliocene highstand of 3.6–5 Ma. The timing of the divergence of *Bothrocophias campbelli* in area B from the ancestor of *Bothrops andianus* and other *Bothrocophias* species in area D overlaps the period of restricted inundation, with a median of 8.69 Ma and $CI_{95\%}$ of 10.78–6.87 Ma (highlighted in Figure 18). In addition, the divergence of the ancestor of *Bothrops brazili* and *B. jararacussu*, in region D plus other regions, from the ancestor of other *Bothrops* species in region B, supports the spatial prediction of this hypothesis but not the temporal prediction (divergence 6.05 Ma, $CI_{95\%}$ = 7.24–4.94 Ma). For the Pirabas basin, this predicts divergence between areas C and E during the marine highstands mentioned above. No nodes matched this prediction. For the Paraná basin, we predicted divergence of areas F from G 8–10 Ma, and no nodes matched this prediction.

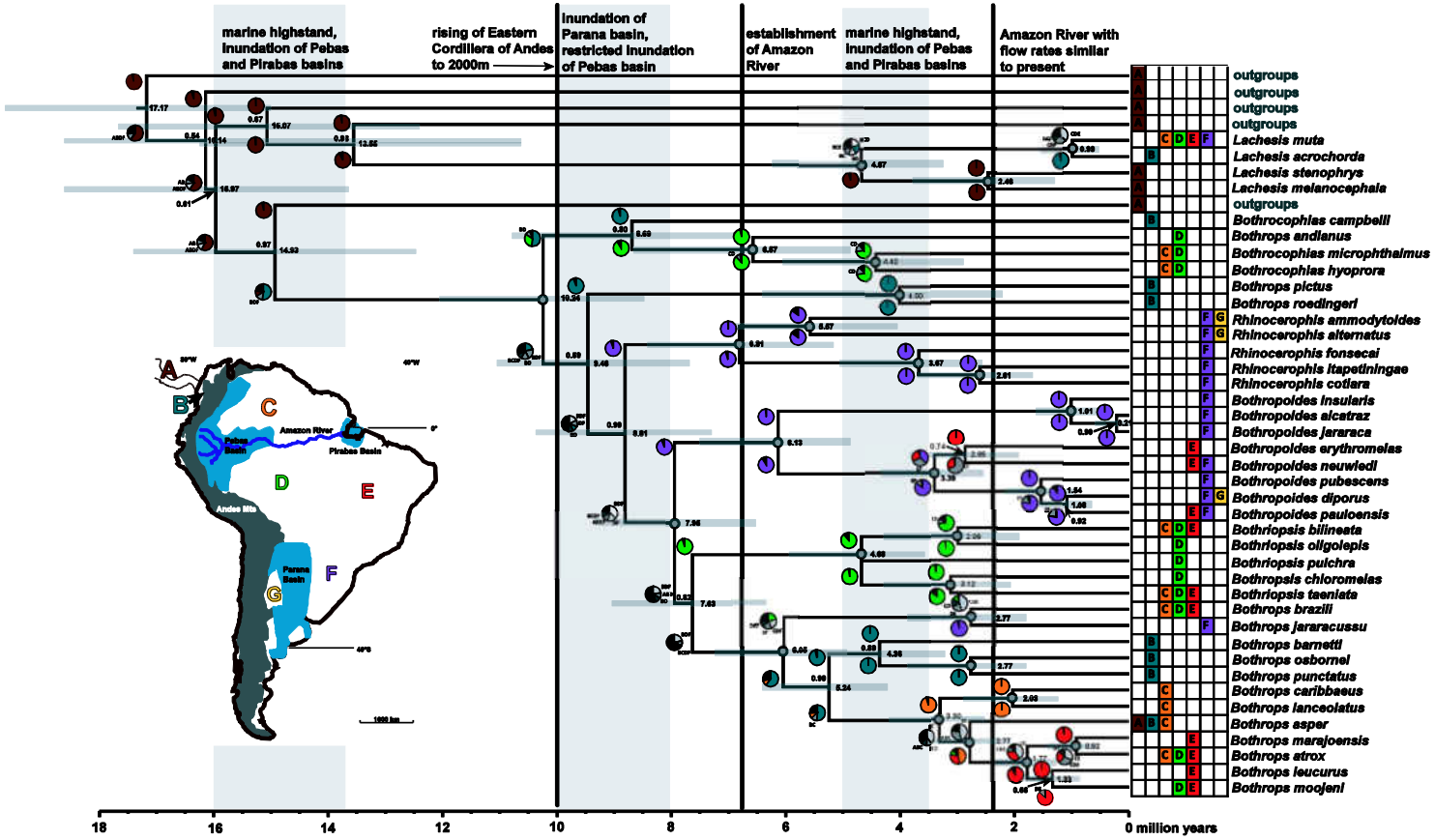

Figure 18. Biogeographic reconstruction obtained using Lagrange for evaluation of allopatric speciation hypotheses (Hyps. 1–3, Table 16). Vertical lines and boxes represent events predicted to drive speciation. Colors correspond to regions delimited by barriers, as seen in inset map: A) Central and North America, B) Pacific versant of Andes mountain range, C) central region north of Amazon River, D) central region south of Amazon River, E) eastern region, F) southern region east of Paraná Basin, G) southern region west of Paraná Basin. Colors to left of species names represent ranges of extant species. Pie graphs represent reconstructions of ancestral nodes; gray sections represent ancestral areas that span more than one region, black sections represent ancestral areas with less than 10% relative probability or those more than two log-likelihood units below the maximum for the node. Gray bars on nodes represent 95% confidence intervals of node ages. Circles on nodes represent 1.0 posterior probability support; lower support is labeled left of node. Yellow bars show median node ages to right and highlight nodes supporting hypotheses; other bars with node ages are discussed in text as groups for further study.

The river barrier hypothesis predicts divergence across the newly formed Amazon River barrier after 7 Ma or after 2.4 Ma, between area C north of the river and southern areas D–E. No nodes matched this prediction (Figure 18).

Parapatry and climate hypotheses

Most node reconstructions were complex, with multiple reconstructions for each node and with ancestral areas estimated to span multiple climate zones (Figure 19).

The Andean altitude hypothesis predicts divergence of Central Andean caliente (CAC) from templada (CAT) climate zones approximately 12 Ma, and the same for the Southern Andes (SAC from SAT). It also predicts divergence of templada from fría zones (CAT from CAF) approximately 10 Ma. One relationship supports this hypothesis (highlighted in Figure 19). The ancestor of bothropoid pitvipers originated 14.93 Ma ($CI_{95\%}$ = 17.4 – 12.49 Ma), and was recovered in CAC. Its descendant lineage, the ancestor of *Bothrocophias*, was recovered in CAT and diverged 10.24 Ma ($CI_{95\%}$ = 12.05 – 8.49 Ma). This expansion upslope, and particularly the divergence of *Bothrocophias,* spans the origin of the templada zone.

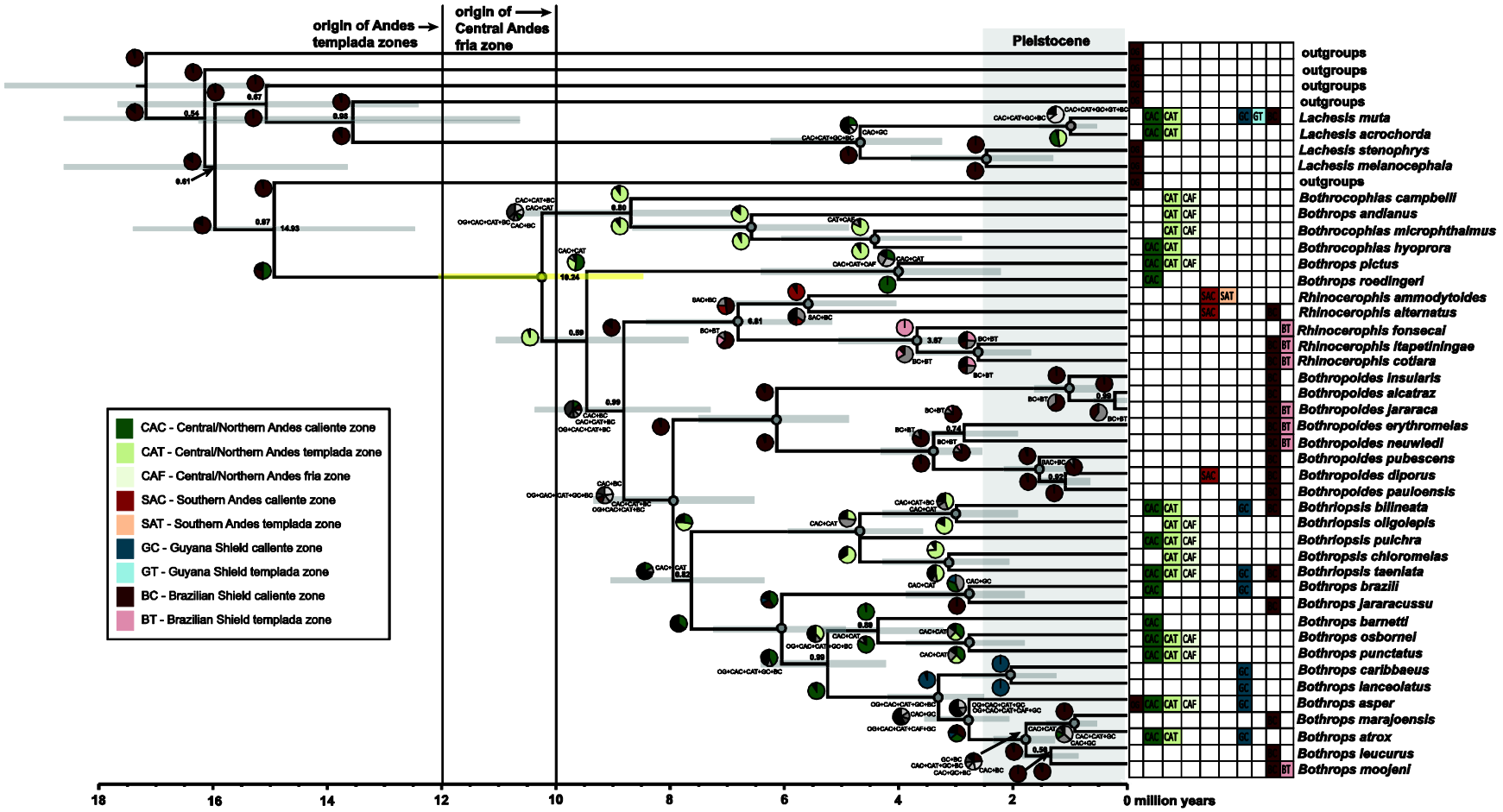

Figure 19. Biogeographic reconstruction obtained using Lagrange for evaluation of parapatric and climate-based speciation hypotheses (Hyps. 4–6, Table 16). Vertical lines and boxes represent events predicted to drive speciation. Colors to left of species names correspond to regions and climate zones. Pie graphs represent reconstructions of ancestral nodes; gray sections represent ancestral areas that span more than one region, black sections represent ancestral areas with less than 10% relative probability or those more than two log-likelihood units below the maximum for the node. Gray bars on nodes represent 95% confidence intervals of node ages. Circles on nodes represent 1.0 posterior probability support; lower support is labeled left of node. Yellow bars show median node ages to right and highlight nodes supporting hypotheses; other bars with node ages are discussed in text as groups for further study.

The museum hypothesis predicts divergence between caliente and templada climate zones (e.g. CAC from CAT) during the Pleistocene, 0.01–2.6 Ma. The divergence-vicariance hypothesis predicts the same, but also predicts divergence between Central Andean templada and fría zones (CAT from CAF) during the Pleistocene. No nodes supported the temporal portions of these predictions (Figure 19). However, one change from an ancestral to descendant range fit the spatial predictions of the museum and divergence-vicariance hypotheses (node ages labeled in Figure 19). The ancestor of *Bothropoides fonsecai, B. itapetiningae* and *B. cotiara* originated 6.81 Ma ($CI_{95\%}$ = 8.4 – 5.91 Ma), and was recovered in the Brazilian Shield caliente zone (BC). Its descendant lineage, the ancestor of *R. fonsecai*, was recovered in the Brazilian Shield templada zone (BT) and diverged 3.67 Ma ($CI_{95\%}$ = 5.03 – 2.59 Ma). This divergence predates the Pleistocene.

Refugia hypothesis

The refugia hypothesis predicts sister lineages inhabiting adjacent and nonoverlapping areas during the Pleistocene, 0.01–2.6 Ma, and one node supported this prediction (highlighted in Figure 20). The ancestor of *Lachesis muta* is recovered in areas DE plus other adjacent regions, with the ancestor of *L. acrochorda* in adjacent area A. The divergence date for these species is 0.99 Ma ($CI_{95\%}$ = 1.54–0.53 Ma).

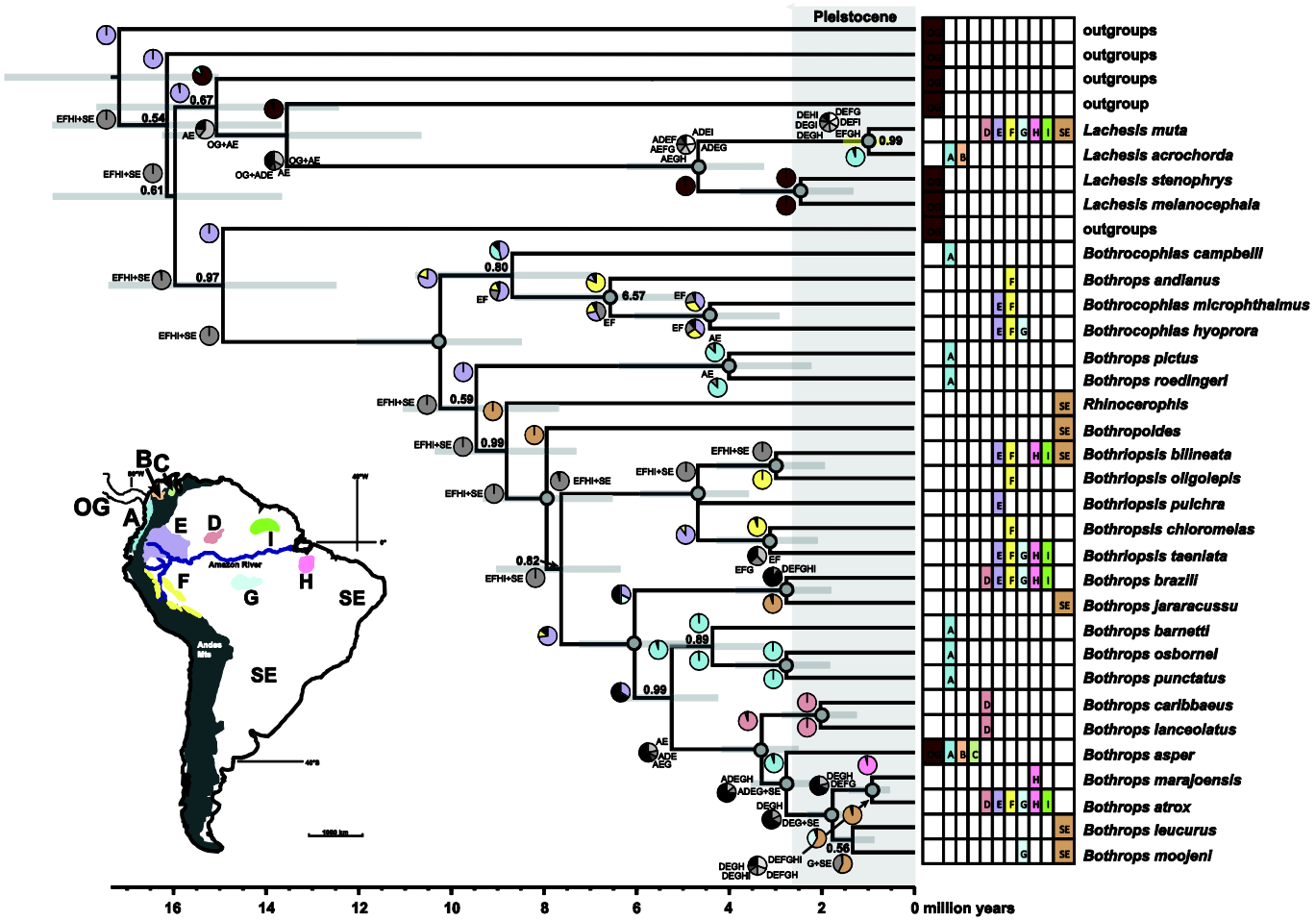

Figure 20. Biogeographic reconstruction obtained using Lagrange for evaluation of refugia hypothesis (Hyp. 7, Table 16). Gray box represents Pleistocene, when climate changes are predicted to drive speciation. Colors correspond to refugial areas defined by Haffer Figure 16and surrounding regions: OG) North and Central America, A) Chocó, B) Nechí, C) Catatumbo, D) Imerí, E) Napo, F) East Peruvian, G) Madeira-Tapajós, H) Belém, I) Guiana, SE) regions south and east of refugia. Colors to left of species names represent ranges of extant species. Pie graphs represent reconstructions of ancestral nodes; gray sections represent ancestral areas that span more than one region, black sections represent ancestral areas with less than 10% relative probability or those more than two log-likelihood units below the maximum for the node. Gray bars on nodes represent 95% confidence intervals of node ages. Circles on nodes represent 1.0 posterior probability support; lower support is labeled left of node. Yellow bars show median node ages to right and highlight nodes supporting hypotheses; other bars with node ages are discussed in text as groups for further study.

Discussion

Overall we find speciation of South American pitvipers to be complex, with no single hypothesis strongly supported. In this system we reject half of the tested hypotheses: the marine incursion hypothesis for the Pirabas and Paraná basins, the river barrier hypothesis, the museum hypothesis, and the divergence-vicariance hypothesis. We find single examples of support for the Andean allopatry hypothesis, the marine incursion hypothesis for the Pebas basin, the Andean altitude hypothesis, and the refugia hypothesis. This results in a more select group of hypotheses with support for testing in other taxa. We discuss our results in detail below and suggest future research avenues.

Phylogenetic relationships

Our evolutionary relationships agree with earlier estimates (Fenwick et al., 2009; Wüster et al., 2002). For example, we find two entrances of pitvipers into South America. The first was the ancestor of bothropoid pitvipers, entering approximately 14.93 Ma ($CI_{95\%}$ = 17.4–12.49 Ma). The second was the ancestor of *Lachesis acrochorda* and *L. muta*, entering approximately 4.67 Ma ($CI_{95\%}$ = 6.21–3.26 Ma). Because we were evaluating species-level relationships we did not investigate the diversification of *Crotalus durissus* in South America (discussed in Wüster et al., 2005) and did not estimate its time of diversification. Both estimated entrances predate the closure of the Isthmus of Panama (Coates and Obando, 1996). Although the Great American Biotic Interchange (Webb, 1976) was hypothesized as the impetus for dispersal and

divergence events in plants (Kay et al., 2005), freshwater fish (Bermingham et al., 1997), reptiles and amphibians (Savage, 2002), and mammals (Cortes-Ortiz et al., 2003; Marshall, 1980), our results mirror the findings of a number of recent studies estimating entrances before the closure of the Isthmus (e.g. Castoe et al., 2009; Daza et al., 2010; Daza et al., 2009; Fuchs et al., 2007; Koepfli et al., 2007; Pinto-Sánchez et al., 2012; Wiens, 2007).

Diversification hypothesis tests

For the Andean allopatry hypothesis (Hyp. 1), we predicted speciation events between the Pacific and Amazonian versants of the mountain ranges approximately 10 Ma when the Central Andes reached the altitude of the current treeline. We found one divergence event across the mountain range occurring 8.69 Ma, between *Bothrocophias campbelli* and its congeners (highlighted in Figure 18). This event overlaps the time of uplift of the Northern Andes (Hoorn et al., 2010) and the earliest estimates predate the closure of passages with tropical climate between Panama and the Amazonian basin (Gregory-Wodzicki, 2000; Hartley, 2003; Hulka et al., 2006). This supports prior predictions for *Bothrocophias* suggesting Andean allopatry was responsible for the divergence of species groups (Gutberlet and Campbell, 2001). The same 8.69 Ma speciation event may also be explained by the inundation of the Pebas Basin surrounding the source of the Amazon River (Hyp. 2 in part). The basin was predicted to be partially filled 8–10 Ma (Marshall et al., 1993), which coincides with the divergence event (Figure 18). Although the effect of the rising of the Andes seems more likely to

result in lineage isolation and speciation, both hypotheses result in the same predictions in this region.

We found approximately equal evidence for effects of environmental changes on speciation (Hyps. 4–7) as those of physical barriers (Hyps. 1–3). For example, one speciation event supported the Andean altitude hypothesis (Hyp. 4). An ancestral bothropoid lineage was recovered in the caliente zone approximately 15 Ma and a direct descendant, the ancestor of *Bothrocophias*, should have inhabited the cooler templada zone approximately 10 Ma. We cannot estimate when the lineage may have reached the cooler climate region, but the branch from ancestor to descendant spans the rising of the Andes into the templada zone approximately 12 Ma, and the divergence time of the descendant overlaps this date. Andean altitudinal change was proposed as a speciation mechanism in *Bothrocophias* (Gutberlet and Campbell, 2001), but was suggested to drive speciation within species groups, not the origin of the genus.

Speciation within South American *Lachesis* species supported the refugia hypothesis (Hyp. 7; Haffer, 1969; Figure 20), which suggests that Pleistocene climate changes isolated populations in pockets of relatively wet, forested habitat. We found diversification across adjacent refugial areas (A vs. E plus other Amazonian regions) during the Pleistocene. The presence of the mountain range complicates interpretation of this divergence, but it supports refugial predictions.

Surprisingly, for most speciation events in the examined phylogeny, we do not find support from our tested hypotheses. Our results support the observations of Rull (2008) that molecular phylogenetic evidence generally does not find strong support for

speciation in particular time periods, and instead may reflect the influence of a number of factors working together to drive lineage evolution.

Diversification in pitvipers

Multiple hypotheses have been cited to explain the expansion of pitvipers across South America, and although we find support for prior proposals in support in toadheaded pitvipers, we do not find support for prior explanations in other genera. We describe our results below.

In agreement with the describers of the genus (Gutberlet and Campbell, 2001), we find that the divergence of species groups of toadheaded pitvipers (*Bothrocophias*) across the Andes may support the Andean allopatry hypothesis. Of the species group consisting of *Bothrocophias campbelli, B. colombianus,* and *B.* myersi, only the first had molecular data available to this study, but we found the divergence of *B. campbelli* to fit Andean vicariance predictions. Gutberlet and Campbell (2001) also suggested altitudinal uplift drove speciation within groups; we did not find evidence for this in the Amazonian group of *B. hyoprora* and *B. microphthalmus* but did find support for altitudinal uplift in the origin of the genus. In agreement with Carrasco et al. (2012) and in contrast to Fenwick et al. (2009), we find *Bothrops andianus* as a member of *Bothrocophias.* We will discuss the phylogenetic and taxonomic implications of this result in upcoming work. The divergence of this species was attributed to Andean uplift, but we do not find support for that explanation here.

Divergence of South American bushmasters (*Lachesis*) from their Central American congeners was attributed to Andean allopatry (Zamudio and Greene, 1997) or

the inundation of the Pebas basin (Werman, 2005). We do not find support for the temporal predictions of these hypotheses, and in fact recover an ancestral range for South American bushmasters spanning the Andes and Pebas basin. We find divergence between the two species of South American *Lachesis* to occur in the Pleistocene, which is best explained by the refugia hypothesis. To our knowledge refugial processes have not been used to explain speciation in this group.

The origin of forest-pitvipers (*Bothriopsis*) was attributed to Andean uplift (Werman, 2005), and diversification within the group was attributed to refugia (Werman, 2005). Isolation in refugia was also suggested to drive speciation in Amazonian lanceheads (*Bothrops*; Werman, 2005; Wüster et al., 1999). Although we find 4 of 5 species-level divergences in *Bothriopsis* and 10 of 11 divergences in *Bothrops* overlap the Pleistocene, we do not find any instances of speciation across adjacent refugia.

Pre-Pleistocene climate change and rain shadow effects of the rising Andes were implicated in the diversification of southern lanceheads (*Rhinocerophis*) and Brazilian lanceheads (*Bothropoides;* Werman, 2005), hypotheses which were not tested in our study. We find no support for our tested hypotheses in these genera.

Considerations in biogeographic hypothesis testing

Because we can only sample extant taxa, the number of sampled speciation events decreases with events further back in time. We therefore expect hypotheses relying on more recent events (5–7) to have more support in the phylogeny than hypotheses relying on earlier events (1–4). Diversification rate analysis should help to

highlight time periods with high rates of speciation compared to expectations, and illuminate if the time periods surrounding any of the events of interest should be further investigated.

Another consideration is how much lag time to expect between the origin of a barrier and the effects on species. If lag time is great between the generation of a barrier and its observed effect on lineage divergence, it will be difficult to attribute speciation events to their appropriate drivers. However, as our focus is on the scale of millions of years we do not expect significant lag between the time estimates of barriers and speciation events influenced by those barriers. In addition, Castoe et al. (2009) did not find lag time effects in biogeographic estimates of Central American highland pitviper diversification. They found tight correlations between the divergence times of multiple genera that were influenced by the same lowland geographic features, times that were similar to the predicted emergence of those features. If South American pitviper species were strongly influenced by particular geological events, we would expect to see the same signature in their divergences. This could be an interesting area for future biogeographic work in this and other taxonomic groups.

Perhaps the complexity of speciation and range evolution seen in South American pitvipers may not be appropriately modeled by current dispersal-extinction-cladogenesis analyses. These methods require the partitioning of geographic ranges into a set of discrete regions, and have been informative on broad scales such as continents, but may be less insightful for relatively continuous habitats where many species ranges

span more than one region. We predict future studies will be able to use more spatially explicit models, with fewer constraints on assigning taxa to specific areas.

Conclusions

We find the diversity of extant pitvipers in South America may be driven by a number of factors, but find only half of our tested hypotheses supported by pitviper speciation events. We predict that with the use of multiple empirical datasets, a select number of hypotheses will gain strong support, with some hypotheses supported by only a few examples, and others rejected. Most of these hypotheses were generated on the basis of patterns seen in one or a few taxa, and now researchers can define specific predictions and test them to understand how well these explanations generalize across the Tree of Life. For pitvipers, a combination of the mainly vicariant processes tested here, dispersal-based events, or even neutral processes may have been responsible for observed diversity. It seems unlikely that such a major geological event such as the rising of the Andes mountains would not leave a stronger signature in the phylogeny of small, terrestrial ectotherms such as pitvipers, which suggests more evaluation of Miocene diversification in this and related groups would better illuminate biological responses to geological change in South America.

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CHAPTER 6: CONCLUSION

As phylogenetics, particularly in reptiles and amphibians, is quickly resolving the evolutionary relationships of genus-level and higher relationships, systematists should focus on estimating the evolution of all species within a group of interest and testing hypotheses using phylogenies (Wiens, 2008). Both of these goals require robust, taxon-dense hypotheses of evolutionary relationships. I resolved relationships of 96% of the 213 species of pitviper, with good resolution of relationships for the 81% of species represented by over 100 characters. For most Asian species, I included phenotypic data in phylogenetic estimation for the first time. In keeping with the traditional roles of phylogeneticists, I evaluated the relationships of South American bothropoid pitvipers and proposed new generic-level taxonomy that describes evolutionarily distinct groups. I also evaluated the phylogenetic placement of a number of newly described species. I combined newly-generated estimated phylogenies with published data to understand biological patterns of the past: 1) I used a phylogeny of vipers in combination with species-level data on egg-laying and livebearing to test the hypothesis of Dollo's Law for the evolution of reproductive mode in vipers. I found that different methods of estimating this character return different results and therefore fail to reject Dollo's Law. 2) I used a phylogeny of South American pitvipers in combination with ranges of extant species to test a number of hypotheses for diversification of South American organisms.

I found the speciation patterns of these snakes to be complex and the regions inhabited by ancestral groups difficult to predict.

Evaluating evolutionary relationships and taxon names

In evaluating the relationships among pitviper species, I utilized a data matrix that should become increasingly common in phylogenetic analysis: four mitochondrial loci for the majority of species, an additional independent genetic locus for a minority of species, and a phenotypic dataset available for practically all species. As expected, the phenotypic dataset made up about 2% of the matrix. The key challenge in this study was that snakes are morphologically conserved (Parkinson et al., 2002) and limbless, leading to a phenotypic matrix of only 100 characters. Although the inclusion of rare and recently-described species in phylogenetic estimation provided some of the first hypotheses for evolutionary relationships of these lineages, adding these highly data-limited species to the analysis reduced the resolution of the tree overall. Prior work suggests that with enough complete characters even data-limited species can be placed in expected phylogenetic positions and may even influence the estimated relationships of nearly data-complete species (Wiens, 2003; Wiens et al., 2010). Therefore, I concluded that the low number of complete characters and potential lack of variation within the phenotypic characters for most groups led to the negative effects of data-limited taxa on phylogenetic resolution. More empirical research will help evaluate the number of characters that lead to good resolution of data-limited lineages across taxonomic groups of various sizes and histories.

I found that adding independent character sets to the well-studied mitochondrial data matrix for pitvipers is beneficial for adding taxa to the analysis and does increase support, but that influence on support is slight and the independent datasets did little to change relationships. Unlike most groups of herpetofauna, intergeneric relationships of pitvipers are not settled, and the addition of a nuclear gene and phenotypic data did not fully resolve the deepest phylogenetic relationships of vipers. It appears that to resolve these deep relationships phylogenomic methods or analysis of many nuclear loci may be required (e.g. Townsend et al., 2011). However, for estimation of species-level relationships and particularly to estimate relationships for as many lineages as possible, the methods used in this study are optimal.

If the inclusion of a maximum number of species is not a goal or if the number of complete phenotypic characters is expected to be low, then the collection of phenotypic data is an extremely inefficient method of bolstering phylogenetic estimation. For this study I examined approximately 1900 individuals and scoured published accounts to include data for 850 others, but even the combination of these data did little to increase understanding of pitviper evolutionary relationships. For example, I did not resolve the sister group of New World vipers and found little support for phylogenetic positions of newly-described species based on morphological data alone. However, I found support from independent datasets for taxonomic proposals and other hypotheses of evolutionary relationship formerly based on single linkage groups (e.g. Malhotra and Thorpe, 2004).

As speciation takes place across extended time periods, the more information a researcher provides to support the divergence between two lineages, the better evidence she has for giving those lineages different names. This idea underpins the general lineage concept of species (de Queiroz, 1998). In the study reported in Chapter 3 and published in 2009, I had support from two independent datasets for the evolutionary distinctiveness of bothropoid pitviper clades, in addition to natural history information supporting their different geographic ranges and ecological requirements. My paper has been cited 41 times, which suggests the new taxonomy is being accepted. Interestingly, a recent critique by Carrasco et al. (2012) finds topological differences in their phylogeny combining mtDNA, ecology and a different set of phenotypic characters. In the interest of taxonomic stability, they suggest lumping the newly described genera and *Bothriopsis* together under *Bothrops*. This proposal limits the biological information contained in the genus named *Bothrops*, as it combines into one genus lineages that range across the continent of South America, from lowlands to highlands, and from the ground to the trees (reviewed in Campbell and Lamar, 2004).

On the opposite end of the spectrum are taxonomic proposals that rely on partial or incomplete data to define groups with questionable biological information and slight taxonomic stability. For example, Hoser (2009) named nine rattlesnake genera based only on a consensus phylogeny suggested by Murphy et al. (2002). The species groups elevated by Hoser were not supported by a particular dataset and therefore had no known synapomorphies. In addition to work finding the new names unavailable under the International Code of Zoological Nomenclature (Wüster and Bernils, 2011),

recent phylogenetic estimation with mitochondrial, nuclear and phenotypic evidence (this study; Fenwick, Diamond, LaDuc and Parkinson, in prep.) finds considerable species-level reassignment would be required to retain Hoser's taxonomy. Similarly, Hoser (2012) erected a new genus to comprise species left *incertae sedis* by the South American bothropoid study in this dissertation (Fenwick et al., 2009). With additional data, we find two of these species to form a distinct group, which may deserve generic recognition. However, we find two other species in divergent phylogenetic positions and do not have enough information to evaluate the relationships of the last species. We recommend rejecting Hoser's many taxonomic proposals.

As the above examples indicate, a middle road is needed between an overly conservative taxonomy that decreases the communication of biological information and a poorly-supported taxonomy that threatens to be too changeable to facilitate good scientific communication. I suggest that my proposed taxonomy for South American bothropoids follows just such a middle road and can serve as a template for new taxonomic revisions.

Hypothesis testing using phylogenies

Natural history data on many aspects of extant species' biology are available in the literature, and the evolution of various traits can be modeled to estimate changes across the history of a group and better understand how the traits evolved. From my study of the evolution of reproductive mode, I found that evaluating evolutionary patterns is like any other hypothesis testing procedure in that using different models with different assumptions is important to generating strong confidence in conclusions.

In this case the use of different models was important to understanding the lack of support for either unidirectional evolution or reversals from derived to ancestral reproductive modes.

In the specific case of Dollo's Law, multiple violations in complex characters found in different organisms (Wiens, 2011 and references therein) suggest that its process of unidirectional evolution is not more common than bidirectional evolution in the Tree of Life. The large number of changes in reproductive mode across squamates suggests that reversals may occur in this system but limitations specific to vipers kept us from finding strong support for rejecting Dollo's Law. The group contains relatively few cases of the ancestral mode of oviparity, which would allow us to detect reversals. Importantly, the deepest relationships among vipers had relatively low support, which complicated character estimation. Increased taxon sampling and filling in missing data among true vipers may help to detect reversals in that subfamily, but I expect support for bidirectional evolution of reproductive mode in squamates must come from a different taxonomic system.

In the specific case of evaluating range evolution in South American pitvipers, I found little insight into diversification patterns using dispersal-extinction-cladogenesis methods (DEC; Ree et al., 2005; Ree and Smith, 2008) to evaluate evolution across the regions defined in this study. Most studies currently using DEC methods define regions with distinct geographic barriers such as, for angiosperms, different island groups (Bendiksby et al., 2010) or continental-scale regions (Xiang and Thomas, 2008). To understand the range evolution of vipers, a focus on distinct geological barriers may

provide more insight. This focus was informative for Central American vipers, where multiple independent groups were influenced by common geographic breaks (Daza et al., 2010). Surprisingly, although the rising of the Andes Mountains should have introduced a major barrier to organismal movement in South America, we find little evidence of its effect in pitvipers.

The study of geographic range evolution is a recent modification of trait evolution methods, and therefore fewer algorithms for modeling historical ranges of lineages are available. In this case I only used one algorithm to understand the evolution of pitviper biogeography in South America. A second method has been recently introduced (Goldberg et al., 2011), and I recommend its use on this pitviper dataset. However, as its assumptions and algorithms are similar to those of Lagrange I expect the ranges predicted by the two methods will agree (Ree et al., 2005; Ree and Smith, 2008) in finding the evolution of South American pitvipers complex and poorly explained by any single diversification hypothesis.

Although future research may be necessary to clarify understanding of South American bothropoid biogeography, the framework of defining spatial and temporal predictions for biogeographic hypotheses and testing them with empirical examples is extremely useful. In the case of South American vipers, using spatial patterns of extant species could have rejected the hypothesis of Amazonian vicariance, but the combination of spatial and temporal estimation was required to evaluate the influence of allopatric factors such as Andes rise and marine incursions compared to climatic factors such as refugial processes. The set of specific predictions tested in this study can

be directly applied to other South American terrestrial animals, and the framework can be applied to systems worldwide. The addition of a temporal component to methods that formerly tested only spatial patterns (e.g. DIVA; Ronquist, 1996) greatly increases the power of biogeographic methods to assess the influence of environmental factors on speciation processes. I recommend the use of specific spatial and temporal predictions for all evaluations of biogeographic effects of distinct events expected to drive vicariant speciation.

The two hypothesis testing studies included in this dissertation represent a tiny fraction of the biological questions that could be addressed in pitvipers through the combination of phylogeny with natural history data. The number of questions that could be addressed using other branches of the Tree of Life is orders of magnitude larger. Taxon-dense, well-supported phylogenies, such as the ones generated by this work, will be used to assess the influence of evolutionary history on phenotype, development, behavior, and ecology and even to account for that evolutionary history in studies of the effects of these factors on the biology of current lineages. This pitviper phylogeny is already being used in comparative methods (Gartner, pers. comm.), and provides an excellent example of the promise of phylogeny to provide insight into the biology of past and current species.

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APPENDIX A:
MORPHOLOGICAL CHARACTERS USED IN STUDIES

Characters 1-76 were taken from Gutberlet and Harvey (2002), and follow the numbering and descriptions therein. Additional characters adapted from other papers are so indicated, along with the number used by the author. Terminology is primarily from Klauber (1972) for squamation and crania, Hofstetter and Gasc (1969) for vertebrae, and Dowling and Savage (1960) for hemipenes.

1. Number of interoculabials.
2. Number of prefoveals.
3. Number of suboculars.
4. Number of supralabials.
5. Number of canthals.
6. Number of intersupraoculars.
7. Number of interrictals.
8. Number of gulars between the chin shields and the first ventral [first ventral defined by Klauber (1972) as the first scale wider then long].
9. Number of ventrals. Ventrals are counted after the method of Dowling (1951), which is different from the method used by Gutberlet and Harvey.
10. Number of middorsal scale rows.
11. Loreal (modified from Gutberlet and Harvey): (0) absent, (1) entire, (2) fragmented vertically.
12. Rostral: (0) broader than high, (1) approximately as broad as high (within 10%) (2) higher than broad.
13. Upper preocular: (0) entire, (1) divided anterior to posterior.
14. Supraocular horn (modified from Gutberlet and Harvey): (0) absent, (1) present, composed of enlarged superciliary scales, (2) present, composed of several fused scales, (3) composed of a single scale.
15. Canthals: (0) flat, (1) raised into small horns.

16. Prelacunal and second supralabial (modified from Gutberlet and Harvey): (0) no prelacunal present, (1) fused, (2) not fused, subfoveals absent, (3) separated by one row of subfoveals, (4) separated by two rows of subfoveals. Based on morphological intermediacy, it can be argued that 0→1→2→3→4 constitutes an ordered transformation series.

17. Scales in parietal region (modified from Gutberlet and Harvey): (0) smooth, (1) keeled, (2) tuberculate.

18. Middle preocular and supralacunal (modified from Gutberlet and Harvey): (0) supralacunal absent/fused to canthals, (1) fused, (2) not fused.

19. Sublacunal (modified from Gutberlet and Harvey): (0) sublacunal absent/fused to canthals, (1) entire, (2) divided with anterior and posterior components.

20. Canthus rostralis: (0) not elevated, (1) elevated to form a distinct ridge.

21. Loreals (modified from Gutberlet and Harvey): (0) absent/fused to canthals, (1) not projecting laterally, (2) projecting laterally.

22. Subcaudals: (0) divided, (1) both divided and entire, (2) entire. Based on morphological intermediacy, it can be argued that 0→1→2 constitutes an ordered transformation series.

23. Papilla protruding from apex of hemipenes: (0) absent, (1) present.

24. Basal and lateral hemipenial spines (modified from Gutberlet and Harvey): (0) many, densely distributed, (1) few, widely spaced (2) none.

25. Calyces on lateral surfaces of hemipenial lobes (modified from Gutberlet and Harvey): (0) restricted to distal portion of lobe, (1) extending proximally to level of crotch, (2) not present.

26. Pleurapophyses of midcaudal vertebrae: (0) long and slender, (1) short and slender, (2) short and wide. Based on morphological intermediacy, it can be argued that 0→1→2 constitutes an ordered transformation series.

27. Haemapophyses of midcaudal vertebrae: (0) not in contact distally, (1) in contact distally.

28. Number of palatine teeth.

29. Number of pterygoid teeth.

30. Number of dentary teeth.

31. Length of maxillary fang: (0) short, maximum length only slightly greater than height on maxilla, (1) long, approximately two times longer than height of maxilla.

32. Medial wall of pit cavity in maxilla (modified from Gutberlet and Harvey): (0) pit cavity absent, (1) notch in wall weakly developed to almost absent, (2) wall with a well-developed notch.

33. Small pit in anterolateral wall of pit cavity in maxilla (modified from Gutberlet and Harvey): (0) pit cavity absent, (1) anterolateral wall simple and lacking projection, (2) anterolateral wall with a small rounded projection, (3) projection with foramen.

34. Anterior foramina of prootic: (0) separated by a bony partition, (1) not separated by a bony partition.

35. Foramen in ventral surface of lateral process of prootic: (0) absent, (1) present.

36. Lateral portion of head of ectopterygoid in dorsal view: (0) broad, (1) intermediate, (2) narrow. Based on morphological intermediacy, it can be argued that 0→1→2 represents an ordered transformation series.

37. Shaft of ectopterygoid: (0) flat, broad, does not taper posteriorly, (1) flat, gradually tapers posteriorly, (2) narrow, does not taper posteriorly. Based on morphological intermediacy, it can be argued that 0→1→2 represents an ordered transformation series.

38. Pits at point of attachment of ectopterygoid retractors on posterior surface of anterior end of ectopterygoid: (0) absent, (1) single, (2) paired.

39. Base of ectopterygoid at point of articulation with pterygoid: (0) with a short, well-defined, fingerlike projection that articulates with pterygoid, (1) with an elongate, less defined projection that broadly overlaps pterygoid, (2) elongate projection present but not set off from rest of bone, i.e., spatulate. Based on morphological intermediacy, it can be argued that 0→1→2 represents an ordered transformation series.

40. Ectopterygoid: (0) shorter than base of pterygoid, (1) approximately equal in length to base of pterygoid (posterior to articulation with ectopterygoid, within 10%), (2) longer than base of pterygoid.

41. Choanal process of palatine (modified from Gutberlet and Harvey): (0) absent, (1) positioned anteriorly, (2) positioned medially, (3) positioned posteriorly. Based on morphological intermediacy, it can be argued that 0→1→2 represents an ordered transformation series.

42. Ventral process of basioccipital: (0) single, (1) bifurcates distally.

43. Lateral processes of prefrontal: (0) directed laterally, (1) directed ventrally.

44. Medial margin of dorsal portion of prefrontal: (0) strongly concave with posteromedial processes longer, (1) moderately concave with anterior and posertior processes of equal length, (2) weakly concave with anteromedial processes longer. Based on morphological intermediacy, it can be argued that 0→1→2 represents an ordered transformation series.

45. Minimum width across both frontals: (0) less than, (1) equal to, or (2) greater than width of skull at anterior end of supratemporals. Based on morphological intermediacy, it can be argued that 0→1→2 represents an ordered transformation series.

46. Dorsal surface of frontals: (0) predominantly flat, (1) with elevated lateral margins.

47. Posterolateral edges of dorsal surface of parietal: (0) slope ventrolaterally, (1) intermediate, with a small lateral shelf of bone, (2) flare laterally and slightly dorsad.

48. Size of postfrontal: (0) large, contributing as much or more to the dorsal margin of the orbit than the parietal does, (1) small, contributing less to the dorsal margin of the orbit than the parietal does. The homology of this bone is in question; it may in fact be the postorbital.

49. Supratemporal: (0) expanded posteriorly but lacking a distinct projection, (1) with small posterolateral projection, (2) with large, hook-like posterolateral projection. The homology of this bone is in question; it may in fact be the squamosal. Based on morphological intermediacy, it can be argued that 0→1→2 represents an ordered transformation series.

50. Supratemporal: (0) thick with a rounded dorsal surface, (1) think with a flat dorsal surface.

51. Meckellian foramen: (0) completely or partially divided into two foramina, (1) single foramen, not divided.

52. Angular and splenial: (0) separate, (1) partially fused, (2) completely fused.

53. Canthorostrals: (0) absent, (1) present. These are small scales between the rostral and the internasals.

54. Dorsal head scales: (0) smooth, (1) keeled.

55. Keel on dorsal scales (modified from Gutberlet and Harvey): (0) absent, (1) typical thin ridge, (2) tuberculate on dorsals on caudal part of body, (3) tuberculate on all dorsals. Based on morphological intermediacy, one may argue that 0→1→2→3 constitutes an ordered transformation series.

56. Keel on parasubcaudals: (0) present, (1) absent.

57. Suboculars: (0) excluded from anteroventral corner of orbit, (1) extend to anteroventral corner of orbit.

58. Sublacunal (modified from Gutberlet and Harvey): (0) absent/fused to canthals, (1) entire, (2) divided with an internal and external component.

59. Loreal (modified from Gutberlet and Harvey): (0) absent/fused to canthals, (1) entire, (2) divided dorsoventrally.

60. Loreal (modified from Gutberlet and Harvey): (0) absent/fused to canthals, (1) contacts canthals, (2) does not contact canthals.

61. Loreal (modified from Gutberlet and Harvey): (0) absent/fused to canthals, (1) longer than high, (2) approximately as long as high (within 10%), (3) higher than long. Based on morphological intermediacy, one may argue that 0→1→2→3 constitutes an ordered transformation series.

62. Number of subcaudals.

63. Nasal pore: (0) present, (1) absent. The nasal pore is a tiny opening on the postnasal scale inside the nostril of most snakes.

64. Loreal pit (modified from Gutberlet and Harvey): (0) absent, (1) crossed by naso-orbital line, (2) ventral to naso-orbital line.

65. Rattle: (0) absent, (1) present.

66. Tail: (0) not prehensile, (1) prehensile.

67. Distinct white spots on posterior infralabials and gulars: (0) absent, (1) present.

68. Orange middorsal stripe: (0) absent, (1) present.

69. Tail pattern: (0) not banded, (1) banded. Specimens with state 1 have distinct black and white bands on the tail, as seen in some rattlesnakes.

70. Dorsum with green ground color: (0) absent, (1) present.

71. Mesial spines on hemipenial lobes: (0) absent, (1) present.

72. Hemipenial lobes: (0) deeply divided, greater than two times longer than base, (1) moderately divided, approximately two times longer than base, (2) partially divided, approximately as long as base, (3) weakly divided, shorter than base. This character was collected but not analyzed due to differences in hemipenis preparation which may have affected lobe length measurements.

73. Calyces on hemipenial lobes (modified from Gutberlet and Harvey): (0) spinulate, (1) smooth, (2) both spinulate and smooth calyces present (3) calyces absent). Most taxa have hemipenes with calyx ridges adorned with tiny spinules (state 0).

74. Size of choanal process of palatine (modified from Gutberlet and Harvey): (0) process absent, (1) greatly reduced, (2) reduced, (3) moderate, (4) attenuate. Based on morphological intermediacy, one may argue that 0→1→2→3→4 constitutes an ordered transformation series.

75. Postfrontal (modified from Gutberlet and Harvey): (0) curves posterolaterally, (1) angles anteriorly, (2) curves to point anteriorly. The homology of this bone is in question; it may in fact be the postorbital.

76. Medial process at posterior end of ectopterygoid: (0) weakly developed, (1) large and prominent.

77. Nasorostrals (modified from Jadin et al. (2010) no. 28): (0) absent, (1) present. Nasorostrals are small scales between the rostral and the prenasal scale.

78. Postnasal (modified from Werman (1992) no. 37): (0) not in contact with first supralabial, (1) in contact with first supralabial, (2) fused to prenasal, (3) fused to prenasal and first supralabial. In state 0 the postnasal is excluded from contact with the first supralabial by the prenasal, prefoveals, or both.

79. Number of scales contacting supraoculars (Wüster et al. (1996) no. 27).

80. Number of scales contacting third supralabial anterior of rictus (Wüster et al. (1996) no. 28). This count includes the supralabials anterior and posterior to the third supralabial.

81. Number of scales across head halfway between supraoculars and internasals (Wüster et al. no. 33 in part). This character is counted in a horizontal line including one canthal from each side.

82. Postorbital stripe: (0) absent, (1) present. (from Campbell and Lamar (2004)). The postorbital stripe is a dark stripe that runs from the posterior corner of the eye towards the back of the head.

83. Postorbital stripe height at rictus. This is the number of scale rows that comprise the postorbital stripe above the rictus of the mouth

84. Postorbital stripe ends: (0) stripe absent, (1) anterior to rictus, (2) at rictus, (3) posterior of head, (4) on neck.

85. Number of supralabials with postorbital stripe.

86. Percent of last supralabial with postorbital stripe. The state of each individual was estimated from visual inspection.

87. Dorsum of head with green ground color: (0) absent, (1) present.

88. deleted

89. Black bars on gulars: (0) absent, (1) present.

90. deleted

91. deleted

92. Percentage of dark pigment on ventrals. The state of each individual was estimated from visual inspection.

93. Number of postcanthals (modified from Gutberlet and Harvey no. 5). Postcanthals are the scales between the most posterior canthal scale and the supraocular.

94. Loreal shape (modified from Harvey (2005)): (0) absent/fused to canthals, (1) subtriangular, (2) rectangular.

95. Number of internasals (Harvey et al., 2005).

96. Apical pits on dorsal scales (0) absent, (1) present. Apical pits are small fenestrae at the tips of scales, easily seen in *Agkistrodon piscivorus*.

97. Parasubcaudals near tip of tail (Hoge and Romano-Hoge, 1981 [dated 1979]): (0) higher than wide, (1) square, (2) wider than high

98. Supratemporals (Hoge and Romano-Hoge, 1981 [dated 1979]): (0) not extending posteriorly past braincase, (1) extending posteriorly past braincase

99. Transition from spines to calyces on hemipenes : (0) abrupt (1) gradual (2) nonexistent.

100. Number of supraoculars.

101. Stripe on dorsal scale row 1 (Sanders et al., 2004): (0) absent (1) present.

102. Lateral projection on lateral head of ectopterygoid: (0) absent, (1) present.

References for Appendix A

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APPENDIX B:
INDIVIDUALS EXAMINED FOR MORPHOLOGICAL DATA

Species used, voucher data, collecting locality, and maorphological data types collected for individuals analyzed in pitviper phylogeny. Examiners are identified by name or initials: AMF = A. Fenwick, KMD = K. Diamond, LaDuc = T. LaDuc. Specimens with data collected from species accounts are identified via citations of publications containing the descriptions; for publications where data were aggregated, the number of specimens used is noted. Institutional abbreviations for vouchers are listed in Leviton, Gibbs, Heal & Dawson (1985).

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Agkistrodon bilineatus	AMNH R-57782, R-64811, R-67141	–			x		AMF
Agkistrodon bilineatus	CAS uncataloged	no data, Steinhart Aquarium			x		AMF
Agkistrodon bilineatus	FMNH 19425, 36253	Mexico: Yucatán	x	x			AMF
Agkistrodon bilineatus	FMNH 236414	Honduras: Valle: San Lorenzo	x	x			AMF
Agkistrodon bilineatus	FMNH 4196	Belize	x	x			AMF
Agkistrodon bilineatus	UCM 40640, 40641, 41792	Mexico: Yucatán: Munic. Tinum	x	x			AMF
Agkistrodon bilineatus	AMNH 125525, 125527	Costa Rica: Guanacaste Prov.		x			Campbell and Lamar 2004
Agkistrodon bilineatus	–	–		x			Campbell and Lamar 2004
Agkistrodon bilineatus	UAZ 41131	Mexico: Colima		x			Campbell and Lamar 2004
Agkistrodon contortrix	AMNH R-77594	USA: New York: Greene Co.			x		AMF
Agkistrodon contortrix	FLMNH 18364	USA: Connecticut: Hartford Co.			x		AMF
Agkistrodon contortrix	FLMNH 37511	USA: Pennsylvania: York Co.			x		AMF
Agkistrodon contortrix	FMNH 178997, 178998	USA: Kansas: Douglas Co.	x	x		x	AMF
Agkistrodon contortrix	UTA R-38098	USA: Arkansas: Colombia Co.			x		AMF
Agkistrodon contortrix	UTA R-40961	USA: Oklahoma: LeFlore Co.			x		AMF
Agkistrodon contortrix	UTA uncataloged	USA: Texas: Freestone Co.			x		AMF
Agkistrodon contortrix	UTT 102, 104, 113, 245, 246, 262, 529	USA: Texas: Smith Co.	x	x			AMF
Agkistrodon contortrix	UTT 154	USA: Texas: Smith Co.	x	x		x	AMF
Agkistrodon contortrix	UTT 516	USA: Texas: Henderson Co.	x	x			AMF
Agkistrodon contortrix	UTT 587	–	x	x			AMF
Agkistrodon contortrix	–	–		x			Campbell and Lamar 2004
Agkistrodon contortrix	–	–	8 inds.		6 inds		Gutberlet 1998
Agkistrodon piscivorus	AMNH R-65481	–				x	AMF
Agkistrodon piscivorus	AMNH R-69108	USA: Florida			x		AMF
Agkistrodon piscivorus	AMNH R-81544	USA: Georgia: SREL			x		AMF
Agkistrodon piscivorus	AMNH R-84486	USA: South Carolina: Jasper Co.			x		AMF
Agkistrodon piscivorus	CLP CLP984	USA: Georgia: Thomas Co.	x	x		x	AMF
Agkistrodon piscivorus	FLMNH 119743, 119745	USA: South Carolina: Jasper Co.	x	x		x	AMF
Agkistrodon piscivorus	FLMNH 74435–74437	USA: Texas	x	x			AMF
Agkistrodon piscivorus	FLMNH 8950	USA: Florida: Alachua Co.			x		AMF
Agkistrodon piscivorus	UCF 2307	USA: Florida: Polk Co.	x	x			AMF
Agkistrodon piscivorus	UCF CLP271	USA: Florida: Osceola Co.	x	x		x	AMF
Agkistrodon piscivorus	UCF CLP934	USA: Florida	x	x			AMF
Agkistrodon piscivorus	UCF CLP942	USA: Georgia: SREL	x	x			AMF
Agkistrodon piscivorus	UTA R-54070	USA: Texas: Rains Co.				x	AMF
Agkistrodon piscivorus	CA 5602	–		x			Campbell and Lamar 2004
Agkistrodon piscivorus	–	–		x			Campbell and Lamar 2004
Agkistrodon taylori	AMNH R-140853	no data, rec. via NY Zool. Soc.			x		AMF
Agkistrodon taylori	CM 147767	Mexico: Tamaulipas			x		AMF
Agkistrodon taylori	CM 147769	Mexico: Tamaulipas	x	x	x		AMF
Agkistrodon taylori	FMNH 250435	Mexico, don. Lincoln Park Zoo	x	x	x		AMF
Agkistrodon taylori	FMNH 28794	Mexico: Tamaulipas	x	x			AMF
Agkistrodon taylori	USNM 209854	Mexico: Tamaulipas: Munic. Aldama	x	x		x	AMF
Agkistrodon taylori	–	–		x			Campbell and Lamar 2004
Atheris ceratophora	CAS 162615–162618	Tanzania: Iringa Region: Mufindi Dist.	x	x			AMF
Atheris ceratophora	CAS 168976	Tanzania: Tanga Region: Lushoto Dist.	x	x			AMF
Atheris ceratophora	CAS 173806	Tanzania: Tanga Region: Muheza Dist.	x				AMF
Atheris ceratophora	CAS 173812	Tanzania: Iringa Region: Mufindi Dist.	x	x			AMF
Atheris ceratophora	FLMNH 66893	Tanzania: Tanga Region: Usambara Mts.	x	x			AMF
Atheris ceratophora	UCF CLP919, CLP920	no data, rec. via A. Cortiz	x	x			AMF
Atheris ceratophora	UTA uncataloged	Tanzania: Usambara Mts.			x		AMF
Atheris nitschei	CAS 178224	Uganda: Rukungiri Dist.: Bwindi Impenetrable Forest Reserve			x		AMF
Atheris nitschei	CAS 201653, 201707, 201708	Uganda: Kabale Dist.: Bwindi Impenetrable Ntl. Park	x	x			AMF
Atheris nitschei	CAS 201654, 201655, 201706	Uganda: Kabale Dist.: Bwindi Impenetrable Ntl. Park	x	x		x	AMF
Atheris nitschei	CAS 85298	Democratic Republic of Congo: Sud-Kivu Prov.: Idjwi Isl.	x	x		x	AMF
Atheris nitschei	CAS 85981	Democratic Republic of Congo	x	x			AMF
Atheris nitschei	FLMNH 80361	Democratic Republic of Congo	x	x			AMF
Atheris nitschei	FMNH 8984	Uganda			x		AMF
Atheris nitschei	FMNH 8987	Uganda: Kigezi Dist.			x		AMF
Atheris nitschei	UCF CLP912	no data, rec. via A. Cortiz	x	x			AMF
Atheris nitschei	UCF CLP913	no data, rec. via A. Cortiz	x				AMF
Atheris squamigera	CAS 197898	Cameroon: East Region: Dja Reserve	x	x			AMF
Atheris squamigera	CAS 207867, 207869	Equatorial Guinea: Bioko Isl.	x	x		x	AMF
Atheris squamigera	FLMNH 72485	–			x		AMF
Atheris squamigera	FLMNH 80384, 80678	Democratic Republic of Congo	x	x		x	AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Atheris squamigera	FLMNH 80389	Democratic Republic of Congo	x	x			AMF
Atheris squamigera	FLMNH 86506, 92249	Kenya	x	x			AMF
Atheris squamigera	UCF CLP914, CLP915	no data, rec. via A. Cortiz	x	x			AMF
Atropoides indomitus	UTA R-52952	Honduras: Dept. Colón	x	x		x	AMF
Atropoides indomitus	–	–	2 inds				Jadin et al. 2010
Atropoides mexicanus	UTA R-12943	Costa Rica; Cartago Prov.: Turrialba Canton: Pavones Dist.				x	AMF
Atropoides mexicanus	UTA R-21967, R-22454	Guatemala: Dept. Baja Verapaz				x	AMF
Atropoides mexicanus	UTA R-24755	Guatemala: Dept. Baja Verapaz	x	x		x	AMF
Atropoides mexicanus	UTA R-24847	Costa Rica: San José Prov.: Puriscal Canton				x	AMF
Atropoides mexicanus	UTA R-38101	Guatemala: Dept. Baja Verapaz			x		AMF
Atropoides mexicanus	UTA R-45500	Guatemala: Dept. Huehuetenango				x	AMF
Atropoides mexicanus	–	–		x			Campbell and Lamar 2004
Atropoides mexicanus	–	–	17 inds				Jadin et al. 2010
Atropoides mexicanus	UTA R35943	Guatemala: Dept. Baja Verapaz		x			Campbell and Lamar 2004
Atropoides nummifer	AMNH R-46475	–			x		AMF
Atropoides nummifer	AMNH R-46962	Honduras			x		AMF
Atropoides nummifer	FLMNH 71065, 71066	Costa Rica			x		AMF
Atropoides nummifer	FMNH 27125	Honduras			x		AMF
Atropoides nummifer	UTA R-16107	Guatemala: Dept. Escuintla	x	x			AMF
Atropoides nummifer	UTA R-24842	Mexico: Hidalgo: La Huasteca Region	x	x		x	AMF
Atropoides nummifer	UTA R-53745	Honduras: Dept. Copán	x	x			AMF
Atropoides nummifer	–	–		x			Campbell and Lamar 2004
Atropoides nummifer	–	–	4 inds				Jadin et al. 2010
Atropoides nummifer	–	–	7 inds.		3 inds.		Gutberlet 1998
Atropoides nummifer	UTA R24843	Mexico: Hidalgo		x			Campbell and Lamar 2004
Atropoides occiduus	UTA R-34158	Guatemala: Dept. Baja Verapaz	x	x		x	AMF
Atropoides occiduus	UTA R-9089	Guatemala: Dept. Escuintla				x	AMF
Atropoides occiduus	–	–		x			Campbell and Lamar 2004
Atropoides occiduus	–	–	5 inds				Jadin et al. 2010
Atropoides occiduus	UTA R12785	Guatemala: Dept. Escuintla		x			Campbell and Lamar 2004
Atropoides olmec	UTA R-25113		x	x		x	AMF
Atropoides olmec	–	–		x			Campbell and Lamar 2004
Atropoides olmec	–	–	6 inds				Jadin et al. 2010
Atropoides olmec	UTA R-6206	Mexico: Oaxaca					Jadin et al. 2010
Atropoides olmec	UTA R25113	Mexico: Veracruz		x			Campbell and Lamar 2004, Jadin et al. 2010
Atropoides picadoi	UCF CLP918	no data, rec. via A. Cortiz	x	x			AMF
Atropoides picadoi	UTA R-18215	Costa Rica				x	AMF
Atropoides picadoi	UTA R-24834	Costa Rica: San José: Moravia Canton				x	AMF
Atropoides picadoi	UTA R-32080	Costa Rica	x	x		x	AMF
Atropoides picadoi	–	–		2 inds			Campbell and Lamar 2004
Atropoides picadoi	–	–	4 inds				Jadin et al. 2010
Atropoides picadoi	UTA R-18215	Costa Rica					Jadin et al. 2010
Atropoides picadoi	UTA R24836	Costa Rica: Heredia Prov.		x			Campbell and Lamar 2004
Azemiops feae	FMNH 152987	Indochina	x	x			AMF
Azemiops feae	FMNH 170643	China: Sikang Prov.	x	x			AMF
Azemiops feae	FMNH 218627, 218628	–	x	x			AMF
Azemiops feae	UCM 57352	China: Fujian Prov.	x	x			AMF
Azemiops feae	UCM 58997, 60500	China: Anhui Prov.	x	x			AMF
Azemiops feae	USNM 84363	China: Sichuan Prov.		x	x	x	AMF
Bitis arietans	AMNH R-51878	Angola: Huíla Prov.	x	x		x	AMF
Bitis arietans	CAS 160773	Botswana: South-East Dist.	x	x			AMF
Bitis arietans	CAS 200970	South Africa: Cape Prov.			x		AMF
Bitis arietans	FLMNH 101242	Democratic Republic of Congo: Kinshasa Prov.	x	x			AMF
Bitis arietans	FLMNH 119853	Mozambique	x	x			AMF
Bitis arietans	FLMNH 58049, 119855	Tanzania	x	x		x	AMF
Bitis arietans	FLMNH 119856	Tanzania: Arusha Dist.	x	x			AMF
Bitis arietans	FLMNH 61114	Togo			x		AMF
Bitis arietans	FLMNH 61976	Tanzania: Morogoro Region			x		AMF
Bitis arietans	FLMNH 71786	Togo			x		AMF
Bitis arietans	FLMNH 85486, 88665	Kenya	x	x			AMF
Bitis arietans	FLMNH 92250	Kenya: Rift Valley Prov.: Baringo Dist.	x	x			AMF
Bitis arietans	FMNH 11006	East Africa			x		AMF
Bitis arietans	FMNH 196152	Liberia			x		AMF
Bitis arietans	FMNH 31316	–			x		AMF
Bitis nasicornis	FLMNH 119868	Ghana	x	x		x	AMF
Bitis nasicornis	FLMNH 21356, 21357, 119869	Kenya	x	x			AMF
Bitis nasicornis	FLMNH 61287, 61484	Togo			x		AMF
Bitis nasicornis	FLMNH 80681	Democratic Republic of Congo	x	x			AMF
Bitis nasicornis	FMNH 3996, 19457	Cameroon			x		AMF
Bitis nasicornis	UCM 17022	Democratic Republic of Congo: Orientale Prov.: Bas-Uele Dist.	x	x			AMF
Bitis nasicornis	UTA uncataloged	–			x		AMF
Bitis nasicornis	UTA, CJF 1257	–			x		AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Bitis peringueyi	CAS 111963, 111964	Namibia: Erongo Region: Namib Desert	x	x			AMF
Bothriechis aurifer	FLMNH 57718	Guatemala			x		AMF
Bothriechis aurifer	FLMNH 87959, 87962, 96309	Guatemala	x	x			AMF
Bothriechis aurifer	KU 187435, 187437	Guatemala: Dept. Baja Verapaz	x	x			AMF
Bothriechis aurifer	KU 187436, 187440	Guatemala: Dept. Baja Verapaz	x	x		x	AMF
Bothriechis aurifer	ROM 42220, 42221	Guatemala: Dept. Baja Verapaz	x	x			AMF
Bothriechis aurifer	UMMZ 91081	Guatemala: Dept. Baja Verapaz	x	x			AMF
Bothriechis aurifer	UTA R-7046, R-35031, R-37226	Guatemala: Dept. Baja Verapaz			x		AMF
Bothriechis aurifer	UTA R-7041	Guatemala: Dept. Baja Verapaz				x	AMF
Bothriechis aurifer	UTA uncataloged	–			x		AMF
Bothriechis aurifer	KU 191201	–					Campbell and Lamar 2004
Bothriechis aurifer	–	–		x			Campbell and Lamar 2004
Bothriechis aurifer	UTA R-7040	Guatemala: Dept. Baja Verapaz		x			Campbell and Lamar 2004
Bothriechis bicolor	FLMNH 64238	Guatemala	x	x			AMF
Bothriechis bicolor	FMNH 20162	Guatemala	x	x			AMF
Bothriechis bicolor	UMMZ 131661	Guatemala: Dept. Chimaltenango	x	x			AMF
Bothriechis bicolor	UMMZ 87707	Mexico: Chiapas: Soconusco Dist.	x	x	x		AMF
Bothriechis bicolor	UMMZ 94644	Mexico: Chiapas	x	x			AMF
Bothriechis bicolor	UTA R-39413, R-39418	Guatemala: Dept. San Marcos: Munic. San Rafael Pie de la Cuesta	x	x			AMF
Bothriechis bicolor	UTA R-39420	–	x	x			AMF
Bothriechis bicolor	UTA R-9353	–			x		AMF
Bothriechis bicolor	–	–		x			Campbell and Lamar 2004
Bothriechis bicolor	–	–	6 inds.		2 inds.		Gutberlet 1998
Bothriechis bicolor	UTA R-42278	–		x			Campbell and Lamar 2004
Bothriechis lateralis	FLMNH 39820, 70571	Costa Rica: San José Prov.	x	x			AMF
Bothriechis lateralis	FLMNH 68976	–			x		AMF
Bothriechis lateralis	FLMNH 88564, 88565	Costa Rica: Alajuela Prov.: San Carlos Canton	x	x			AMF
Bothriechis lateralis	FLMNH 88566	Costa Rica	x	x			AMF
Bothriechis lateralis	UMMZ 101783, 101784, 147782	Panama: Chiriquí Prov.	x	x			AMF
Bothriechis lateralis	UTA R-14537	Costa Rica: San José Prov.			x	x	AMF
Bothriechis lateralis	UTA R-2811	–			x		AMF
Bothriechis lateralis	UTA R-3660	Costa Rica: San José Prov.: Patarrá Dist.			x	x	AMF
Bothriechis lateralis	–	–		x			Campbell and Lamar 2004
Bothriechis lateralis	–	–	7 inds.		3 inds.		Gutberlet 1998
Bothriechis marchi	FLMNH 144679	Honduras: Dept. Cortés	x	x		x	AMF
Bothriechis marchi	FLMNH 51160	Honduras			x		AMF
Bothriechis marchi	FLMNH 52554, 52555	Honduras	x	x			AMF
Bothriechis marchi	FMNH 21777, 21892, 34732, 34733, 36000, 37217, 38542, 41621	Honduras: Yoro	x	x			AMF
Bothriechis marchi	FMNH 31291, 31292	Honduras: Yoro			x		AMF
Bothriechis marchi	FMNH 31304	Honduras, don. Chicago Zool. Soc.			x		AMF
Bothriechis marchi	–	–		x			Campbell and Lamar 2004
Bothriechis nigroviridis	FLMNH 103499	Costa Rica: San José Prov.: San José	x	x			AMF
Bothriechis nigroviridis	FLMNH 70573	Costa Rica	x	x			AMF
Bothriechis nigroviridis	FLMNH 80252, 87335	Costa Rica: San José Prov.	x	x			AMF
Bothriechis nigroviridis	FLMNH 85313	Costa Rica	x	x		x	AMF
Bothriechis nigroviridis	LACM 154552	Costa Rica: Puntarenas Prov.	x	x			AMF
Bothriechis nigroviridis	LACM 154554	Costa Rica: Cartago Prov.	x	x			AMF
Bothriechis nigroviridis	UMMZ 117734	Costa Rica: San José Prov.	x	x	x		AMF
Bothriechis nigroviridis	UMMZ 131330	Costa Rica: Limon Prov.: Siquirres Canton	x	x			AMF
Bothriechis nigroviridis	UMMZ 138816	Costa Rica: San José Prov.			x		AMF
Bothriechis nigroviridis	UMMZ 147776	Panama: Chiriquí Prov.	x	x			AMF
Bothriechis nigroviridis	UTA R-9635	Costa Rica: San José Prov.			x		AMF
Bothriechis nigroviridis	UTA R-9636	–			x		AMF
Bothriechis nigroviridis	–	–		x			Campbell and Lamar 2004
Bothriechis nigroviridis	–	–	6 inds.		3 inds.		Gutberlet 1998
Bothriechis rowleyi	AMNH R-102894, 102895	Mexico: Oaxaca	x	x			AMF
Bothriechis rowleyi	FLMNH 52553	Mexico: Chiapas	x	x			AMF
Bothriechis rowleyi	UTA R-12565	–			x		AMF
Bothriechis rowleyi	UTA R-7707	–	x		x		AMF
Bothriechis rowleyi	–	–		x			Campbell and Lamar 2004
Bothriechis schlegelii	AMNH R-35777	Colombia			x		AMF
Bothriechis schlegelii	FLMNH 141057	Honduras: Dept. Gracias a Dios	x	x			AMF
Bothriechis schlegelii	FLMNH 150141	Honduras: Dept. Cortés	x	x			AMF
Bothriechis schlegelii	FLMNH 22254	Ecuador	x	x			AMF
Bothriechis schlegelii	FLMNH 30499	Costa Rica: Heredia Prov.	x	x			AMF
Bothriechis schlegelii	FLMNH 39829	Costa Rica: Guanacaste Prov.: La Cruz Canton	x	x			AMF
Bothriechis schlegelii	FLMNH 68031	Ecuador	x	x			AMF
Bothriechis schlegelii	FLMNH 69924	Costa Rica	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Bothriechis schlegelii	FLMNH 71068	Costa Rica			x		AMF
Bothriechis schlegelii	FMNH 2524	Costa Rica			x		AMF
Bothriechis schlegelii	FMNH 51688	Panama: Bocas del Toro Prov.	x		x		AMF
Bothriechis schlegelii	UMMZ 177670, 176988	Costa Rica: San José Prov.: Salitral Dist.	x	x			AMF
Bothriechis schlegelii	UMMZ 177671, 176989	Costa Rica: San José Prov.: Salitral Dist.	x	x	x		AMF
Bothriechis schlegelii	UMMZ 80725	Belize: Cayo Dist.	x	x			AMF
Bothriechis schlegelii	–	–	14 inds.		4 inds.		Gutberlet 1998
Bothriechis schlegelii	–	Colombia: Dept. Cauca		2 inds.			Campbell and Lamar 2004
Bothriechis schlegelii	–	Costa Rica: Limon Prov.		2 inds.			Campbell and Lamar 2004
Bothriechis schlegelii	UCR no number	Costa Rica: Puntarenas Prov.		x			Campbell and Lamar 2004
Bothriechis schlegelii	–	Ecuador		x			Campbell and Lamar 2004
Bothriechis schlegelii	–	Ecuador: Pichincha Prov.		x			Campbell and Lamar 2004
Bothriechis schlegelii	UTA R41195	Guatemala: Dept. Izabal		x			Campbell and Lamar 2004
Bothriechis schlegelii	UTA R12957	Guatemala: Dept. Izabal: Munic. Los Amates		x			Campbell and Lamar 2004
Bothriechis schlegelii	–	Peru: Tumbes Prov.		x			Campbell and Lamar 2004
Bothriechis supraciliaris	AMNH R-147743	Panama: Chiriquí Prov.	x	x			AMF
Bothriechis supraciliaris	UTA R-30289, R-35193, R-35246	Costa Rica; Puntarenas Prov.	x	x			AMF
Bothriechis supraciliaris	UTA R-35192	Costa Rica; Puntarenas Prov.	x	x		x	AMF
Bothriechis supraciliaris	UCR 14010	Costa Rica: Puntarenas Prov.: Dist. San Vito de Coto Brus		x			Campbell and Lamar 2004
Bothriechis supraciliaris	UCR no number	Costa Rica: Puntarenas Prov.: Dist. San Vito de Coto Brus		2 inds.			Campbell and Lamar 2004
Bothriechis supraciliaris	–	Costa Rica: Puntarenas Prov.: Dist. San Vito de Coto Brus		2 inds.			Campbell and Lamar 2004
Bothriechis thalassinus	FLMNH 142530	Honduras	x	x			AMF
Bothriechis thalassinus	FMNH 154530	Guatemala	x	x			AMF
Bothriechis thalassinus	UTA R-38220	Guatemala: Dept. Zacapa	x	x			AMF
Bothriechis thalassinus	UTA R-38891, R-39251, R-42259, R-46526	Guatemala: Dept. Izabal: Munic. Morales	x	x			AMF
Bothriechis thalassinus	UTA R-44438	Guatemala: Dept. Zacapa	x	x		x	AMF
Bothriechis thalassinus	–	–		x			Campbell and Lamar 2004
Bothriechis thalassinus	UTA R-46526	–		x			Campbell and Lamar 2004
Bothriopsis bilineata	AMNH R-53422, R-140856, R-140859	–			x		AMF
Bothriopsis bilineata	ANSP 7015	Peru: Loreto Region	x	x			AMF
Bothriopsis bilineata	FLMNH 119435	–	x	x			AMF
Bothriopsis bilineata	FLMNH 61281, 61283	Suriname			x		AMF
Bothriopsis bilineata	FLMNH 78036	Suriname	x	x		x	AMF
Bothriopsis bilineata	FLMNH 83837	Ecuador: Napo Prov.	x	x			AMF
Bothriopsis bilineata	LACM 104360	Peru: Maynas Prov.	x	x			AMF
Bothriopsis bilineata	LACM 73359	Ecuador: Napo Prov.	x	x			AMF
Bothriopsis bilineata	LACM 76790	Peru: Pasco Region	x	x			AMF
Bothriopsis bilineata	MCZ 149525	Suriname	x	x			AMF
Bothriopsis bilineata	MCZ 20891	Brazil: Espírito Santo	x	x			AMF
Bothriopsis bilineata	UCF CLP no number	Colombia: Dept. Amazonas				x	AMF
Bothriopsis bilineata	UTA R-15645, R-15647, R-15650	Suriname, Marowijne Dist.	x	x			AMF
Bothriopsis bilineata	UTA R-16084, R-19490	Suriname	x	x			AMF
Bothriopsis bilineata	UTA R-22581	Ecuador	x	x			AMF
Bothriopsis bilineata	UTA R-2468	Peru: Loreto Region	x	x			AMF
Bothriopsis bilineata	UTA R-34144	Peru	x	x			AMF
Bothriopsis bilineata	UTA R-34145	–	x	x			AMF
Bothriopsis bilineata	UTA R-3588	Colombia, Dept. Vaupés	x	x			AMF
Bothriopsis bilineata	–	–		2 inds.			Campbell and Lamar 2004
Bothriopsis chloromelas	AMNH R-104298	Peru: Huánuco Prov.	x	x			AMF
Bothriopsis chloromelas	CM R-373	Peru: Loreto Region	x	x			AMF
Bothriopsis chloromelas	FMNH 59205	Peru: Junín Region; Chanchamayo Prov.	x	x		x	AMF
Bothriopsis chloromelas	LSUMZ 41037	Peru: Pasco Region	x	x			AMF
Bothriopsis chloromelas	USNM 119020	Peru: Loreto Region	x	x			AMF
Bothriopsis chloromelas	–	–		x			Campbell and Lamar 2004
Bothriopsis medusa	AMNH R-64914	Venezuela: Aragua: Munic. Tovar	x	x			AMF
Bothriopsis medusa	USNM 129585	Venezuela	x	x			AMF
Bothriopsis medusa	–	–		x			Campbell and Lamar 2004
Bothriopsis oligolepis	FMNH 68597	Peru: Tambopata Prov.	x	x			AMF
Bothriopsis oligolepis	–	–		x			Campbell and Lamar 2004
Bothriopsis pulchra	KU 121347, 121348	Ecuador: Tungurahua	x	x			AMF
Bothriopsis pulchra	LSUMZ 39316	Peru: Dept. Amazonas			x		AMF
Bothriopsis pulchra	UMMZ 105894	Ecuador: Pastaza Prov.	x	x			AMF
Bothriopsis pulchra	UMMZ 82900	Ecuador: Zamora-Chinchipe Prov.	x	x			AMF
Bothriopsis pulchra	USNM 165183–165185, 165188	Ecuador	x	x			AMF
Bothriopsis pulchra	–	–		x			Campbell and Lamar 2004
Bothriopsis taeniata	FLMNH 119978	Suriname: Nickerie Dist.	x	x			AMF
Bothriopsis taeniata	FLMNH 83839	Suriname	x	x			AMF
Bothriopsis taeniata	FMNH 74043	Venezuela	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Bothriopsis taeniata	KU 128263	Brazil: Pará	x	x			AMF
Bothriopsis taeniata	UTA R-10501, R-10502, R-30817	Suriname, Sipaliwini Dist.	x	x			AMF
Bothriopsis taeniata	UTA R-15618	Suriname, Marowijne Dist.	x	x		x	AMF
Bothriopsis taeniata	UTA R-29687	Brazil, Rondonia	x	x			AMF
Bothriopsis taeniata	UTA R-32087	–			x		AMF
Bothriopsis taeniata	UTA R-32088	–	x	x			AMF
Bothriopsis taeniata	UTA uncataloged	no data, don. Dallas Zoo			x		AMF
Bothriopsis taeniata	–	–		x			Campbell and Lamar 2004
Bothrocophias campbelli	AMNH R-22094	Ecuador	x	x			AMF
Bothrocophias campbelli	USNM 165322, 165340	Ecuador: Manabí Prov.: Pichincha Canton	x	x			AMF
Bothrocophias campbelli	–	–		x			Campbell and Lamar 2004
Bothrocophias colombianus	AMNH R-130550	Colombia: Dept. Cauca: Munic. Tambo	x	x			AMF
Bothrocophias colombianus	FMNH 55898	Colombia	x	x			AMF
Bothrocophias colombianus	UTA R-25949	Colombia		x			AMF
Bothrocophias colombianus	–	–		x			Campbell and Lamar 2004
Bothrocophias hyoprora	AMNH R-54141	Peru			x		AMF
Bothrocophias hyoprora	KU 222208	Peru: Loreto Region	x	x			AMF
Bothrocophias hyoprora	KU 222209	Peru: Loreto Region	x	x		x	AMF
Bothrocophias hyoprora	MCZ R163236	Ecuador: Sucumbíos Prov.: Cuyabeno Canton	x	x			AMF
Bothrocophias hyoprora	USNM 165297, 165299, 165301, 165302, 165304–165307, 165309, 165310	Ecuador	x	x			AMF
Bothrocophias hyoprora	USNM 165298	Ecuador		x			AMF
Bothrocophias hyoprora	–	–		x			Campbell and Lamar 2004
Bothrocophias microphthalmus	FLMNH 38922	Peru: Loreto Region	x	x			AMF
Bothrocophias microphthalmus	FMNH 5580, 40242	Peru: Canta Prov.: Santa Rosa de Quives Dist.	x	x			AMF
Bothrocophias microphthalmus	FMNH 63740	Peru			x		AMF
Bothrocophias microphthalmus	KU 211621	Peru: San Martín Region: San Martín Prov.	x	x			AMF
Bothrocophias microphthalmus	LACM 76791	–	x	x			AMF
Bothrocophias microphthalmus	LSUMZ 43286	Peru: Pasco Region	x	x			AMF
Bothrocophias microphthalmus	MCZ 45920	Peru: Loreto Region	x	x			AMF
Bothrocophias microphthalmus	USNM 165303	Ecuador	x				AMF
Bothrocophias microphthalmus	YPM R7812	Ecuador: Oriente Region	x	x			AMF
Bothrocophias microphthalmus	–	–		x			Campbell and Lamar 2004
Bothrocophias myersi	AMNH R-107919, R-107920, R-109812	Colombia: Dept. Cauca	x	x			AMF
Bothrocophias myersi	FMNH 165586, 165588, 165590–165592, 165596	–	x	x			AMF
Bothrocophias myersi	FMNH 165587, 165589, 165594, 165595	Colombia: Dept. Valle del Cuaca	x	x			AMF
Bothrocophias myersi	FMNH 165593	Colombia: Dept. Valle del Cuaca	x	x	x		AMF
Bothrocophias myersi	UTA R-21689	Colombia: Dept. Valle del Cuaca	x	x		x	AMF
Bothrocophias myersi	–	–		x			Campbell and Lamar 2004
Bothropoides alcatraz	–	–		x			Campbell and Lamar 2004
Bothropoides alcatraz	IB 62545	Brazil: Sao Paulo: Alcatrazes Isl.	x	x			Marques et al. 2002
Bothropoides diporus	ANSP 7013	Argentina: Buenos Aires Prov.: Dept. La Plata	x	x			AMF
Bothropoides diporus	MCZ 47029	Paraguay: Dept. Central: Dist. Villeta	x	x			AMF
Bothropoides diporus	MVZ 127510	Argentina: Jujuy Prov.: Dept. Ledesma	x	x			AMF
Bothropoides diporus	MVZ 134155	Argentina, Chaco Prov., General Belgrano Dept.	x	x			AMF
Bothropoides diporus	MVZ 134156	Argentina, Cordoba Prov.	x	x			AMF
Bothropoides diporus	TNHC 44863, 44877, 44989	Argentina: Catamarca Prov.	x	x		x	AMF
Bothropoides diporus	TNHC 46875, 46876	Argentina: La Rioja Prov.: Chamical Dept.	x	x		x	AMF
Bothropoides diporus	–	–		x			Campbell and Lamar 2004
Bothropoides diporus	–	–					Silva and Rodrigues 2008
Bothropoides diporus	–	–					Carrasco et al. 2010
Bothropoides diporus	IBSP 5320	Argentina: Santiago del Estero Prov.		x			Silva and Rodrigues 2008
Bothropoides erythromelas	AMNH R-131808	Brazil: Bahia	x	x			AMF
Bothropoides erythromelas	LSUMZ 24446	Brazil: Ceará: Munic. Limoeiro do Norte	x	x			AMF
Bothropoides erythromelas	–	–		x			Campbell and Lamar 2004
Bothropoides erythromelas	IB 3030, 3031	Brazil: Bahia	2 inds.	x			Amaral 1923
Bothropoides insularis	CM R 2862	Brazil, São Paulo, Ilha da Queimada Grande	x	x			AMF
Bothropoides insularis	MCZ 17620, 17622, 17625–17627	Brazil, São Paulo, Ilha da Queimada Grande	x	x			AMF

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Bothropoides insularis	MCZ 17623	Brazil, São Paulo, Ilha da Queimada Grande	x	x		x	AMF
Bothropoides insularis	MVZ 176399	Brazil, São Paulo, Ilha da Queimada Grande	X	x		x	AMF
Bothropoides insularis	UMMZ 58505, 58506	Brazil, São Paulo	x	x			AMF
Bothropoides insularis	–	–		x			Campbell and Lamar 2004
Bothropoides jararaca	AMNH R-27464, R-27465	Brazil			x		AMF
Bothropoides jararaca	ANSP 7030	Brazil	x	x			AMF
Bothropoides jararaca	FLMNH 39813	Peru: Loreto Region: Maynas Prov.	x	x			AMF
Bothropoides jararaca	FLMNH 39814	Brazil: São Paulo: Cubatão City	x	x			AMF
Bothropoides jararaca	FLMNH 39817	Brazil: Minas Gerais: Juiz de Floridaora City	x	x			AMF
Bothropoides jararaca	FLMNH 39821	Brazil: Bahia: Munic. Itapetinga	x	x			AMF
Bothropoides jararaca	FMNH 69951	Brazil: São Paulo			x		AMF
Bothropoides jararaca	KU 124651	Brazil: Santa Catarina	x	x			AMF
Bothropoides jararaca	KU 124655	Brazil: Paraná	x	x			AMF
Bothropoides jararaca	KU 125036	Brazil: São Paulo	x	x			AMF
Bothropoides jararaca	LACM 14601	Argentina: Misiones Prov.	x	x			AMF
Bothropoides jararaca	USNM 71139	Brazil	x	x			AMF
Bothropoides jararaca	–	–		x			Campbell and Lamar 2004
Bothropoides lutzi	–	–		x			Campbell and Lamar 2004
Bothropoides lutzi	IBSP 1672	Brazil: Paraná: Fazenda Rio Grande		x			Silva and Rodrigues 2008
Bothropoides lutzi	IBSP 561	–		x			Silva and Rodrigues 2008
Bothropoides marmoratus	UTA R-28232	Brazil, Goiás, Munic. Pires do Rio	x	x			AMF
Bothropoides marmoratus	–	–		x			Campbell and Lamar 2004
Bothropoides marmoratus	IBSP 55055	Brazil: Goiás: Munic. Ipameri	x	x			Silva and Rodrigues 2008
Bothropoides mattogrossensis	FMNH 140199, 140200	Bolivia: Mamoré Prov.: Dept. Beni	x	x			AMF
Bothropoides mattogrossensis	FMNH 161558–161560	Bolivia	x	x			AMF
Bothropoides mattogrossensis	FMNH 35743	Bolivia			x		AMF
Bothropoides mattogrossensis	KU 183007	Argentina: Salta Prov.	x	x		x	AMF
Bothropoides mattogrossensis	KU 73475	Paraguay: Dept. Boquerón	x	x		x	AMF
Bothropoides mattogrossensis	MCZ 11857, 20620, 29229, 29231	Bolivia, Dept. Santa Cruz	x	x			AMF
Bothropoides mattogrossensis	MCZ 182691	Paraguay	x	x			AMF
Bothropoides mattogrossensis	MCZ 34211, 34212	Paraguay	x	x			AMF
Bothropoides mattogrossensis	–	–		x			Campbell and Lamar 2004
Bothropoides mattogrossensis	MZUSP 6478	Bolivia: Dept. Santa Cruz		x			Silva and Rodrigues 2008
Bothropoides mattogrossensis	IBSP 3011	Brazil: Matto Grosso do Sul: Munic. Miranda		x			Silva and Rodrigues 2008
Bothropoides neuwiedi	AMNH R-29256	Brazil: São Paulo			x		AMF
Bothropoides neuwiedi	FLMNH 45712	Argentina			x		AMF
Bothropoides neuwiedi	FMNH 171255	Brazil	x	x			AMF
Bothropoides neuwiedi	KU 124658	Brazil: São Paulo	x	x			AMF
Bothropoides neuwiedi	MCZ 20923	Brazil: São Paulo	x	x			AMF
Bothropoides neuwiedi	MCZ 20938, R-54645	Brazil: Paraná	x	x			AMF
Bothropoides neuwiedi	MVZ 134157	Brazil: São Paulo	x	x			AMF
Bothropoides neuwiedi	UTA R-35938	Brazil: Paraná: Munic. Telêmaco Borba	x	x			AMF
Bothropoides neuwiedi	UTA R-35939	Brazil: Paraná: Munic. Piraquara	x	x			AMF
Bothropoides neuwiedi	UTA R-38283	Brazil: São Paulo	x	x			AMF
Bothropoides neuwiedi	UTA R-38284	Brazil: Paraná: Jaguariaíva	x	x			AMF
Bothropoides neuwiedi	MZUSP 4917	–					Silva and Rodrigues 2008
Bothropoides neuwiedi	–	–		x			Campbell and Lamar 2004
Bothropoides neuwiedi	ZSM 2348/0	Brazil: Bahia		x			Silva and Rodrigues 2008
Bothropoides neuwiedi	IBSP 3016	Brazil: Goiás		x			Silva and Rodrigues 2008
Bothropoides neuwiedi	IBSP 3015	Brazil: Matto Grosso		x			Silva and Rodrigues 2008
Bothropoides neuwiedi	IBSM 3014	Brazil: Paraná		x			Silva and Rodrigues 2008
Bothropoides neuwiedi	IBSP 7806	Brazil: Rio de Janeiro		x			Silva and Rodrigues 2008
Bothropoides neuwiedi	IBSP 3012	Brazil: Bahia		x			Silva and Rodrigues 2008
Bothropoides pauloensis	FMNH 171277	Brazil	x	x			AMF
Bothropoides pauloensis	MCZ 17729, 17731	Brazil	x	x			AMF
Bothropoides pauloensis	MCZ 20919	Brazil: São Paulo	x	x			AMF
Bothropoides pauloensis	UTA R-31000	Brazil: Goiás, Goiânia	x	x			AMF
Bothropoides pauloensis	–	–		x			Campbell and Lamar 2004
Bothropoides pauloensis	–	–		x			Silva and Rodrigues 2008
Bothropoides pauloensis	IBSP 3013	Brazil: São Paulo		x			Silva and Rodrigues 2008
Bothropoides pubescens	CAS 90737	Brazil: Rio Grande do Sul: Munic. Porto Alegre	x	x			AMF
Bothropoides pubescens	FMNH 10245, 10503	Uruguay	x	x			AMF
Bothropoides pubescens	UTA R-41141	Brazil: Rio Grande do Sul	x	x			AMF
Bothropoides pubescens	YPM R13345	Uruguay: Dept. Cerro Largo	x	x		x	AMF
Bothropoides pubescens	–	–		x			Campbell and Lamar 2004
Bothropoides pubescens	MZUSP 1476	Brazil: Rio Grande do Sul		x			Silva and Rodrigues 2008
Bothrops andianus	FLMNH 83845	–	x	x			AMF
Bothrops andianus	FMNH 62943	Peru: Cuzco Prov.	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Bothrops andianus	KU 135212	Peru: Cuzco Prov.	x	x			AMF
Bothrops andianus	MCZ 12415	Peru: Cuzco Prov.	x	x			AMF
Bothrops andianus	USNM 267836, 267837	Peru: Puno Prov.	x	x		x	AMF
Bothrops andianus	USNM 538554	Peru	x	x			AMF
Bothrops andianus	UTA R-26719	Peru: Puno Prov.	x	x			AMF
Bothrops andianus	UTA R-39104	Bolivia: Dept. Santa Cruz	x	x			AMF
Bothrops andianus	UTA R-39107	Bolivia: Dept. La Paz	x	x			AMF
Bothrops andianus	–	–		x			Campbell and Lamar 2004
Bothrops asper	FLMNH 11521	Colombia: Choco Mus. Comp. Zool.			x		AMF
Bothrops asper	FLMNH 37176	Costa Rica: Limón Prov.			x		AMF
Bothrops asper	FLMNH 99289	Honduras			x		AMF
Bothrops asper	FMNH 197882	Ecuador: Pichincha Prov.			x		AMF
Bothrops asper	FMNH 20641	Honduras: Dept. Atlantida			x		AMF
Bothrops asper	FMNH 31167	Panama			x		AMF
Bothrops asper	FMNH 3480	Belize			x		AMF
Bothrops asper	FMNH 51689	Panama: Chiriquí Prov.			x		AMF
Bothrops asper	KU 112957, 112958	Nicaragua: Dept. Zelaya	x	x			AMF
Bothrops asper	KU 23915, 23995	Mexico: Veracruz	x	x			AMF
Bothrops asper	USNM 220377	Costa Rica			x		AMF
Bothrops asper	UTA R-12920, R-12996	Costa Rica: Limón Prov.	x	x			AMF
Bothrops asper	UTA R-12932, R-12936, R-14507–R-14510	Costa Rica: Cartago Prov.	x	x			AMF
Bothrops asper	UTA R-16961	–			x		AMF
Bothrops asper	UTA R-17095	Mexico: Quintana Roo				x	AMF
Bothrops asper	UTA R-17862, R-22345	Trinidad	x	x			AMF
Bothrops asper	UTA R-32494	Costa Rica: Puntarenas Prov.	x	x			AMF
Bothrops asper	UTA R-34157	Costa Rica	x	x			AMF
Bothrops asper	UTA R-40320, R-40321	Guatemala: Dept. Izabal	x	x			AMF
Bothrops asper	UTA R-41026	Panama: Chiriquí Prov.	x	x			AMF
Bothrops asper	UTA R-52545	Honduras, Dept. Gracias a Dios	x	x		x	AMF
Bothrops asper	UTA R-6770	Colombia	x	x			AMF
Bothrops asper	–	–		x			Campbell and Lamar 2004
Bothrops asper	–	–	6 inds.		4 inds.		Gutberlet 1998
Bothrops atrox	CM 91926	–			x		AMF
Bothrops atrox	FMNH 51658	Brazil			x		AMF
Bothrops atrox	LSUMZ 39317	Peru: Amazonas			x		AMF
Bothrops atrox	MCZ 1189	Brazil: Bahia	x	x			AMF
Bothrops atrox	MCZ 1211	Brazil: Pará	x	x			AMF
Bothrops atrox	MCZ 45911, 54638	Peru: Dept. Junín	x	x			AMF
Bothrops atrox	SDNHM 59509, 59589	–			x		AMF
Bothrops atrox	SDNHM 59573	Panama			x		AMF
Bothrops atrox	UTA R-30826	Venezuela: Amazonas	x	x			AMF
Bothrops atrox	UTA R-3377, R-3378, R-3590, R-3771, R-5848	Colombia: Dept. Meta	x	x		x	AMF
Bothrops atrox	UTA R-3610, R-3772, R-3852, R-5219, R-5850, R-5853, R-5862, R-7196	Colombia: Dept. Meta	x	x			AMF
Bothrops atrox	UTA R-52552–R-52554	Guyana: Rupununi Region	x	x			AMF
Bothrops atrox	UTA R-9328	Colombia	x	x		x	AMF
Bothrops atrox	UTA R-9345	Colombia: Dept. Vichada	x	x			AMF
Bothrops atrox	–	–		x			Campbell and Lamar 2004
Bothrops barnetti	CAS 14570	Peru: Tumbes Prov.	x	x			AMF
Bothrops barnetti	CAS 92343	Peru		x			AMF
Bothrops barnetti	FMNH 9777, 9778, 9787–9789, 11013	Peru	x	x			AMF
Bothrops barnetti	FMNH 41603	Peru: Piura Region	x	x			AMF
Bothrops barnetti	LSUMZ 39318	Peru	x	x		x	AMF
Bothrops barnetti	–	–		x			Campbell and Lamar 2004
Bothrops brazili	FMNH 165563	Colombia			x		AMF
Bothrops brazili	KU 222206	Peru: Dept. Loreto	x	x			AMF
Bothrops brazili	LSUMZ 26851	Peru: Dept. Loreto			x		AMF
Bothrops brazili	MVZ 163340	Peru: Dept. Amazonas	x	x		x	AMF
Bothrops brazili	MVZ 163341, 163344, 163346	Peru: Dept. Amazonas			x		AMF
Bothrops brazili	MVZ 163342, 163343, 163345	Peru: Dept. Amazonas	x	x			AMF
Bothrops brazili	UTA R-29977	Surinam: Sipaliwini Dist.	x	x			AMF
Bothrops brazili	UTA R-3764	Colombia: Dept. Vaupés	x	x		x	AMF
Bothrops brazili	UTA R-3765	Colombia: Dept. Vaupés				x	AMF
Bothrops brazili	–	–		x			Campbell and Lamar 2004
Bothrops caribbaeus	AMNH R-90164	St. Lucia			x		AMF
Bothrops caribbaeus	FLMNH 66043	St. Lucia: Windward Isls.			x		AMF
Bothrops caribbaeus	KU 268957	St. Lucia: Anse-la-Raye Quarter	x	x			AMF
Bothrops caribbaeus	MCZ 70194, 70196, 70200	St Lucia	x	x			AMF
Bothrops caribbaeus	UTA R-16311	–	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Bothrops caribbaeus	UTA R-3850, R-7304, R-8351–R-8353	St Lucia	x	x			AMF
Bothrops caribbaeus	–	–		x			Campbell and Lamar 2004
Bothrops jararacussu	AMNH R-14530	Brazil			x		AMF
Bothrops jararacussu	FMNH 171283, 171300	Brazil: São Paulo	x	x			AMF
Bothrops jararacussu	FMNH 51659, 51660	Brazil			x		AMF
Bothrops jararacussu	KU 124656	Brazil: Espirito Santo	x	x			AMF
Bothrops jararacussu	KU 290723	Paraguay: Dept. Cazaapá	x	x			AMF
Bothrops jararacussu	KU 68959	Brasil: Santa Catarina	x	x			AMF
Bothrops jararacussu	LACM 146081	Argentina: Misiones Prov.: Dept. El Dorado	x	x			AMF
Bothrops jararacussu	UTA R-32425	Brazil	x	x		x	AMF
Bothrops jararacussu	UTA R-37700	Brazil: São Paulo	x	x			AMF
Bothrops jararacussu	UTA R-38295, R-38296	Brazil: Santa Catarina	x	x		x	AMF
Bothrops jararacussu	–	–		x			Campbell and Lamar 2004
Bothrops lanceolatus	ANSP 7016–7018, 7022	West Indies	x	x			AMF
Bothrops lanceolatus	CM S-6390	Martinique	x	x			AMF
Bothrops lanceolatus	KU 268958	Martinique	x	x			AMF
Bothrops lanceolatus	USNM 10116, 10122	Tobago	x	x			AMF
Bothrops lanceolatus	USNM 11317, 11318	Martinique	x	x			AMF
Bothrops lanceolatus	–	–		x			Campbell and Lamar 2004
Bothrops lanceolatus	–	–			2 inds.		Brattstrom 1964
Bothrops leucurus	CAS 116342	Brazil: Espírito Santo	x	x			AMF
Bothrops leucurus	CM 50981	Brazil: Espírito Santo	x	x			AMF
Bothrops leucurus	KU 124659	Brazil: Espírito Santo	x	x			AMF
Bothrops leucurus	USNM 165505, 165506	Brazil	x	x			AMF
Bothrops leucurus	UTA R-19512, R-38299	Brazil: Espírito Santo	x	x			AMF
Bothrops leucurus	UTA R-38290	Brazil, Bahia	x	x			AMF
Bothrops leucurus	UTA R-38300, R-38301	Brazil: Espírito Santo	x	x		x	AMF
Bothrops leucurus	–	–		x			Campbell and Lamar 2004
Bothrops lojanus	KU 135213	Ecuador: Loja Prov.	x	x			AMF
Bothrops lojanus	MCZ 93587	Ecuador: Loja Prov.	x	x			AMF
Bothrops lojanus	USNM 98927, 98935, 232519	Ecuador	x	x			AMF
Bothrops lojanus	UTA R-23529	Ecuador: Zamora-Chinchipe Prov.	x	x			AMF
Bothrops lojanus	–	–		x			Campbell and Lamar 2004
Bothrops marajoensis	–	–		x			Campbell and Lamar 2004
Bothrops moojeni	AMNH R-62581	Brazil: Goiás			x		AMF
Bothrops moojeni	FMNH 171278	Brazil: São Paulo	x	x	x		AMF
Bothrops moojeni	FMNH 2617a–d	Brazil: São Paulo	x	x			AMF
Bothrops moojeni	KU 124657	Brazil: Paraná	x	x			AMF
Bothrops moojeni	UTA R-28231	Brazil: Goiás	x	x			AMF
Bothrops moojeni	UTA R-35940	Brazil: Paraná	x	x		x	AMF
Bothrops moojeni	UTA R-38297	Brazil: São Paulo: Pirassunuga	x	x			AMF
Bothrops moojeni	UTA R-38298	Brazil: São Paulo	x	x			AMF
Bothrops moojeni	–	–		x			Campbell and Lamar 2004
Bothrops osbornei	KU 218462	Ecuador: Chimborazo Prov.: Pallatanga Canton	x	x			AMF
Bothrops osbornei	USNM 310822	Ecuador	x	x			AMF
Bothrops osbornei	–	–		x			Campbell and Lamar 2004
Bothrops pictus	ANSP 11521, 11522, 11524	Peru	x	x			AMF
Bothrops pictus	FLMNH 39826	Peru: Cajamarca Prov.	x	x		x	AMF
Bothrops pictus	FMNH 229982	Peru: Dept. Lima	x	x			AMF
Bothrops pictus	FMNH 39990	Peru: Madre de Dios Region	x	x			AMF
Bothrops pictus	FMNH 5662, 5663, 39991	Peru	x	x			AMF
Bothrops pictus	USNM 49992	Peru	x	x			AMF
Bothrops pictus	–	–		x			Campbell and Lamar 2004
Bothrops pirajai	–	–		x			Campbell and Lamar 2004
Bothrops pirajai	IB 3008	Brazil: Bahia	x	x			Amaral 1923
Bothrops punctatus	CAS 119594, 119921	Colombia: Dept. Chocó	x	x			AMF
Bothrops punctatus	FMNH 165384	Colombia: Dept. Valle del Cuaca	X	x		x	AMF
Bothrops punctatus	FMNH 165385	Colombia: Dept. Valle del Cuaca	X	x			AMF
Bothrops punctatus	FMNH 55888	Colombia: Dept. Caldas	x	x	x		AMF
Bothrops punctatus	FMNH 55894	Colombia: Dept. Caldas	x	x			AMF
Bothrops punctatus	USNM 20629	Ecuador	x	x			AMF
Bothrops punctatus	USNM 72355	Colombia	x	x			AMF
Bothrops punctatus	–	–		x			Campbell and Lamar 2004
Bothrops roedingeri	–	–		x			Campbell and Lamar 2004
Bothrops sanctaecrucis	MCZ 17699, 20619	Bolivia: Dept. Santa Cruz: Santa Cruz de la Sierra	x	x			AMF
Bothrops sanctaecrucis	MCZ 20618	Bolivia: Dept. Santa Cruz	x	x			AMF
Bothrops sanctaecrucis	UMMZ 68027a–c, 68028, 68031	Bolivia: Dept. Santa Cruz	x	x			AMF
Bothrops sanctaecrucis	USNM 48931	Brazil	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Bothrops sanctaecrucis	–	–		x			Campbell and Lamar 2004
Bothrops venezuelensis	KU 133536	Venezuela: Dept. Chuquisaca: Sucre	x	x		x	AMF
Bothrops venezuelensis	KU 182734	Venezuela: Aragua State	x	x		x	AMF
Bothrops venezuelensis	TCWC 58959–58963	Venezuela: Miranda State	x	x			AMF
Bothrops venezuelensis	USNM 129583, 259175	Venezuela: Aragua State	x	x			AMF
Bothrops venezuelensis	–	–		x			Campbell and Lamar 2004
Calloselasma rhodostoma	CM 145553	Thailand: South Thailand Region			x		AMF
Calloselasma rhodostoma	CM 20456	Indonesia	x	x			AMF
Calloselasma rhodostoma	CM 53552	Thailand	x	x			AMF
Calloselasma rhodostoma	FLMNH 83783	Malaysia: Perak State: Kerian Dist.: Parit Buntar	x	x			AMF
Calloselasma rhodostoma	FLMNH 83784	Thailand: Bangkok	x	x		x	AMF
Calloselasma rhodostoma	FLMNH 83785, 83786	Thailand	x	x			AMF
Calloselasma rhodostoma	FLMNH 83787	Thailand	x	x	x		AMF
Calloselasma rhodostoma	FMNH 11522a	Vietnam: Cochinchina Region					AMF
Calloselasma rhodostoma	FMNH 259196	Cambodia	x	x			AMF
Calloselasma rhodostoma	MCZ 84911	Indonesia: West Java Prov.: Java	x	x	x		AMF
Calloselasma rhodostoma	MVZ 222323	Vietnam: Dac Lat Prov.: Buon Ma Thuot	x	x			AMF
Calloselasma rhodostoma	USNM 22970	Thailand: Trang Prov.			x		AMF
Calloselasma rhodostoma	UTA R-12970	–		x		x	AMF
Calloselasma rhodostoma	CA 5602	–		x			Vogel 2006
Causus defilippi	AMNH R-44312	Malawi	x	x			AMF
Causus defilippi	FLMNH 59799, 59800, 59802	Tanzania: Morogoro Region	x	x		x	AMF
Causus defilippi	FLMNH 59801, 59803	Tanzania: Morogoro Region	x	x		x	AMF
Causus defilippi	FLMNH 66950	Tanzania	x	x			AMF
Causus resimus	AMNH R-48466	Tanzania	x	x		x	AMF
Causus resimus	CAS 141432, 150928	Kenya: Kisumu Dist.: Chemelil	x	x			AMF
Causus resimus	CAS 141447	Kenya: Kakamega Dist.: Mumias	x	x		x	AMF
Causus resimus	CAS 148044, 152792	Kenya: Kisumu Dist.: Chemelil	x	x		x	AMF
Causus resimus	CAS 153440, 153446	Somalia: Lower Juba Region				x	AMF
Causus resimus	CAS 153441	Somalia: Lower Juba Region	x	x			AMF
Causus resimus	CAS 153442	Somalia: Lower Juba Region	x	x		x	AMF
Causus resimus	FMNH 153073	Sudan: Upper Nile Prov.: Paloidh	x	x			AMF
Causus resimus	FMNH 153081	Sudan: Upper Nile Prov.	x	x			AMF
Causus resimus	FMNH 62183	Sudan: Eastern Equatorial State: Torit			x		AMF
Causus rhombeatus	AMNH R-2392	South Africa: Natal Region	x	x			AMF
Causus rhombeatus	AMNH R-93674	South Africa: Eastern Cape Prov.: East London	x	x		x	AMF
Causus rhombeatus	FLMNH 119902	Liberia	x	x			AMF
Causus rhombeatus	FLMNH 119903	Liberia: Gbarnga Dist.: Suakoko	x	x			AMF
Causus rhombeatus	FLMNH 57049	Liberia			x		AMF
Causus rhombeatus	FLMNH 99044	Kenya			x		AMF
Causus rhombeatus	FMNH 164744	–			x		AMF
Causus rhombeatus	FMNH 2268	Nairobi			x		AMF
Causus rhombeatus	USNM 297462	–	x	x	x	x	AMF
Cerastes cerastes	AMNH R-38194, R-66253, R-66254	Egypt	x	x			AMF
Cerastes cerastes	FLMNH 119907	Algeria	x	x		x	AMF
Cerastes cerastes	FLMNH 13986	Israel	x	x		x	AMF
Cerastes cerastes	FLMNH 61163	Algeria	x	x			AMF
Cerastes cerastes	FLMNH 61284	Algeria			x		AMF
Cerastes cerastes	FMNH 142986, 142990, 142991, 142993, 143994, 143995, 153114	Egypt			x		AMF
Cerastes cerastes	FMNH 164721, 164723	Egypt: Red Sea Gov.: Wadi Abu Shih	x	x			AMF
Cerastes cerastes	UCF CLP917	–	x	x			AMF
Cerastes cerastes	UCM 37401, 37412	Tunisia: Gafsa Gov.	x	x			AMF
Cerastes gasperettii	CAS 84440, 145303, 145340, 145341	Saudi Arabia	x	x			AMF
Cerastes gasperettii	CAS 84481, 84490	Saudi Arabia: Eastern Prov.: Abqaiq	x	x			AMF
Cerastes gasperettii	CAS 84503, 84560	Saudi Arabia: Eastern Prov.: Dhahran	x	x			AMF
Cerastes gasperettii	CAS 97826	United Arab Emirates: Abu Dhabi: Beda Azan	x	x			AMF
Cerastes gasperettii	CAS 97827, 97829	United Arab Emirates: Abu Dhabi	x	x			AMF
Cerastes gasperettii	UCF CLP910, CLP911	–	x	x			AMF
Cerrophidion godmani	UTA R-14535	Guatemala: Depto. Baja Verapaz			x		AMF
Cerrophidion godmani	UTA R-42266	Guatemala: Depto. Quiche				x	AMF
Cerrophidion godmani	UTA R-6642	Mexico: Oaxaca				x	AMF
Cerrophidion godmani	–	Guatemala: Dept. Quiche	8 inds.	9 inds.			Jadin 2010
Cerrophidion godmani	–	Guatemala: Dept. San Marcos	10 inds.	10 inds.			Jadin 2010
Cerrophidion godmani	–	Mexico: Oaxaca	6 inds.	7 inds.			Jadin 2010

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Cerrophidion petlalcalensis	UNAM LTH 3451–3455	Mexico: Veracruz: Munic. San Andres Tenejapan	5 inds.	2 inds.			Lopez-Luna et al. 1999
Cerrophidion petlalcalensis	–	–		x			Campbell and Lamar 2004
Cerrophidion sasai	UTA R-51403	Costa Rica; San José Prov.				x	AMF
Cerrophidion sasai	–	Costa Rica: San José Prov.	5 inds.	5 inds.			Jadin 2010
Cerrophidion tzotzilorum	UTA R-21971, R-21979	Mexico: Chiapas	x	x			AMF
Cerrophidion tzotzilorum	UTA R-4529, R-9641	Mexico: Chiapas	x	x		x	AMF
Cerrophidion tzotzilorum	UTA R-9640	Mexico: Chiapas			x		AMF
Cerrophidion tzotzilorum	–	–	18 inds.	x			Campbell 1985
Cerrophidion tzotzilorum	–	–		x			Campbell and Lamar 2004
Cerrophidion wilsoni	YPM R14017, R14021	El Salvador: Depto. Santa Ana: Municip. Santa Ana	x	x			AMF
Cerrophidion wilsoni	–	El Salvador: Dept. Chalatenango	5 inds.	5 inds.			Jadin 2010
Cerrophidion wilsoni	–	Honduras: Sierra de Omoa	7 inds.	7 inds.			Jadin 2010
Crotalus adamanteus	AMNH R-69123, R-69725	USA: Florida			x		AMF/KMD
Crotalus adamanteus	AMNH R-85755, R-86956	USA: South Carolina: Jasper Co.			x		AMF/KMD
Crotalus adamanteus	FMNH 31050, 31051	USA: Georgia			x		AMF/KMD
Crotalus adamanteus	UCF 2312, 2325, 2331, 2333, 2334	USA: Florida: Orange Co.	x	x			AMF/KMD
Crotalus adamanteus	UCF 2313	Florida: Osceola Co.	x	x			AMF/KMD
Crotalus adamanteus	UCF 2324	USA: Florida: Brevard Co.	x	x		x	AMF/KMD
Crotalus adamanteus	UCF CLP936	USA: Georgia	x	x			AMF/KMD
Crotalus adamanteus	UCF CLP937	USA	x	x		x	AMF/KMD
Crotalus adamanteus	–	–		x			Campbell and Lamar 2004
Crotalus aquilus	FLMNH 87873	Mexico: Queretaro	x	x			AMF/KMD
Crotalus aquilus	LSUMZ 321, 322	Mexico: San Luis Potosi: Xilitla Region	x	x			AMF/KMD
Crotalus aquilus	LSUMZ 325, 4192	Mexico: San Luis Potosi	x	x			AMF/KMD
Crotalus aquilus	LSUMZ 4193	Mexico: San Luis Potosi	x	x		x	AMF/KMD
Crotalus aquilus	SDNHM 46795	Mexico: Hidalgo: Munic. Jacala	x	x			AMF/KMD
Crotalus aquilus	SDNHM 6575	Mexico: San Luis Potosi	x	x			AMF/KMD
Crotalus aquilus	UMMZ 75867	Mexico: Guanajuato	x	x			AMF/KMD
Crotalus aquilus	UTA R-12595	Mexico: Hidalgo				x	AMF/KMD
Crotalus aquilus	UTA R-18341	Mexico: Queretaro				x	AMF/KMD
Crotalus aquilus	UTA R-22596	Mexico: Guanajuato	x	x		x	AMF/KMD
Crotalus aquilus	UTA R-4540, R-6115	Mexico: Hidalgo			x	x	AMF/KMD
Crotalus aquilus	UTA R-6179	Mexico: Michoacán			x		AMF/KMD
Crotalus aquilus	–	–		x			Campbell and Lamar 2004
Crotalus aquilus	UTA R-17904	Mexico: Hidalgo		x			Campbell and Lamar 2004
Crotalus armstrongi	UTA R-12591	Mexico: Jalisco		x			Campbell and Lamar 2004
Crotalus atrox	AMNH R-124109	USA: Texas: Palo Pinto Co.			x		AMF/KMD
Crotalus atrox	AMNH R-57433	USA: Texas: Brewster Co.			x		AMF/KMD
Crotalus atrox	AMNH R-71199	USA: Arizona: Pima Co.			x		AMF/KMD
Crotalus atrox	AMNH R-81495	USA: New Mexico			x		AMF/KMD
Crotalus atrox	AMNH R-82420	USA: Louisiana: St. John the Baptist Parish			x		AMF/KMD
Crotalus atrox	AMNH R-90666	USA: New Mexico: Grant Co.			x		AMF/KMD
Crotalus atrox	CAS 156174	USA: Arizona: Yavapai Co.			x		AMF/KMD
Crotalus atrox	CAS 50515	Mexico: Baja California Sur: Isla Tortuga	x	x			AMF/KMD
Crotalus atrox	FLMNH 120169	Mexico	x	x			AMF/KMD
Crotalus atrox	FLMNH 24810	Mexico: Coahuila	x	x		x	AMF/KMD
Crotalus atrox	FLMNH 42593	Mexico: Sinaloa	x	x			AMF/KMD
Crotalus atrox	FLMNH 42594	Mexico: Sinaloa	x	x		x	AMF/KMD
Crotalus atrox	FLMNH 42597	Mexico	x	x		x	AMF/KMD
Crotalus atrox	FLMNH 60768	Mexico: Veracruz-Llave	x	x			AMF/KMD
Crotalus atrox	SDNHM 3006, 6595, 6597, 26798, 27077, 28377, 42013	Mexico: Baja California Sur: Isla Tortuga	x	x			AMF/KMD
Crotalus atrox	SDNHM 27410, 28551	Mexico: Baja California Sur: Isla Tortuga	x	x		x	AMF/KMD
Crotalus atrox	UCF 2338–2340	USA: Texas: Brewster Co.	x	x			AMF/KMD
Crotalus atrox	UTA R-16283	USA: Texas: Wise Co.				x	AMF/KMD
Crotalus atrox	UTA R-5092	USA: Texas: Coleman Co.				x	AMF/KMD
Crotalus atrox	–	–		x			Campbell and Lamar 2004
Crotalus atrox	–	–			2 inds.		LaDuc
Crotalus atrox	–	–			2 inds.		Brattstrom 1964
Crotalus atrox	–	–		x			Campbell and Lamar 2004
Crotalus basiliscus	AMNH R-75094	–			x		AMF/KMD
Crotalus basiliscus	CAS C.basiliscus uncat.	–			x		AMF/KMD
Crotalus basiliscus	FLMNH 120172, 120173	–	x	x			AMF/KMD
Crotalus basiliscus	FLMNH 120174, 19050, 19169	Mexico	x	x			AMF/KMD
Crotalus basiliscus	FLMNH 16783	Mexico: Nayarit	x	x			AMF/KMD
Crotalus basiliscus	FMNH 31299	Mexico: Michoacán			x		AMF/KMD
Crotalus basiliscus	LACM 37329, 104457	Mexico: Sinaloa	x	x		x	AMF/KMD
Crotalus basiliscus	LACM 7222, 38213	Mexico: Sinaloa	x	x			AMF/KMD

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Crotalus basiliscus	UTA R-6120	Mexico: Michoacán				x	AMF/KMD
Crotalus basiliscus	–	–		x			Campbell and Lamar 2004
Crotalus basiliscus	–	Mexico: Colima		x			Campbell and Lamar 2004
Crotalus catalinensis	CAS SU-15631	Mexico: Baja California Sur: Isla Santa Catalina	x	x			AMF/KMD
Crotalus catalinensis	FMNH 1169	Mexico: Baja California Sur: Isla Santa Catalina	x	x			AMF/KMD
Crotalus catalinensis	SDNHM 44352	Mexico: Baja California Sur: Isla Santa Catalina	x	x		x	AMF/KMD
Crotalus catalinensis	SDNHM 44353, 48020, 53050	Mexico: Baja California Sur: Isla Santa Catalina	x	x			AMF/KMD
Crotalus catalinensis	UCM 25953, 31446	Mexico: Baja California Sur: Isla Santa Catalina	x	x			AMF/KMD
Crotalus catalinensis	–	–		x			Campbell and Lamar 2004
Crotalus catalinensis	SDNHM no number	–			2 inds.		LaDuc
Crotalus cerastes	AMNH R-72633	USA: Arizona: Maricopa Co.		x	x		AMF/KMD
Crotalus cerastes	AMNH R-73719, R-75704	USA: California: Riverside Co.			x		AMF/KMD
Crotalus cerastes	CAS 156177, 201522	USA: California: San Bernardino Co.			x		AMF/KMD
Crotalus cerastes	CAS SU-7287	USA: Arizona: Maricopa Co.	x	x			AMF/KMD
Crotalus cerastes	FLMNH 141569	USA: Arizona	x	x			AMF/KMD
Crotalus cerastes	FLMNH 24672	USA: California: Riverside Co.	x	x			AMF/KMD
Crotalus cerastes	FLMNH 57647	USA: Arizona	x	x		x	AMF/KMD
Crotalus cerastes	FLMNH 75230	USA: California	x	x			AMF/KMD
Crotalus cerastes	FLMNH 81904	USA: Nevada: Clark Co.	x	x			AMF/KMD
Crotalus cerastes	FLMNH 81907	USA: Nevada: Clark Co.	x	x		x	AMF/KMD
Crotalus cerastes	FMNH 26122	USA: California: Imperial Co.			x		AMF/KMD
Crotalus cerastes	FMNH 75802	USA: Arizona: Pima Co	x	x			AMF/KMD
Crotalus cerastes	KU 77991	Mexico: Sonora	x	x		x	AMF/KMD
Crotalus cerastes	KU 77994	Mexico: Sonora	x	x			AMF/KMD
Crotalus cerastes	UTA R-8015	–				x	AMF/KMD
Crotalus cerastes	–	–		x			Campbell and Lamar 2004
Crotalus cerberus	SDNHM 4923	USA: Arizona: Yavapai Co.	x	x		x	AMF/KMD
Crotalus culminatus	FMNH 126616	Mexico: Michoacán	x	x			AMF/KMD
Crotalus culminatus	FMNH 38496	Mexico: Guerrero	x	x			AMF/KMD
Crotalus culminatus	FMNH 38502	Mexico: Guerrero	x	x		x	AMF/KMD
Crotalus culminatus	–	–					Klauber 1972
Crotalus durissus	AMNH R-137172, R-140806	–			x		AMF/KMD
Crotalus durissus	AMNH R-147320	Brazil: Matto Grosso				x	AMF/KMD
Crotalus durissus	AMNH R-62579	Brazil: Goiás: Anápolis Region			x		AMF/KMD
Crotalus durissus	AMNH R-62580	Colombia: Dept. Meta: Munic. Villavicencio			x		AMF/KMD
Crotalus durissus	AMNH R-73161	Lesser Antilles: Kingdom of Netherlands: Aruba			x		AMF/KMD
Crotalus durissus	FLMNH 132639	Venezuela	x	x			AMF/KMD
Crotalus durissus	FLMNH 132640	Venezuela	x	x		x	AMF/KMD
Crotalus durissus	FLMNH 16157, 16160	Guyana	x	x			AMF/KMD
Crotalus durissus	FLMNH 16159, 16161	Guyana	x	x		x	AMF/KMD
Crotalus durissus	FLMNH 29388	Colombia	x	x		x	AMF/KMD
Crotalus durissus	FLMNH 29389	Venezuela	x	x			AMF/KMD
Crotalus durissus	FLMNH 57243	Colombia: Dept. Magdalena				x	AMF/KMD
Crotalus durissus	FLMNH 61623	Brazil	x	x		x	AMF/KMD
Crotalus durissus	FLMNH 65975	Venezuela	x	x			AMF/KMD
Crotalus durissus	FLMNH 83821	Colombia	x	x			AMF/KMD
Crotalus durissus	FMNH 51664	Brazil			x		AMF/KMD
Crotalus durissus	UTA R-7322, R-9633	Lesser Antilles: Kingdom of Netherlands: Aruba				x	AMF/KMD
Crotalus durissus	–	–		10 inds.			Campbell and Lamar 2004
Crotalus enyo	CAS SU-14021	Mexico: Baja California Sur: Isla Cerralvo (Jacques Cousteau Isl)	x	x			AMF/KMD
Crotalus enyo	FLMNH 120176	Mexico: Baja California Sur	x	x		x	AMF/KMD
Crotalus enyo	FLMNH 120177	Mexico: Baja California Sur	x	x			AMF/KMD
Crotalus enyo	LACM 107223	Mexico: Baja California	x	x			AMF/KMD
Crotalus enyo	LACM 126268	Mexico: Baja California Sur	x	x		x	AMF/KMD
Crotalus enyo	LACM 132134	Mexico: Baja California Norte	x	x		x	AMF/KMD
Crotalus enyo	LACM 74024	Mexico: Baja California Norte	x	x			AMF/KMD
Crotalus enyo	UCM 51220	Mexico: Baja California Sur	x	x			AMF/KMD
Crotalus enyo	UMMZ 174666–174669	–	x	x	x		AMF/KMD
Crotalus enyo	–	–		x			Campbell and Lamar 2004
Crotalus enyo	CJB 1064	–					LaDuc
Crotalus enyo	–	–			2 inds.		LaDuc
Crotalus enyo	–	–			2–6 inds.		Brattstrom 1964
Crotalus ericsmithi	UTA R-55372	Mexico: Guerrero: Sierra Madre del Sur	x	x		x	AMF/KMD
Crotalus horridus	AMNH R-81547, R-123907	USA: New York: Rockland Co.			x		AMF/KMD
Crotalus horridus	AMNH R-75173	USA: Virginia: Giles Co.				x	AMF/KMD
Crotalus horridus	AMNH R-97641	–				x	AMF/KMD
Crotalus horridus	FLMNH 116096, 116098, 116099	USA: Kansas: Atchison Co.	x	x			AMF/KMD

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Crotalus horridus	FLMNH 116166	USA: Oklahoma: LeFlore Co.	x	x			AMF/KMD
Crotalus horridus	FLMNH 140945	USA: Florida: Hamilton Co.			x		AMF/KMD
Crotalus horridus	FLMNH 14442-2	USA: Connecticut: Hartford Co.			x		AMF/KMD
Crotalus horridus	FLMNH 144643	USA: Florida: Alachua Co.	x	x			AMF/KMD
Crotalus horridus	FLMNH 14577	USA: Illinois: Jackson Co.	x	x			AMF/KMD
Crotalus horridus	FLMNH 16018, 74513	USA: Illinois	x	x			AMF/KMD
Crotalus horridus	FLMNH 19734	USA: Florida: Suwanee Co.	x	x		x	AMF/KMD
Crotalus horridus	FLMNH 42566, 67009	USA: Florida: Baker Co.	x	x			AMF/KMD
Crotalus horridus	FLMNH 67017	USA: Florida: Columbia Co.	x	x		x	AMF/KMD
Crotalus horridus	FLMNH 72645	USA: Oklahoma	x	x		x	AMF/KMD
Crotalus horridus	FLMNH 81527	USA: Florida: Alachua Co.	x	x		x	AMF/KMD
Crotalus horridus	FMNH 3502	USA: Mississippi: Bolivar Co.			x		AMF/KMD
Crotalus horridus	–	–		x			Campbell and Lamar 2004
Crotalus horridus	UTA R22358	USA: Texas: Ellis Co.		x			Campbell and Lamar 2004
Crotalus intermedius	FLMNH 52552	Mexico: Puebla	x	x			AMF/KMD
Crotalus intermedius	FMNH 100749	Mexico: Veracruz	x	x			AMF/KMD
Crotalus intermedius	LACM 20024	Mexico: Hidalgo	x	x			AMF/KMD
Crotalus intermedius	LSUMZ 10780, 10781	Mexico, Veracruz	x	x			AMF/KMD
Crotalus intermedius	UCM 40075, 41224, 52587	Mexico: Oaxaca: Cerro San Felipe	x	x			AMF/KMD
Crotalus intermedius	UCM 52512	Mexico: Oaxaca: Ixtlan Dist.	x	x			AMF/KMD
Crotalus intermedius	UTA R-4538, R-4707	Mexico: Guerrero				x	AMF/KMD
Crotalus intermedius	–	–		x			Campbell and Lamar 2004
Crotalus lannomi	BYU 23800	Mexico: Jalisco: Puerto Los Mazos	x	x			Campbell and Flores-Villela 2008, Tanner 1966, Campbell and Lamar 2004
Crotalus lannomi	MZFC 22941	Mexico: Colima	x	x			Reyes-Velasco et al. 2010, Jadin et al. 2010
Crotalus lannomi	UTA DC-4002, DC-4003, DC-4005, DC-4006	Mexico: Colima	x	x			Reyes-Velasco et al. 2010
Crotalus lepidus	FLMNH 149088	Mexico: Chihuahua	x	x		x	AMF/KMD
Crotalus lepidus	FMNH 23787	USA: Texas: Brewster Co.			x		AMF/KMD
Crotalus lepidus	FMNH 900	USA: Arizona: Cochise Co.			x		AMF/KMD
Crotalus lepidus	LSUMZ 35156	Mexico: Durango	x	x			AMF/KMD
Crotalus lepidus	LSUMZ 36635, 36636	Mexico: Zacatecas	x	x			AMF/KMD
Crotalus lepidus	LSUMZ 36637	Mexico: Durango	x	x		x	AMF/KMD
Crotalus lepidus	UTA R-12789, R-18351	Mexico: Durango				x	AMF/KMD
Crotalus lepidus	UTA R-17836	Mexico: Sinaloa				x	AMF/KMD
Crotalus lepidus	UTA R-18347	Mexico: Chihuahua				x	AMF/KMD
Crotalus lepidus	UTA R-25394	Mexico: Aguascalientes	x	x			AMF/KMD
Crotalus lepidus	UTA R-25395	Mexico: Aguascalientes	x	x		x	AMF/KMD
Crotalus lepidus	UTA R-7186	USA: Arizona: Cochise Co.				x	AMF/KMD
Crotalus lepidus	–	–		x			Campbell and Lamar 2004
Crotalus lepidus morulus	SDNHM 43322	Mexico: Tamaulipas: Gomez Farias Munic.	x	x		x	AMF/KMD
Crotalus lepidus morulus	UMMZ 101559, 104307	Mexico: Tamaulipas	x	x			AMF/KMD
Crotalus mitchellii	FLMNH 120184	USA: California: San Diego Co.	x	x		x	AMF/KMD
Crotalus mitchellii	FMNH 1159	Mexico: Baja California			x		AMF/KMD
Crotalus mitchellii	LACM 28018, 134442	USA: California: Riverside Co.	x	x		x	AMF/KMD
Crotalus mitchellii	LACM 25083	Mexico: Baja California Sur: Isla Cerralvo	x	x		x	AMF/KMD
Crotalus mitchellii	LACM 52593	USA: California: San Diego Co.	x	x		x	AMF/KMD
Crotalus mitchellii	LACM 74029	Mexico: Baja California Sur	x	x		x	AMF/KMD
Crotalus mitchellii	SDNHM 37446	Mexico: Baja California Norte: Isla El Muerto (Isla Miramar)	x	x		x	AMF/KMD
Crotalus mitchellii	SDNHM 51991	Mexico: Baja California Norte: Isla Angel de la Guarda	x	x		x	AMF/KMD
Crotalus mitchellii	YPM R490	Mexico: Baja California Sur	x	x			AMF/KMD
Crotalus mitchellii	–	–		x			Campbell and Lamar 2004
Crotalus molossus	AMNH R-68715	USA: New Mexico: Catron Co.			x		AMF/KMD
Crotalus molossus	AMNH R-74472, R-74787	–				x	AMF/KMD
Crotalus molossus	AMNH R-74861, 75467	USA: Arizona: Cochise Co.			x		AMF/KMD
Crotalus molossus	CAS 156574, 156576	USA: Arizona: Cochise Co.			x		AMF/KMD
Crotalus molossus	FLMNH 24796, 120190	Mexico: Coahuila	x	x		x	AMF/KMD
Crotalus molossus	FLMNH 48171	Mexico: Durango	x	x			AMF/KMD
Crotalus molossus	FMNH 4770	USA: Texas: El Paso Co.			x		AMF/KMD
Crotalus molossus	SDNHM 41123	Mexico: Durango	x	x		x	AMF/KMD
Crotalus molossus	SDNHM 49968	Mexico: Sonora: Isla San Esteban	x	x			AMF/KMD
Crotalus molossus	UCF 2346	USA: Texas	x	x			AMF/KMD
Crotalus molossus	UCF CLP968, M505	–	x	x			AMF/KMD
Crotalus molossus	UMMZ 77834, 77835	Mexico: Zacatecas	x	x			AMF/KMD
Crotalus molossus	UTA R-12572, R-12579, R-12582, R-15295	Mexico: Puebla				x	AMF/KMD

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Crotalus molossus	UTA R-33	USA: Texas: Brewster Co.				x	AMF/KMD
Crotalus molossus	UTA R-7411	Mexico: Michoacán				x	AMF/KMD
Crotalus molossus	UTA R-9360	Mexico: Oaxaca				x	AMF/KMD
Crotalus molossus	–	–		x			Campbell and Lamar 2004
Crotalus molossus	UTA R-25852	Mexico: Oaxaca		x			Campbell and Lamar 2004
Crotalus oreganus	AMNH R-69935, R-74870	USA: California: Riverside Co			x		AMF/KMD
Crotalus oreganus	AMNH R-75411	USA: California: Riverside Co				x	AMF/KMD
Crotalus oreganus	CAS 165770	USA: California: San Bernardino Co.			x		AMF/KMD
Crotalus oreganus	CAS 200965	USA: California: Alameda Co.			x		AMF/KMD
Crotalus oreganus	CAS 201490	USA: California: San Diego Co.			x		AMF/KMD
Crotalus oreganus	FLMNH 21346	USA: Washington: Grant Co.			x		AMF/KMD
Crotalus oreganus	FMNH 1272	Mexico: Baja California Sur: San José	x	x			AMF/KMD
Crotalus oreganus	FMNH 922, 923	USA: Colorado: Mesa Co.	x	x			AMF/KMD
Crotalus oreganus	SDNHM 4924	Mexico: Baja California Norte: Islas de Los Coronados	x	x		x	AMF/KMD
Crotalus oreganus	SDNHM 57127	Mexico: Baja California Norte	x	x			AMF/KMD
Crotalus oreganus	YPM R-607, R-6258, R-6263	USA: Washington: Snohomish Co.	x	x			AMF/KMD
Crotalus oreganus	–	–		7 inds.			Campbell and Lamar 2004
Crotalus polystictus	FMNH 106074–106076	Mexico	x	x			AMF/KMD
Crotalus polystictus	UMMZ 96873	Mexico	x	x		x	AMF/KMD
Crotalus polystictus	UTA R-12583	–			x		AMF/KMD
Crotalus polystictus	UTA R-40482	Mexico: Jalisco			x		AMF/KMD
Crotalus polystictus	UTA R-8270	–			x		AMF/KMD
Crotalus polystictus	–	–		x			Campbell and Lamar 2004
Crotalus polystictus	–	–					LaDuc
Crotalus polystictus	UTA R-12583	Mexico: Jalisco		x			Campbell and Lamar 2004
Crotalus pricei	CAS SU-1702	USA: Arizona: Pima Co.	x	x			AMF/KMD
Crotalus pricei	FLMNH 87340	USA: Arizona	x	x			AMF/KMD
Crotalus pricei	FLMNH 90054	USA: Arizona: Cochise Co.	x	x			AMF/KMD
Crotalus pricei	FMNH 30849, 30850	Mexico: Nuevo Leon	x	x			AMF/KMD
Crotalus pricei	LSUMZ 28547, 36631, 79916, 79922	Mexico: Durango	x	x		x	AMF/KMD
Crotalus pricei	LSUMZ 35365	Mexico: Durango	x	x			AMF/KMD
Crotalus pricei	UTA R-6769, R-7432, R-9241, R-9242	–			x		AMF/KMD
Crotalus pricei	–	–		x			Campbell and Lamar 2004
Crotalus pricei	UNAM NL	Mexico: Aguascalientes: Munic. San José Prov. de Gracia		x			Campbell and Lamar 2004
Crotalus pusillus	FMNH 37042, 39097, 39112, 39113, 39117, 39120, 39121, 39127, 40818, 40824	Mexico: Michoacán	x	x			AMF/KMD
Crotalus pusillus	FMNH 37048	Mexico: Michoacán: Munic. Tancítaro	x	x	x		AMF/KMD
Crotalus pusillus	UTA R-4530, R-5846, R-9358	Mexico: Michoacán				x	AMF/KMD
Crotalus pusillus	–	–		x			Campbell and Lamar 2004
Crotalus pusillus	–	–			10 inds.		Brattstrom 1964
Crotalus ravus	FMNH 113016	Mexico: Veracruz			x		AMF/KMD
Crotalus ravus	LACM 64446	Mexico: Oaxaca	x	x		x	AMF/KMD
Crotalus ravus	UMMZ 95175, 99839, 99847	Mexico: Districto Federal	x	x			AMF/KMD
Crotalus ravus	UTA R-12634	Mexico: Morelos		x		x	AMF/KMD
Crotalus ravus	YPM R7797	Mexico: Puebla State: Munic. Oriental	x	x			AMF/KMD
Crotalus ravus	YPM R7798	Mexico: Puebla State: Munic. Oriental	x	x		x	AMF/KMD
Crotalus ravus	UTEP 959	–					LaDuc
Crotalus ravus	–	–		x			Campbell and Lamar 2004
Crotalus ravus	–	–			2 inds.		LaDuc
Crotalus ravus	–	–			10 inds.		Brattstrom 1964
Crotalus ruber	AMNH R-141158, R-75259	–			x		AMF/KMD
Crotalus ruber	AMNH R-69061	–				x	AMF/KMD
Crotalus ruber	CAS 200259	USA: California: Riverside Co.			x		AMF/KMD
Crotalus ruber	CAS 45888	Mexico: Baja California: Agua Caliente	x	x			AMF/KMD
Crotalus ruber	FLMNH 2949	USA: California: San Diego Co.	x	x		x	AMF/KMD
Crotalus ruber	FLMNH 2950	USA: California: San Diego Co.	x	x			AMF/KMD
Crotalus ruber	FLMNH 87325	USA: California	x	x			AMF/KMD
Crotalus ruber	FMNH 31290	western USA			x		AMF/KMD
Crotalus ruber	FMNH 5997, 8050	USA: California: San Diego Co.			x		AMF/KMD
Crotalus ruber	LACM 122109, 122110, 138224	USA: California: Riverside Co.	x	x		x	AMF/KMD
Crotalus ruber	LACM 20017	USA: California: San Bernardino Co.	x	x		x	AMF/KMD
Crotalus ruber	LACM 2465	Mexico: Baja California Sur: Isla de Cedros	x	x			AMF/KMD
Crotalus ruber	SDNHM 49961	Mexico: Baja California Norte: Isla San Lorenzo Sur	x	x			AMF/KMD

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Crotalus ruber	–	–		x			Campbell and Lamar 2004
Crotalus scutulatus	AMNH R-110177, 114719	USA: Arizona: Cochise Co.			x		AMF/KMD
Crotalus scutulatus	CAS 156166, 156169	USA: Nevada: Clark Co.			x		AMF/KMD
Crotalus scutulatus	CAS 156172	USA: Arizona: Yavapai Co.			x		AMF/KMD
Crotalus scutulatus	CAS 156267	USA: California: Kern Co.			x		AMF/KMD
Crotalus scutulatus	FLMNH 120196	Mexico: Puebla	x	x			AMF/KMD
Crotalus scutulatus	FLMNH 120197–120200	Mexico: Durango	x	x			AMF/KMD
Crotalus scutulatus	FLMNH 24785, 24787	Mexico: Zacatecas	x	x			AMF/KMD
Crotalus scutulatus	UTA R-14465	USA: Arizona: Pima Co.				x	AMF/KMD
Crotalus scutulatus	UTA R-4554	Mexico: Chihuahua				x	AMF/KMD
Crotalus scutulatus	UTA R-504	USA: New Mexico: Luna Co.				x	AMF/KMD
Crotalus scutulatus	–	–		x			Campbell and Lamar 2004
Crotalus scutulatus	–	Mexico: Veracruz		x			Campbell and Lamar 2004
Crotalus simus	FLMNH 73641	Costa Rica: Guanacaste	x	x			AMF/KMD
Crotalus simus	FLMNH 83824	Honduras: Dept. Morazan	x	x			AMF/KMD
Crotalus simus	FMNH 1731	Costa Rica: Cartago Prov.: Tres Rios			x		AMF/KMD
Crotalus simus	FMNH 20160	Guatemala: Dept. Escuintla: Munic. Tiquisate			x		AMF/KMD
Crotalus simus	–	–		x			Campbell and Lamar 2004
Crotalus stejnegeri	KU 78972	Mexico: Sinaloa	x	x		x	AMF/KMD
Crotalus stejnegeri	LACM 37718	Mexico: Sinaloa	x	x			AMF/KMD
Crotalus stejnegeri	SDNHM 41120	Mexico: Durango	x	x		x	AMF/KMD
Crotalus stejnegeri	SDNHM 41121	Mexico: Durango	x	x			AMF/KMD
Crotalus stejnegeri	UTA R-10499	Mexico: Sinaloa: Munic. Rosario			x		AMF/KMD
Crotalus stejnegeri	UTA R-5926, R-6234	Mexico: Sinaloa: Munic. Rosario	x	x		x	AMF/KMD
Crotalus stejnegeri	–	–		x			Campbell and Lamar 2004
Crotalus stejnegeri	–	–			4 inds.		Brattstrom 1964
Crotalus stephensi	AMNH R-124110	–			x		AMF/KMD
Crotalus stephensi	CAS 156575	USA: Nevada: Lincoln Co.			x		AMF/KMD
Crotalus tancitarensis	FMNH 39115	Mexico: Michoacán: Munic. Tancitaro	x	x			AMF/KMD
Crotalus tancitarensis	UTA R-52401	Mexico	x	x			AMF/KMD
Crotalus tancitarensis	INIRENA 309	Mexico: Michoacán: Cerro Tancitaro	x	x			Alvarado-Diaz and Campbell 2004
Crotalus tigris	AMNH R-59500	USA: Arizona: Pima Co.				x	AMF/KMD
Crotalus tigris	FLMNH 120201	–	x	x			AMF/KMD
Crotalus tigris	FLMNH 16784	Mexico: Sonora	x	x			AMF/KMD
Crotalus tigris	FLMNH 19126	USA: Arizona	x	x		x	AMF/KMD
Crotalus tigris	LSUMZ 28545	Mexico: Sonora	x	x			AMF/KMD
Crotalus tigris	LSUMZ 28650, 38523	USA: Arizona: Pima Co.	x	x		x	AMF/KMD
Crotalus tigris	NAUQSP 7381	–					LaDuc
Crotalus tigris	–	–		x			Campbell and Lamar 2004
Crotalus tigris	–	–			6 inds.		LaDuc
Crotalus tigris	–	–			4 inds.		Brattstrom 1964
Crotalus totonacus	FLMNH 83826, 83829	Mexico: Tamaulipas	x	x		x	AMF/KMD
Crotalus totonacus	FLMNH 83827, 83828	Mexico: Tamaulipas	x	x			AMF/KMD
Crotalus totonacus	SDNHM 43323	Mexico: Tamaulipas: Munic. Gómez Farias	x	x		x	AMF/KMD
Crotalus totonacus	–	–		x			Campbell and Lamar 2004
Crotalus totonacus	–	Mexico: Queretaro		x			Campbell and Lamar 2004
Crotalus transversus	FMNH 100129, 100710	Mexico: Morelos	x	x			AMF/KMD
Crotalus transversus	UCM 51421–51423	Mexico: Morelos: Lagunas de Zempoala Ntl. Park	x	x			AMF/KMD
Crotalus transversus	–	–					Campbell and Lamar 2004
Crotalus triseriatus armstrongi	LACM 25944	Mexico: Jalisco	x	x			AMF/KMD
Crotalus triseriatus armstrongi	UTA R-12589	Mexico: Jalisco			x	x	AMF/KMD
Crotalus triseriatus armstrongi	UTA R-7232	Mexico: Jalisco			x		AMF/KMD
Crotalus triseriatus armstrongi	UTA R-9357	Mexico: Jalisco				x	AMF/KMD
Crotalus triseriatus triseriatus	FLMNH 85096	Mexico: Veracruz-Llave	x	x			AMF/KMD
Crotalus triseriatus triseriatus	FMNH 126618	Mexico	x	x		x	AMF/KMD
Crotalus triseriatus triseriatus	FMNH 126619	Mexico	x	x			AMF/KMD
Crotalus triseriatus triseriatus	LACM 66951	Mexico: Puebla	x	x			AMF/KMD
Crotalus triseriatus triseriatus	UTA R-12599	Mexico: Morelos: Lagunas de Zempoala Ntl. Park			x		AMF/KMD
Crotalus triseriatus triseriatus	UTA R-12600, 12601	Mexico: Morelos				x	AMF/KMD
Crotalus triseriatus triseriatus	UTA R-7398	Mexico: Mexico			x		AMF/KMD
Crotalus tzabcan	FMNH 36168, 40728	Mexico: Yucatán	x	x			AMF/KMD
Crotalus tzabcan	FMNH 49367	Mexico: Yucatán	x	x			AMF/KMD

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Crotalus viridis	AMNH R-147321	USA: Montana: Glacier Co.				x	AMF/KMD
Crotalus viridis	AMNH R-69043	USA: Oklahoma: Texas Co.			x		AMF/KMD
Crotalus viridis	AMNH R-88396	USA: New Mexico: Grant Co.			x		AMF/KMD
Crotalus viridis	FLMNH 41573	USA: New Mexico: Luna Co.			x		AMF/KMD
Crotalus viridis	FLMNH 62550	USA: Arizona: Coconino Co.			x		AMF/KMD
Crotalus viridis	FLMNH 99947	USA: NE Arizona			x		AMF/KMD
Crotalus viridis	LSUMZ 20584	USA: Oklahoma: Texas Co.	x	x		x	AMF/KMD
Crotalus viridis	LSUMZ 38635	USA: Texas: Concho Co.	x	x			AMF/KMD
Crotalus viridis	LSUMZ 40916	USA: Oklahoma: Cimarron Co.	x	x			AMF/KMD
Crotalus viridis	LSUMZ 82043	USA: Texas: Brewster Co.	x	x			AMF/KMD
Crotalus viridis	LSUMZ 82179	USA: Arizona: Navajo Co.	x	x			AMF/KMD
Crotalus viridis	UTA R-14224	USA: Texas: Sherman Co.				x	AMF/KMD
Crotalus viridis	–	–		x			Campbell and Lamar 2004
Crotalus viridis	UTA 18255	USA: New Mexico: Union Co.		x			Campbell and Lamar 2004
Crotalus willardi	AMNH R-119010	–			x		AMF/KMD
Crotalus willardi	FLMNH 48331, 56864	–			x		AMF/KMD
Crotalus willardi	FLMNH 60656	Mexico: Sonora	x	x			AMF/KMD
Crotalus willardi	FMNH 1493	Mexico: Durango	x	x			AMF/KMD
Crotalus willardi	FMNH 902	USA: Arizona: Cochise Co.	x	x			AMF/KMD
Crotalus willardi	LACM 67265	USA: New Mexico: Hidalgo Co.	x	x			AMF/KMD
Crotalus willardi	SDNHM 3207, 40888, 44056	USA: Arizona: Cochise Co.	x	x			AMF/KMD
Crotalus willardi	UMMZ 193361	USA: Arizona: Cochise Co.			x		AMF/KMD
Crotalus willardi	UMMZ 78450, 78452	Mexico: Sonora	x	x			AMF/KMD
Crotalus willardi	UMMZ 78451	Mexico: Sonora	x	x		x	AMF/KMD
Crotalus willardi	UTA R-18425, R-6942	Mexico: Sonora				x	AMF/KMD
Crotalus willardi	UTA R-40529	–			x	x	AMF/KMD
Crotalus willardi	UTA R-9356	Mexico: Durango				x	AMF/KMD
Crotalus willardi	–	–		5 inds.			Campbell and Lamar 2004
Cryptelytrops albolabris	AMNH R-27946	China: Hainan			x		AMF
Cryptelytrops albolabris	CAS 215394	Myanmar: Sagaing Region				x	AMF
Cryptelytrops albolabris	CAS 233005	Myanmar: Kachin State: Myitkyina Dist.	x	x		x	AMF
Cryptelytrops albolabris	CAS 239623	Myanmar: Bago Region: Pyi Dist.	x	x			AMF
Cryptelytrops albolabris	CAS 243024	Myanmar: Maguay Region: Pakhokku Dist.	x	x		x	AMF
Cryptelytrops albolabris	FLMNH 65613, 65615, 88585, 90855, 120225	Thailand	x	x			AMF
Cryptelytrops albolabris	FLMNH 61846	Thailand: Kanchanaburi Prov.	x	x			AMF
Cryptelytrops albolabris	FLMNH 65614	Thailand	x	x		x	AMF
Cryptelytrops albolabris	FLMNH 69255–69258	Thailand			x		AMF
Cryptelytrops albolabris	FMNH 255251	Laos	x	x	x	x	AMF
Cryptelytrops albolabris	FMNH 255252, 255255, 255256	Laos				x	AMF
Cryptelytrops albolabris	FMNH 263013	Cambodia: Mondolkiri Prov.	x	x		x	AMF
Cryptelytrops albolabris	FMNH 270451	Laos: Khammouan Prov.: Nakai Dist.	x	x			AMF
Cryptelytrops albolabris	FMNH 6710	China			x		AMF
Cryptelytrops albolabris	FMNH 6713	China: Hainan Prov.			x		AMF
Cryptelytrops albolabris	UMMZ 227454	Indonesia: Sumatra	x	x			AMF
Cryptelytrops albolabris	YPM R9151	China: Guangdong Prov.: Nan'ao Isl.	x	x			AMF
Cryptelytrops albolabris	YPM R9501	Hong Kong: Lantau Isl.	x	x			AMF
Cryptelytrops albolabris	–	–		x			Vogel 2006
Cryptelytrops andersonii	ZSI 3057	India: Andaman Isl.		x			Theobald 1868
Cryptelytrops andersonii	–	–		x			Vogel 2006
Cryptelytrops andersonii	–	India: Middle Andaman Isl.		2 inds.			Gumprecht et al. 2004
Cryptelytrops andersonii	–	India: North Andaman Isl.		x			Gumprecht et al. 2004
Cryptelytrops andersonii	–	India: South Andaman Isl.		4 inds.			Gumprecht et al. 2004
Cryptelytrops cantori	USNM 29445	India: Nicobar Isls.: Camorta Isl.	x	x			AMF
Cryptelytrops cantori	–	Nicobar Isls.		x			Theobald 1868
Cryptelytrops cantori	–	–		x			Vogel 2006
Cryptelytrops cantori	–	–					Malhotra and Thorpe 2004
Cryptelytrops cardamomensis	FMNH 259191-259192	Cambodia: Koh Kong Prov.: Cardamom Mtns.	x	x			Malhotra et al. 2011
Cryptelytrops cardamomensis	–	Cambodia: Cardamom Mts.		2 inds.			Malhotra et al. 2011
Cryptelytrops cardamomensis	–	Cambodia: Koh Kong Prov.: Kampong Saom Bay		2 inds.			Malhotra et al. 2011
Cryptelytrops cardamomensis	–	Thailand: Chantaburi Prov.: Khao Kitchakut Ntl. Park		2 inds.			Malhotra et al. 2011
Cryptelytrops erythrurus	AMNH R-2158	–			x		AMF
Cryptelytrops erythrurus	CAS 213410, 213412	Myanmar: Yangon Region	x	x	x		AMF
Cryptelytrops erythrurus	CAS 216423, 220254	Myanmar: Rakhine State	x	x		x	AMF
Cryptelytrops erythrurus	CAS 216575, 220336	Myanmar: Rakhine State	x	x			AMF
Cryptelytrops erythrurus	CAS SU8864	Myanmar: Yangon Region	x	x	x		AMF
Cryptelytrops erythrurus	TCWC 81398	India	x	x			AMF
Cryptelytrops erythrurus	–	–		x			Vogel 2006
Cryptelytrops erythrurus	–	–		x			Malhotra and Thorpe 2004

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Cryptelytrops fasciatus	ZRC 2.5620	Indonesia: Sulawesi Selatan Prov.: Tanahjampea Isl.	x				David et al. 2003
Cryptelytrops fasciatus	MNHN 1999.9071, 2000.0401	Indonesia: Sulawesi Selatan Prov.: Tanahjampea Isl.	x				David et al. 2003
Cryptelytrops fasciatus	BMNH 96.4.29.46	Indonesia: Sulawesi Selatan Prov.: Tanahjampea Isl.	x				David et al. 2003
Cryptelytrops fasciatus	ZMFK Specimens 1–2	Indonesia: Sulawesi Selatan Prov.: Tanahjampea Isl.	x				David et al. 2003
Cryptelytrops honsonensis	UNS 0353–0355	Vietnam: Kien Giang Prov.: Hon Son Isl.	x	x			Grismer et al. 2008
Cryptelytrops insularis	FLMNH 28223	Indonesia: Komodo Isl.			x		AMF
Cryptelytrops insularis	FLMNH 28690, 28692, 28696–28698, 28703, 28709	Indonesia: Komodo Isl.	x	x			AMF
Cryptelytrops insularis	FLMNH 28694, 28710, 28711	Indonesia: Komodo Isl.	x	x		x	AMF
Cryptelytrops insularis	FLMNH 30128, 30149	Indonesia: Lesser Sundas: Flores Isl.	x	x		x	AMF
Cryptelytrops insularis	FLMNH 30129, 30142	Indonesia: Lesser Sundas: Flores Isl.	x	x			AMF
Cryptelytrops insularis	FLMNH 36446	Indonesia: Timor	x	x			AMF
Cryptelytrops insularis	–	–		x			Vogel 2006
Cryptelytrops kanburiensis	FLMNH 85089, 85090, 89608, 89609	Thailand	x	x			AMF
Cryptelytrops kanburiensis	USNM 297337, 297452, 345537–345539	–	x	x			AMF
Cryptelytrops kanburiensis	–	–		x			Vogel 2006
Cryptelytrops kanburiensis	–	–					Malhotra and Thorpe 2004
Cryptelytrops kanburiensis	QSMI 508, 509	Thailand: Kanchanaburi Prov.	x	x			David et al. 2004
Cryptelytrops kanburiensis	BMNH 1988.383	Thailand: Kanchanaburi Prov.	x	x			David et al. 2004
Cryptelytrops kanburiensis	BMNH 1946.1.8.91	Thailand: Kanchanaburi Prov.		x			David et al. 2004
Cryptelytrops kanburiensis	BMNH 1987.943, 1992.535	Thailand: Kanchanaburi Prov.: Sai Yok Dist.	x	x			David et al. 2004
Cryptelytrops labialis	USNM 29444	India: Nicobar Isls: Nancowry Isl.	x	x			AMF
Cryptelytrops labialis	–	India: Andaman Isls.		3 inds.			Vogel 2006
Cryptelytrops labialis	–	India: Central Nicobar Isl.: Nancowry Grp.		4 inds.			Vogel 2006
Cryptelytrops macrops	CM 156455–156458	Thailand	x	x			AMF
Cryptelytrops macrops	FMNH 258957, 258958	Laos: Champasak Prov.: Paksong Dist.	x	x			AMF
Cryptelytrops macrops	FMNH 259189	Cambodia: Kampong Speu Prov.: Phnom Sruoch Dist.	x	x			AMF
Cryptelytrops macrops	FMNH 262715	Cambodia: Stung Treng Prov.: Siem Pang Dist.	x	x			AMF
Cryptelytrops macrops	–	Thailand		2 inds.			Vogel 2006
Cryptelytrops macrops	FMNH 180271	Thailand: Nakhon Nayok Prov.					Guo et al. 2010
Cryptelytrops macrops	–	Thailand: Nakhon Ratchesima Prov.: Khao Yai Ntl. Park		x			Vogel 2006
Cryptelytrops purpureomaculatus	CAS 212242, 212244	Myanmar: Ayeyarwady Region: Myaungmya Dist.			x		AMF
Cryptelytrops purpureomaculatus	FLMNH 48828, 48830, 48833, 48834	Myanmar: Yangon Region	x	x		x	AMF
Cryptelytrops purpureomaculatus	FLMNH 48829, 48831, 48832	Myanmar: Yangon Region	x	x			AMF
Cryptelytrops purpureomaculatus	FMNH 80157	Singapore	x	x			AMF
Cryptelytrops purpureomaculatus	UMMZ 126386, 126387	Thailand	x	x			AMF
Cryptelytrops purpureomaculatus	–	–		x			Vogel 2006
Cryptelytrops purpureomaculatus	–	–			4 inds.		Brattstrom 1964
Cryptelytrops purpureomaculatus	–	Thailand		x			Vogel 2006
Cryptelytrops purpureomaculatus	–	West Malaysia		x			Vogel 2006
Cryptelytrops rubeus	FMNH 262717, 262720, 262721	Cambodia: Mondulkiri Prov.: Ou Reang Dist.	x	x		x	AMF
Cryptelytrops rubeus	FMNH 262718	Cambodia: Mondulkiri Prov.: Ou Reang Dist.	x	x			Malhotra et al. 2011
Cryptelytrops rubeus	–	Cambodia: Mondulkiri Prov.: Ou Reang Dist.		2 inds.			Malhotra et al. 2011
Cryptelytrops rubeus	–	South Vietnam		2 inds.			Malhotra et al. 2011
Cryptelytrops rubeus	–	Vietnam: Nam Cat Tien Ntl Park		x			Malhotra et al. 2011
Cryptelytrops rubeus	–	Vietnam		2 inds.			Malhotra et al. 2011
Cryptelytrops septentrionalis	CAS 135750	Nepal: Hyangcha	x	x			AMF
Cryptelytrops septentrionalis	FMNH 131953	Nepal	x	x			AMF
Cryptelytrops septentrionalis	FMNH 83083	Nepal: Gorkha Dist.	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Cryptelytrops septentrionalis	–	–					Malhotra and Thorpe 2004
Cryptelytrops septentrionalis	–	India: Uttarakhand		x			Vogel 2006
Cryptelytrops septentrionalis	–	Nepal		x			Vogel 2006
Cryptelytrops venustus	USNM 81860	Thailand: Surat Thani Prov.	x	x			AMF
Cryptelytrops venustus	ZMB 48045	Thailand: Nakhon Si Thammarat Prov.		x			David et al. 2004, Vogel 1991
Cryptelytrops venustus	ZMB 48046	Thailand: Nakhon Si Thammarat Prov.		x			David et al. 2004
Cryptelytrops venustus	–	–		x			Vogel 2006
Cryptelytrops venustus	MNHN 1990.9091–9095	–		x			David et al. 2004
Cryptelytrops venustus	ZMFK 79783–79784	–		x			David et al. 2004
Cryptelytrops venustus	SMF 82550–82552	–		x			David et al. 2004
Cryptelytrops venustus	BMNH 1983.384–386, 1987.944–945	Thailand: Nakhon Si Thammarat Prov.		x			David et al. 2004
Cryptelytrops venustus	QSMI 352–353, 383–384, 512–513	Thailand: Nakhon Si Thammarat Prov.		x			David et al. 2004
Cryptelytrops venustus	PSGV 600, 662	Thailand: Nakhon Si Thammarat Prov.: Lan Saka Dist.		x			David et al. 2004
Cryptelytrops venustus	QSMI 354–357, 517–518	Thailand: Nakhon Si Thammarat Prov.: Thung Song Dist.		x			David et al. 2004
Cryptelytrops venustus	ZSM 127.1990	Thailand: Nakhon Si Thammarat Prov.: Thung Song Dist.		x			David et al. 2004
Daboia palaestinae	UCF CLP905	–	x	x			AMF
Daboia russelii	FLMNH 74263, 120377	India	x	x			AMF
Daboia russelii	FLMNH 54074	Pakistan			x		AMF
Daboia russelii	FLMNH 70644	Pakistan: Sind Prov.: Tatta Dist.	x	x		x	AMF
Daboia russelii	FLMNH 71133, 73350, 73356, 78405	Pakistan	x	x			AMF
Daboia siamensis	CAS 206671	Myanmar: Sagaing Region	x	x		x	AMF
Daboia siamensis	CAS 210536	Myanmar: Magway Region	x	x			AMF
Daboia siamensis	CAS 210836	Myanmar: Magway Region	x	x		x	AMF
Daboia siamensis	CAS 210838	Myanmar: Magway Region: Minbu Twnsp.	x	x		x	AMF
Daboia siamensis	CAS 215924	Myanmar: Mandalay Region: Myin Gyan Dist.	x	x			AMF
Daboia siamensis	FLMNH 87944	Thailand	x	x			AMF
Daboia siamensis	UCF CLP902, CLP903	–	x	x			AMF
Deinagkistrodon acutus	CM 147733	China	x	x			AMF
Deinagkistrodon acutus	CM 147735	China	x	x	x		AMF
Deinagkistrodon acutus	FLMNH 120204	China	x	x			AMF
Deinagkistrodon acutus	FLMNH 24083, 120205	Taiwan	x	x			AMF
Deinagkistrodon acutus	FLMNH 50805, 51120	China: Fukien Prov.			x		AMF
Deinagkistrodon acutus	FMNH 25177	China: Fukien Prov.			x		AMF
Deinagkistrodon acutus	–	–		x			Vogel 2006
Deinagkistrodon acutus	CIB no number	China: Jiangxi Prov., Fujian Prov.			3 inds.		Guo et al. 1999
Echis carinatus multisquamatus	CAS 179124, 179145	Turkmenistan: Lebap Prov.: Repetek Nature Reserve	x	x		x	AMF
Echis carinatus multisquamatus	CAS 179144, 179514	Turkmenistan: Lebap Prov.: Repetek Nature Reserve	x	x			AMF
Echis carinatus multisquamatus	CAS 179737, 179741	Turkmenistan: Mary Prov.	x	x		x	AMF
Echis carinatus multisquamatus	CAS 179738–179740, 179742	Turkmenistan: Mary Prov.	x	x			AMF
Echis carinatus multisquamatus	UCF CLP906, CLP907	–	x	x			AMF
Echis pyramidum	CAS 131532	South Sudan: Ilemi Triangle	x	x		x	AMF
Echis pyramidum	CAS 174027, 174028	South Sudan: Central Equatoria	x	x		x	AMF
Echis pyramidum	FLMNH 62318	Kenya: Rift Valley Prov.	x	x			AMF
Echis pyramidum	UCF CLP908	–	x	x			AMF
Garthius chaseni	FMNH 71860	North Borneo	x	x			AMF
Garthius chaseni	MCZ 43615, 43616	Malaysia: Sabah: Borneo	x	x			AMF
Garthius chaseni	MCZ 43618	Malaysia: Sabah: Borneo: Kiau: Mt. Kinabalu	x	x			AMF
Garthius chaseni	USNM 134126	Malaysia: Sabah: Borneo: Kiau: Mt. Kinabalu	x	x			AMF
Garthius chaseni	–	–		x			Vogel 2006
Gloydius blomhoffii	CAS 14622	China: Munic. Shanghai			x		AMF
Gloydius blomhoffii	FLMNH 24025, 119550, 120207	Japan: Kantō Region: Honshu Isl.: Saitama Pref.	x	x		x	AMF
Gloydius blomhoffii	FLMNH 120208	Japan: Kantō Region: Honshu Isl.: Saitama Pref.	x	x			AMF
Gloydius blomhoffii	FLMNH 24024, 120210	Japan: Kantō Region: Honshu Isl.: Saitama Pref.				x	AMF
Gloydius blomhoffii	FLMNH 24023	Japan: Hachijō-jima Isl.				x	AMF
Gloydius blomhoffii	FMNH 7164, 7165	China: Anhui Prov.	x	x			AMF
Gloydius blomhoffii	FMNH 7167	China: Anhui Prov.				x	AMF
Gloydius blomhoffii	FMNH 7171	China: Anhui Prov.	x	x	x		AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Gloydius blomhoffii	FMNH 73968, 73970, 73971	Japan	x	x			AMF
Gloydius blomhoffii	FMNH 73969	Japan	x	x	x		AMF
Gloydius blomhoffii	–	–		x			Vogel 2006
Gloydius blomhoffii	–	–	2 inds.		3 inds.		Gutberlet 1998
Gloydius brevicaudus	AMNH R-147936, R-147937	Korea			x		AMF
Gloydius brevicaudus	AMNH R-17438	China			x		AMF
Gloydius brevicaudus	CM 69430	Korea	x	x			AMF
Gloydius brevicaudus	KU 208078	China: Sichuan Prov.	x	x			AMF
Gloydius brevicaudus	KU 215579	South Korea: Gyeonggi Prov.	x	x		x	AMF
Gloydius brevicaudus	KU 38798	China: Sichuan Prov.	x	x		x	AMF
Gloydius brevicaudus	UMMZ 113464	South Korea: Gyeonggi Prov.	x	x			AMF
Gloydius brevicaudus	UMMZ 168336	China	x	x			AMF
Gloydius brevicaudus	UTA R-16873	Korea	x	x		x	AMF
Gloydius brevicaudus	UTA R-18699	Korea	x	x			AMF
Gloydius brevicaudus	YPM R9828	China: Guangdong Prov.: Nan'ao Isl.	x	x		x	AMF
Gloydius brevicaudus	–	–		x			Vogel 2006
Gloydius halys	AMNH R-143775	–			x		AMF
Gloydius halys	CAS 183387	Kazakhstan: Aral Sea	x	x		x	AMF
Gloydius halys	CM 69431	Azerbaijan	x	x			AMF
Gloydius halys	FMNH 141634, 141635	Iran: Mazandaran Prov.	x	x			AMF
Gloydius halys	FMNH 170638	China: Sichuan Prov.	x	x		x	AMF
Gloydius halys	FMNH 230008, 230009	Kyrgyzstan and Tajikistan	x	x			AMF
Gloydius halys	FMNH 234287	Kyrgyzstan	x	x			AMF
Gloydius halys	FMNH 7127	Mongolia	x	x		x	AMF
Gloydius halys	FMNH 7128	Mongolia	x	x			AMF
Gloydius halys	FMNH 7161, 7163	China: Chihli: Hsing Sung Shan	x	x			AMF
Gloydius halys	–	–			2 inds.		Brattstrom 1964
Gloydius himalayanus	FLMNH 70651–70657, 70668	Pakistan: Khyber Pakhtunkhwa: Kaghan Valley	x	x			AMF
Gloydius himalayanus	FLMNH 70658	Pakistan: Khyber Pakhtunkhwa: Kaghan Valley	x	x		x	AMF
Gloydius himalayanus	FLMNH 82634	Pakistan: Khyber Pakhtunkhwa: Hazara Region	x	x			AMF
Gloydius himalayanus	KU 129591	India: Uttar Pradesh: Nag Tiba: 9200	x	x			AMF
Gloydius himalayanus	UMMZ 50086	India: Himachal Pradesh: Kullu Dist.	x	x			AMF
Gloydius himalayanus	–	–		x			Vogel 2006
Gloydius intermedius	AMNH R-108505	Korea	x	x		x	AMF
Gloydius intermedius	AMNH R-108507, R-140532	Korea	x	x			AMF
Gloydius intermedius	CAS 31540	North Korea: North Hamgyong Prov.: Chongjin			x		AMF
Gloydius intermedius	FMNH 11484	Korea: Songdo			x		AMF
Gloydius intermedius	FMNH 230006, 230007, 230013	Russia: Primorsky Krai	x	x			AMF
Gloydius intermedius	KU 87848	Kyrgyzstan	x	x			AMF
Gloydius intermedius	ROM 20462, 20467	China: Jilin Prov.: Kouqian Twnsp.	x	x			AMF
Gloydius intermedius	ROM 20465, 20466	China: Jilin Prov.: Kouqian Twnsp.	x	x		x	AMF
Gloydius intermedius	–	–		x			Vogel 2006
Gloydius intermedius	CIB no number	China: Jilin Prov., Liaoning Prov.			3 inds.		Guo et al. 1999
Gloydius intermedius	CIB no number	China: Xinjiang Uyghur Autonomous Region			5 inds.		Guo et al. 1999
Gloydius monticola	AMNH R-21020	China: Yunnan Prov.: Jade Dragon Snow Mt.	x	x			AMF
Gloydius monticola	–	–		x			Vogel 2006
Gloydius shedaoensis	–	–		x			Vogel 2006
Gloydius shedaoensis	–	–	var. inds.	x			Zhao 1979
Gloydius shedaoensis	CIB no number	China: Liaoning Prov.			4 inds.		Guo et al. 1999
Gloydius strauchi	FMNH 15134, 15172	China: Sichuan Prov.	x	x			AMF
Gloydius strauchi	FMNH 15171	China: Sichuan Prov.	x	x		x	AMF
Gloydius strauchi	MVZ 216678, 216680, 216826, 216829, 216830	China: Sichuan Prov.	x	x			AMF
Gloydius strauchi	–	–		x			Vogel 2006
Gloydius strauchi	CIB no number	China: Shaanxi Prov.			2 inds.		Guo et al. 1999
Gloydius strauchi	CIB no number	China: Sichuan Prov.			3 inds.		Guo et al. 1999
Gloydius tsushimaensis	OMNH R-3934	Japan: Nagasaki Pref.: Tsushima Isl.	x	x			Isogawa et al. 1994
Gloydius tsushimaensis	–	–		x			Vogel 2006
Gloydius tsushimaensis	–	Japan: Nagasaki Pref.	32 inds.	x			Isogawa et al. 1994
Gloydius ussuriensis	FMNH 11470, 11475, 11478	North Korea: North Hwanghae Prov.: Munic. Kaesŏng	x	x			AMF
Gloydius ussuriensis	FMNH 229985–229988	Russia: Primorsky Krai	x	x			AMF
Gloydius ussuriensis	ROM 20454, 20456	China: Jilin Prov.: Yongji Co.	x	x		x	AMF
Gloydius ussuriensis	UTA R-19421	Russia: Primorsky Krai	x	x			AMF
Gloydius ussuriensis	–	–		x			Vogel 2006
Gloydius ussuriensis	CIB no number	China: Jilin Prov.			4 inds.		Guo et al. 1999
Himalayophis tibetanus	CAS 177460, 177471, 177472, 177573, 177574, 177677	China: Tibet Aut. Region: Shigatse Pref.	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Himalayophis tibetanus	FU 80001, 80002	China: Xizang Prov.: Nielamou Dist.	x	x			David and Tong 1997
Himalayophis tibetanus	–	–				x	Malhotra and Thorpe 2004
Himalayophis tibetanus	–	Nepal: Central Region: Phulchoki Mtn.		2 inds.			Vogel 2006
Himalayophis tibetanus	–	Nepal: Bagmati Zone: Sindhupalchok Dist.		x			Vogel 2006
Hypnale hypnale	AMNH R-96081	Sri Lanka: North Western Prov.: Kurunegala Dist.	x	x			AMF
Hypnale hypnale	CM 151343	India: Tamil Nadu: Tirunelveli Dist.	x	x			AMF
Hypnale hypnale	CM 151796	India: Kerala	x	x			AMF
Hypnale hypnale	CM 67694, 67695	Sri Lanka: Uva Prov.	x	x			AMF
Hypnale hypnale	CM 67813	Sri Lanka: North Western Prov.	x	x			AMF
Hypnale hypnale	CM 67996	Sri Lanka: Central Prov.: Kandy Dist.	x	x			AMF
Hypnale hypnale	FMNH 120932–120934, 120936	Sri Lanka: Central Prov.	x	x			AMF
Hypnale hypnale	FMNH 121450	Sri Lanka	x	x			AMF
Hypnale hypnale	FMNH 165058	Sri Lanka: Western Prov.: Colombo Dist.	x	x			AMF
Hypnale hypnale	FMNH 217683, 217686, 217687	India: Kerala: Trivandrum Dist.	x	x			AMF
Hypnale hypnale	WHT 5857	–	x				Maduwage et al. 2009
Hypnale hypnale	–	–		x			Vogel 2006
Hypnale hypnale	WHT 5852	Sri Lanka: Southern Prov.: Galle Dist.	x				Maduwage et al. 2009
Hypnale nepa	AMNH R-99385	Sri Lanka: Southern Prov.	x	x			AMF
Hypnale nepa	CAS 16916	Sri Lanka	x	x			AMF
Hypnale nepa	WHT 6515	Sri Lanka	x	x			Maduwage et al. 2009
Hypnale nepa	–	–		2 inds.			Vogel 2006
Hypnale nepa	WHT 6082	Sri Lanka	x				Maduwage et al. 2009
Hypnale zara	AMNH R-94469	Sri Lanka: Western Prov.	x	x			AMF
Hypnale zara	CM S6383	Sri Lanka	x	x			AMF
Hypnale zara	KU 24143	Sri Lanka	x	x			AMF
Hypnale zara	UMMZ 65626	Sri Lanka	x	x			AMF
Hypnale zara	BMNH 1946.1.19.96	–	x	x			Maduwage et al. 2009
Hypnale zara	WHT 6089	–	x				Maduwage et al. 2009
Hypnale zara	WHT 2198	Sri Lanka: Southern Prov.: Galle Dist.	x				Maduwage et al. 2009
Hypnale zara	WHT 5848	Sri Lanka	x				Maduwage et al. 2009
Lachesis acrochorda	AMNH R-63419	Colombia: Dept. Chocó: Munic. Tadó			x		AMF
Lachesis acrochorda	KU 112608	Panama: Canal Zone	x	x			AMF
Lachesis acrochorda	KU 117479	Panama: Darién Prov.			x		AMF
Lachesis acrochorda	UTA R-51433	Colombia: Dept. Valle	x	x			AMF
Lachesis acrochorda	UTA R-56349	Ecuador: Esmeraldas Prov.	x	x			AMF
Lachesis acrochorda	UTA R-7234	Colombia	x	x			AMF
Lachesis acrochorda	–	–		x			Campbell and Lamar 2004
Lachesis acrochorda	UTA R7593	Colombia: Dept. Chocó	x				Campbell and Lamar 2004
Lachesis melanocephala	FLMNH 120209	Costa Rica: Puntarenas Prov.: Rincón de Osa	x	x			AMF
Lachesis melanocephala	KU 102539	Costa Rica: Puntarenas Prov.	x	x			AMF
Lachesis melanocephala	LACM 154666	Costa Rica: Puntarenas Prov.: Buenos Aires Canton	x	x			AMF
Lachesis melanocephala	SDNHM 46013	Costa Rica: Puntarenas Prov.	x	x			AMF
Lachesis melanocephala	–	–		x			Campbell and Lamar 2004
Lachesis melanocephala	–	–		x			Fernandes et al. 2004
Lachesis muta	AMNH R-75737	Trinidad: Arima Valley			x		AMF
Lachesis muta	AMNH R-85310	Trinidad			x		AMF
Lachesis muta	FLMNH 120217	Surinam	x	x		x	AMF
Lachesis muta	FLMNH 56383	Guyana			x		AMF
Lachesis muta	FMNH 54183, 59182, 68603	Peru	x	x			AMF
Lachesis muta	ROM 23318	Trinidad and Tobago: St. George: Arima Ward Twnsp.	x	x			AMF
Lachesis muta	–	–		x			Campbell and Lamar 2004
Lachesis muta	UTA R40468	–	x				Campbell and Lamar 2004
Lachesis muta	–	Brazil: Atlantic Forest		x			Fernandes et al. 2004
Lachesis muta	–	Brazil: Espírito Santo: Munic. Vitória		x			Campbell and Lamar 2004
Lachesis muta	–	Brazil: Matto Grosso		x			Fernandes et al. 2004
Lachesis muta	–			2 inds			Fernandes et al. 2004
Lachesis muta	–	Suriname: Paramaribo Dist.		x			Campbell and Lamar 2004
Lachesis stenophrys	FLMNH 120215, 120216	Panama: Canal Zone	x	x			AMF
Lachesis stenophrys	FLMNH 52873	Costa Rica: Limón Prov.	x	x			AMF
Lachesis stenophrys	FLMNH 83585	Costa Rica: Cartago Prov.			x		AMF
Lachesis stenophrys	FLMNH 88663, 88883	Costa Rica	x	x			AMF
Lachesis stenophrys	FMNH 31748–31751	Panama			x		AMF
Lachesis stenophrys	UTA R-12944	Costa Rica: Cartago Prov.				x	AMF
Lachesis stenophrys	–	–		x			Campbell and Lamar 2004
Lachesis stenophrys	–	–		x			Fernandes et al. 2004
Lachesis stenophrys	UTA R-15415	Costa Rica: Cartago Prov.		x			Campbell and Lamar 2004
Lachesis stenophrys	UTA R-12945	Costa Rica: Limón Prov.		x			Campbell and Lamar 2004
Macrovipera lebetina	UTA R-6678, R-14073	–	x	x		x	AMF
Macrovipera lebetina	UTA R-7297, R-8022	–	x	x			AMF
Mixcoatlus barbouri	UTA R-6231, R-15558	Mexico: Guerrero	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Mixcoatlus barbouri	USNM 46347	–	x				Jadin et al. 2011
Mixcoatlus barbouri	MZFC 2881	–	x				Jadin et al. 2011
Mixcoatlus barbouri	–	–		x			Campbell and Lamar 2004
Mixcoatlus barbouri	–	–	14 inds.	1 ind.			Jadin et al. 2011
Mixcoatlus browni	UTA R-56264	Mexico: Guerrero: Sierra Madre del Sur	x	x			AMF
Mixcoatlus browni	MCZ 42678, 42679	–					Jadin et al. 2011
Mixcoatlus browni	UTA 56265	–		x			Jadin et al. 2011
Mixcoatlus browni	–	–	13 inds.				Jadin et al. 2011
Mixcoatlus browni	UTA R-4450	–	x				Jadin et al. 2011
Mixcoatlus melanurus	FMNH 100407, 120234	Mexico: Puebla	x	x			AMF
Mixcoatlus melanurus	FMNH 105726	Mexico	x	x			AMF
Mixcoatlus melanurus	LACM 128520	Mexico: Puebla			x		AMF
Mixcoatlus melanurus	UTA R-34604	–			x	x	AMF
Mixcoatlus melanurus	UTA R-34605, R-34606	–			x		AMF
Mixcoatlus melanurus	–	–		x			Campbell and Lamar 2004
Mixcoatlus melanurus	–	–	31 inds.		4 inds.		Gutberlet 1998
Mixcoatlus melanurus	UTA R-34606	–					Campbell and Lamar 2004
Mixcoatlus melanurus	UTA R-12557	Mexico: Puebla		x			Campbell and Lamar 2004
Ophryacus undulatus	FMNH 38505	Mexico: Guerrero: Munic. Chilpancingo			x		AMF
Ophryacus undulatus	UTA R-4517	Mexico: Guerrero: Omilteme	x	x			AMF
Ophryacus undulatus	UTA R-4518	Mexico: Guerrero: Omilteme	x	x		x	AMF
Ophryacus undulatus	UTA R-4641	Mexico: Guerrero: Omilteme			x		AMF
Ophryacus undulatus	UTA R-5810	Mexico: Oaxaca	x	x		x	AMF
Ophryacus undulatus	–	–		x			Campbell and Lamar 2004
Ophryacus undulatus	–	–	44 inds.		3 inds.		Gutberlet 1998
Ophryacus undulatus	UTA R-4108	Mexico: Guerrero		x			Campbell and Lamar 2004
Ovophis monticola	AMNH R-34294	China: Fukien Prov.	x	x			AMF
Ovophis monticola	CAS 224376	Myanmar: Kachin State: Putao Dist.: Nagmung Twnsp.	x	x			AMF
Ovophis monticola	CAS 224424	Myanmar: Kachin State: Putao Dist.: Nagmung Twnsp.	x	x	x		AMF
Ovophis monticola	CAS 233203	Myanmar: Chin State: Phalum Dist.: Haka Twnsp.	x	x	x	x	AMF
Ovophis monticola	CAS 233241	Myanmar: Chin State: Phalum Dist.: Phalum Twnsp.	x	x	x		AMF
Ovophis monticola	CAS SU12920	Malaysia: Pahang: Cameroon Highlands	x	x	x		AMF
Ovophis monticola	FMNH 18760	China: Szechuan: Mouping			x		AMF
Ovophis monticola	FMNH 25187	China			x		AMF
Ovophis monticola	FMNH 258632	Laos	x	x		x	AMF
Ovophis monticola	KU 156296	Nepal: Dhankuta Dist.	x	x			AMF
Ovophis monticola	MCZ 7392	Taiwan: Mt. Arizan	x	x			AMF
Ovophis monticola	–	–		x			Vogel 2006
Ovophis monticola	SCUM 035030	China: Sichuan: An Co.			x		Guo and Zhao 2006, Guo et al. 2010
Ovophis monticola	AFS 06.30	China			x		Guo et al. 2009
Ovophis monticola	SCU M035047, 035052	China: Sichuan			2 inds.		Guo and Zhao 2006
Ovophis monticola	SCUM 035040, 035082, 035083	China: Sichuan: Huili Co.			x		Guo and Zhao 2006, Guo et al. 2010
Ovophis monticola	AFS 06.49	Nepal			x		Guo et al. 2010
Ovophis okinavensis	CAS 21927	Japan: Kagoshima Pref.: Ryukyu Isls.: Amami Isls.			x		AMF
Ovophis okinavensis	CM 147772	Japan	x	x			AMF
Ovophis okinavensis	CM 25918	Japan	x	x		x	AMF
Ovophis okinavensis	FLMNH 120357	Japan: Kagoshima Pref.: Ryukyu Isls.: Amami Isls.	x	x			AMF
Ovophis okinavensis	FLMNH 120358	Japan: Kagoshima Pref.: Ryukyu Isls.	x	x		x	AMF
Ovophis okinavensis	FLMNH 24037–24040	Japan: Kagoshima Pref.: Ryukyu Isls.: Amami Isl.	x	x			AMF
Ovophis okinavensis	FLMNH 24041	Japan: Kagoshima Pref.: Ryukyu Isls.: Amami Isls.	x	x		x	AMF
Ovophis okinavensis	FLMNH 45643	–			x		AMF
Ovophis okinavensis	FMNH 45074	Japan: Ryukyu Isls.			x		AMF
Ovophis okinavensis	–	–		x			Vogel 2006
Ovophis okinavensis	CAS 21927	Japan			x		Guo et al. 2009, Guo et al. 2010
Ovophis okinavensis	FMNH 45074	Japan			x		Guo et al. 2010
Ovophis okinavensis	KUZ R-19071, R-19248	Japan			x		Guo et al. 2010
Parias flavomaculatus	AM 01	Philippines, Luzon Isl.			x		Guo et al. 2010
Parias flavomaculatus	RTV 35	Philippines, Luzon Isl.			x		Guo et al. 2009, Guo et al. 2010
Parias flavomaculatus	AFS 06.35	Philippines, Luzon Isl.			x		Guo et al. 2010
Parias f. flavomaculatus	FLMNH 51015, 51016, 54645, 54945	Philippines: Luzon Isls.: Luzon: Camarines Sur Prov.	x	x			AMF
Parias f. flavomaculatus	FLMNH 53430	Philippines: Luzon Isls.: Luzon: Camarines Sur Prov.			x		AMF
Parias f. flavomaculatus	FLMNH 54654, 54655	Philippines: Luzon Isls.: Luzon: Catanduanes Prov.	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Parias f. flavomaculatus	KU 313904	Philippines: Luzon Isls.: Luzon: Camarines Norte Prov.	x	x			AMF
Parias f. flavomaculatus	–	–				x	Malhotra and Thorpe 2004
Parias f. flavomaculatus	–	Philippines		x			Vogel 2006
Parias f. flavomaculatus	–	Philippines: Bicol Prov.: Sorsogon Prov.		x			Vogel 2006
Parias f. flavomaculatus	–	Philippines: NW of Panay Isl.		x			Vogel 2006
Parias f. flavomaculatus	–	Philippines: NW of Panay Isl.		2 inds.			Vogel 2006
Parias f. flavomaculatus	–	Philippines: NW of Panay Isl.		x			Vogel 2006
Parias flavomaculatus halieus	CAS 62407–62410, 62576	Philippines: Polillo Isl.	x	x			AMF
Parias flavomaculatus halieus	FMNH 15043	Philippines: Polillo Isls.	x	x			AMF
Parias flavomaculatus mcgregori	CAS 60525	Philippines: Batanes Isls.: Batanes Prov.: Batan Isl.	x	x			AMF
Parias flavomaculatus mcgregori	MCZ 173403	Philippines: Luzon Isls.: Luzon	x				AMF
Parias flavomaculatus mcgregori	USNM 291414, 291415, 291417, 328683	Philippines: Batanes Isls.: Batanes Prov.: Batan Isl.	x	x			AMF
Parias flavomaculatus mcgregori	USNM 291416	Philippines: Batanes Isls.: Batanes Prov.: Batan Isl.	x	x		x	AMF
Parias flavomaculatus mcgregori	–	–				x	Malhotra and Thorpe 2004
Parias flavomaculatus mcgregori	–	Philippines: Batanes Isls.		4 inds.			Vogel 2006
Parias flavomaculatus mcgregori	AM 03	Philippines: Batanes Prov.: Batan Isl.			x		Guo et al. 2010
Parias flavomaculatus mcgregori	AFS 06.28, 06.31	Philippines: Batanes Prov.: Batan Isl.			x		Guo et al. 2010
Parias hageni	CAS 16831	Malaysia: Pahang State	x	x			AMF
Parias hageni	UMMZ 227032	Indonesia: Sumatra	x	x		x	AMF
Parias hageni	UMMZ 227773	Indonesia: Sumatra	x	x			AMF
Parias hageni	USNM 23770, 95959	Thailand	x	x			AMF
Parias hageni	UTA R-55256, R-55257	Malaysia	x	x			AMF
Parias hageni	–	–		x			Vogel 2006
Parias hageni	–	–					Malhotra and Thorpe 2004
Parias hageni	AM 06	Malaysia			x		Guo et al. 2010
Parias hageni	AFS 06.52	Sumatra			x		Guo et al. 2010
Parias hageni	AFS 06.19	Sumatra			x		Guo et al. 2009, Guo et al. 2010
Parias malcolmi	MCZ 43605, 43606	Malaysia: Borneo: Sabah	x	x			AMF
Parias malcolmi	SM no number	Malaysia: Borneo: Sabah: Ranau Dist.		7 inds.			Struebing and Inger 1998
Parias malcolmi	–	–		x			Vogel 2006
Parias schultzei	CM R-2265–R-2268	Philippines: Palawan Prov.: Balabac Isl.	x	x			AMF
Parias schultzei	FLMNH 67914–69176	Philippines: Palawan Prov.: Palawan Isl.	x	x			AMF
Parias schultzei	FMNH 15045, 53560	Philippines: Palawan Prov.: Palawan Isl.	x	x			AMF
Parias schultzei	FMNH 53561	Philippines: Palawan Prov.: Palawan Isl.	x	x		x	AMF
Parias schultzei	–	–		x			Vogel 2006
Parias schultzei	–	–				x	Malhotra and Thorpe 2004
Parias sumatranus	FMNH 71643, 76326, 138687, 138690, 148829	Malaysia: Borneo: Sarawak	x	x			AMF
Parias sumatranus	FMNH 230064	Malaysia: Borneo: Sabah: Lahad Datu Dist.	x	x			AMF
Parias sumatranus	FMNH 239948	Malaysia: Borneo: Sabah: Kota Marudu Dist.	x	x			AMF
Parias sumatranus	FMNH 239954, 239957, 239958	Malaysia: Borneo: Sabah: Tenom Dist.	x	x			AMF
Parias sumatranus	FMNH 239959	Malaysia: Borneo: Sabah: Sipitang Dist.	x	x			AMF
Parias sumatranus	FMNH 249756	Malaysia: Borneo: Sabah: Tawau Dist.	x	x			AMF
Parias sumatranus	FMNH 71644	Malaysia: Borneo: Sarawak			x		AMF
Parias sumatranus	MCZ 43625	Indonesia: North Sumatra Prov.: Nias Isl.	x	x			AMF
Parias sumatranus	UMMZ 173496	Malaysia: Pahang	x	x			AMF
Parias sumatranus	UMMZ 225044	Indonesia			x		AMF
Parias sumatranus	UMMZ 225449	Indonesia: Sumatra	x	x			AMF
Parias sumatranus	–	–				x	Malhotra and Thorpe 2004
Parias sumatranus	–	Borneo		x			Vogel 2006
Parias sumatranus	–	Malaysia: Borneo: Sabah: Mt. Kinabalu		x			Vogel 2006
Parias sumatranus	–	Indonesia: Sumatra: Bengkulu Prov.		2 inds.			Vogel 2006
Parias sumatranus	AFS 06.33	Sumatra			x		Guo et al. 2010
Parias sumatranus	AFS 06.57	Sumatra			x		Guo et al. 2009, Guo et al. 2010
Peltopelor macrolepis	AMNH R-43332	India	x	x			AMF
Peltopelor macrolepis	CAS 17276	India: Anaimalai	x				AMF
Peltopelor macrolepis	MCZ 3864	India: Tamil Nadu	x	x			AMF
Peltopelor macrolepis	TCWC 11781, 11783	South India	x	x			AMF
Peltopelor macrolepis	TCWC 11782	–	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Peltopelor macrolepis	USNM 42465, 42466	India: Kerala	x	x			AMF
Peltopelor macrolepis	–	–		x			Vogel 2006
Peltopelor macrolepis	–	–				x	Malhotra and Thorpe 2004
Peltopelor macrolepis	AFS 06.45	South India			x		Guo et al. 2010
Peltopelor macrolepis	AM 02	South India			x		Guo et al. 2010
Popeia barati	–	–		x			Vogel 2006
Popeia barati	–	–				x	Malhotra and Thorpe 2004
Popeia barati	–	Sumatra	19 inds.	x			Vogel et al. 2004
Popeia buniana	ZRC 2.6176	Malaysia: Pahang: Tioman Isl.	x	x			Grismer et al. 2006
Popeia buniana	ZRC 2.3439	Malaysia: Pahang: Tioman Isl.	x				Grismer et al. 2006
Popeia buniana	BMNH uncataloged, 2007	Malaysia: Pahang: Tioman Isl.	x	x			Grismer et al. 2006
Popeia buniana	ZRC 2.6177	Malaysia: Pahang: Tioman Isl.	x				Grismer et al. 2006
Popeia buniana	LSUDPC 1135	–		x			Grismer et al. 2006
Popeia fucata	CAS 242721	Myanmar: Mon State: Thaton Dist.	x	x			AMF
Popeia fucata	CM S-6377	Malaysia: Perak	x	x			AMF
Popeia fucata	FMNH 263429	Thailand: Prachuap Khiri Khan Prov.	x	x			AMF
Popeia fucata	USNM 141751	Malaysia: Selangor	x	x			AMF
Popeia fucata	MNHN 1990.4283	Thailand: Nakhon Si Thammarat Prov	x	x			Vogel et al. 2004
Popeia fucata	ZRC 2.2876, 2.2881, 2.3493	–	x	x			Vogel et al. 2004
Popeia fucata	PSGV 274	–	x	x			Vogel et al. 2004
Popeia fucata	QSMI 510, 511, 519, 520	–	x	x			Vogel et al. 2004
Popeia fucata	BMNH 1974.4995–1974.5000	–	x	x			Vogel et al. 2004
Popeia fucata	BMNH 1988.879–1988.884	–	x	x			Vogel et al. 2004
Popeia fucata	MNHN 1990.4247, 1990.4280, 1990.4281, 1990.4284	–	x	x			Vogel et al. 2004
Popeia fucata	IRSNB 2588, 2589	–	x	x			Vogel et al. 2004
Popeia fucata	ZSM 4/2004	–	x	x			Vogel et al. 2004
Popeia fucata	ZFMK 82855	–	x	x			Vogel et al. 2004
Popeia fucata	–	–		x			Vogel 2006
Popeia nebularis	CAS SU-8863	Malaysia: Pahang: Cameron Highlands	x	x	x		AMF
Popeia nebularis	USNM 142425	Malaysia: Pahang: Cameron Highlands: Mt. Batu Brinchang	x	x			Vogel et al. 2004
Popeia nebularis	ZRC 2.2884, 2.2885, 2.2887	Malaysia: Pahang: Cameron Highlands	x	x			Vogel et al. 2004
Popeia nebularis	PSGV 626	Malaysia: Pahang: Cameron Highlands	x	x			Vogel et al. 2004
Popeia nebularis	MNHN 2004.0501	Malaysia: Pahang: Cameron Highlands	x	x			Vogel et al. 2004
Popeia nebularis	IRSNB 2627	Malaysia: Pahang: Cameron Highlands	x	x			Vogel et al. 2004
Popeia nebularis	ZFMK 82856	Malaysia: Pahang: Cameron Highlands: Mt. Batu Brinchang	x	x			Vogel et al. 2004
Popeia nebularis	–	Malaysia: Pahang: Cameron Highlands		x			Vogel 2006
Popeia nebularis	–	Malaysia: Pahang		x			Vogel 2006
Popeia popeiorum	CAS 205847	Myanmar: Bago Div.	x	x	x		AMF
Popeia popeiorum	CAS 216609, 222195	Myanmar: Mon State	x	x	x		AMF
Popeia popeiorum	CAS 239273	Myanmar: Ayeyarwady Div.: Pathein Dist.	x	x		x	AMF
Popeia popeiorum	FMNH 178655, 178656	Thailand: Chiang Mai Prov.	x	x			AMF
Popeia popeiorum	FMNH 265805	Thailand: Loei Prov.	x	x		x	AMF
Popeia popeiorum	FMNH 271590	Thailand: Nan Prov.: Bo Kluea Dist.	x	x			AMF
Popeia popeiorum	USNM 145481	Malaysia	x	x			AMF
Popeia popeiorum	–	–		x			Vogel 2006
Popeia popeiorum	–	–					Malhotra and Thorpe 2004
Popeia popeiorum	AM 05	Thailand: Chiang Mai Prov.			x		Guo et al. 2009, Guo et al. 2010
Popeia sabahi	CAS 8316	Malaysia: Borneo: Sabah	x	x			AMF
Popeia sabahi	FMNH 240512	Malaysia: Borneo: Sabah: Sipitang Dist.	x	x			AMF
Popeia sabahi	FMNH 67273	Malaysia: Borneo: Sarawak	x		x		AMF
Popeia sabahi	MCZ 43607, 43609, 43610	Malaysia: Borneo: Sabah	x	x			AMF
Popeia sabahi	MCZ 43612	Malaysia: Borneo: Sabah	x	x	x		AMF
Popeia sabahi	UMMZ 82925	Malaysia: Borneo: Sabah	x	x			AMF
Popeia sabahi	USNM 130253	Malaysia: Borneo	x	x			AMF
Popeia sabahi	USNM 134128	Malaysia: Borneo: Sabah	x	x			AMF
Popeia sabahi	–	–				x	Malhotra and Thorpe 2004
Popeia sabahi	–	–		x			Vogel 2006
Popeia sabahi	AFS 06.47	Thailand: Fraser's Hill			x		Guo et al. 2010
Popeia sabahi	AFS 06.36	Malaysia: Selangor			x		Guo et al. 2010
Popeia toba	MSNG 30988, 54282, 54338	Indonesia: Sumatra: North Sumatra Prov.	x	x			David et al. 2009
Popeia toba	NMBE 1018072–1018074	Indonesia: Sumatra: North Sumatra Prov.	x	x			David et al. 2009
Porthidium arcosae	UTA R-55938	Ecuador: Manabí Prov.	x	x			AMF
Porthidium arcosae	–	–		x			Campbell and Lamar 2004

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Porthidium dunni	FMNH 73392	Mexico: Oaxaca: Tehuantepec Dist.	x	x			AMF
Porthidium dunni	UMMZ 82739	Mexico: Oaxaca	x				Campbell and Lamar 2004
Porthidium dunni	–	–		x			Campbell and Lamar 2004
Porthidium hespere	UTA R-4443	Mexico: Colima	x	x			AMF
Porthidium hespere	UTA R4443	Mexico: Colima: Munic. Ixtlahuacan	x				Campbell and Lamar 2004
Porthidium hespere	–	–		x			Campbell and Lamar 2004
Porthidium lansbergii	FMNH 21797	Honduras: Yoro: Subriana Valley	x	x			AMF
Porthidium lansbergii	–	–		x			Campbell and Lamar 2004
Porthidium nasutum	AMNH R-46958	Honduras			x		AMF
Porthidium nasutum	FLMNH 61010	Guatemala or Honduras			x		AMF
Porthidium nasutum	FLMNH 99121, 99200	Honduras			x		AMF
Porthidium nasutum	UTA R-14180	Costa Rica: Cartago Prov.: Turrialba Canton: Pavones Dist.	x	x		x	AMF
Porthidium nasutum	UTA R-14183	Costa Rica: Cartago Prov.: Turrialba Canton: Pavones Dist.				x	AMF
Porthidium nasutum	UTA R-23066, R-24515	–	x	x			AMF
Porthidium nasutum	UTA R-24516	Guatemala: Izabal Dept.	x	x			AMF
Porthidium nasutum	UTA R-31057	Costa Rica: Cartago Prov.	x	x		x	AMF
Porthidium nasutum	–	–		x			Campbell and Lamar 2004
Porthidium nasutum	–	–	29 inds.		2 inds.		Gutberlet 1998
Porthidium nasutum	UTA R-23065	Guatemala: Dept. Izabal		x			Campbell and Lamar 2004
Porthidium ophryomegas	UTA R-14532	–			x		AMF
Porthidium ophryomegas	UTA R-39755	Guatemala: Zacapa Dept.: Cabañas Munic.	x	x		x	AMF
Porthidium ophryomegas	–	–		x			Campbell and Lamar 2004
Porthidium ophryomegas	–	–	9 inds.		x		Gutberlet 1998
Porthidium ophryomegas	UTA R46502	Guatemala: Dept. Zacapa	x				Campbell and Lamar 2004
Porthidium porrasi	UTA R-59119	Costa Rica: Puntarenas Prov.	x	x			AMF
Porthidium porrasi	UTA R-30829	Costa Rica: Puntarenas Prov.: Osa Peninsula	x	x			Lamar and Sasa 2003
Porthidium porrasi	–	–		x			Campbell and Lamar 2004
Porthidium volcanicum	UTA R-24828–R-24830	Costa Rica: Puntarenas Prov.	x	x			AMF
Porthidium volcanicum	UCR 11642	–		x			Campbell and Lamar 2004
Porthidium volcanicum	–	–		x			Campbell and Lamar 2004
Porthidium yucatanicum	FMNH 544, 20621	Mexico: Yucatán	x	x			AMF
Porthidium yucatanicum	FMNH 36181	Mexico: Yucatán			x		AMF
Porthidium yucatanicum	UTA R-16960	Mexico: Campeche	x	x		x	AMF
Porthidium yucatanicum	–	–		x			Campbell and Lamar 2004
Protobothrops cornutus	–	–		x			Vogel 2006
Protobothrops cornutus	MNHN 1937.35	Vietnam	x				Herrmann et al. 2004
Protobothrops cornutus	BMNH 1946.1.19.25	Vietnam: Lai Chau Prov.: Mt. Fan Si Pan	x				Herrmann et al. 2004
Protobothrops cornutus	ZMFK 75067	Vietnam: Mquang Binh Prov.: Phong Nha-Ke Bang Ntl. Park	x	x			Herrmann et al. 2004
Protobothrops elegans	CAS 21946	Japan: Okinawa Pref.: Ryukyu Isls.: Ishigaki Isl.			x		AMF
Protobothrops elegans	CAS 21947, 21954–21956, 21958, 21961, 21962, 21966, 21970	Japan: Okinawa Pref.: Ryukyu Isls.: Ishigaki Isl.	x	x			AMF
Protobothrops elegans	FMNH 75170	Japan: Ryukyu Isls.	x	x		x	AMF
Protobothrops elegans	USNM 133984	Japan: Ryukyu Isls.: Yaeyama Isls.			x		AMF
Protobothrops elegans	–	–		x			Vogel 2006
Protobothrops elegans	AM 07–09	Japan			x		Guo et al. 2010
Protobothrops elegans	AFS 06.27	Japan			x		Guo et al. 2010
Protobothrops elegans	RTV 10	Japan			x		Guo et al. 2010
Protobothrops flavoviridis	–	–		x			Vogel 2006
Protobothrops flavoviridis	SCUM 035056	Japan			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops flavoviridis	FMNH 72584	Japan			x		Guo et al. 2010
Protobothrops flavoviridis	KUZ R48345	Japan			x		Guo et al. 2010
Protobothrops flavoviridis	FLMNH 24047, 24050, 24052, 120226, 120229, 120233	Japan: Kagoshima Pref.: Ryukyu Isls.: Amami Isls.	x	x			AMF
Protobothrops flavoviridis	FLMNH 24049	–	x	x			AMF
Protobothrops flavoviridis	FMNH 72584	Japan: Ryukyu Isls.			x		AMF
Protobothrops flavoviridis	FMNH 74895	Japan: Okinawa Pref.: Ryukyu Isls.: Kume Isl.	x	x			AMF
Protobothrops flavoviridis	TCWC 86183	–			x		AMF
Protobothrops flavoviridis	USNM 133986	–			x		AMF
Protobothrops flavoviridis	USNM 137287	Japan: Ryukyu Isls.	x	x		x	AMF
Protobothrops flavoviridis	USNM 139985	Japan: Ryukyu Isls.			x		AMF
Protobothrops flavoviridis	USNM 297391	–	x	x	x	x	AMF
Protobothrops jerdonii	CAS 224428, 224429	Myanmar: Kachin State: Putao Dist.	x	x			AMF
Protobothrops jerdonii	CAS 90668	Nepal: Central Region: Janakpur Zone	x	x			AMF
Protobothrops jerdonii	FMNH 28199	China			x		AMF
Protobothrops jerdonii	MCZ 163258	China: Hubei Prov.	x	x		x	AMF
Protobothrops jerdonii	UCF CLP921	–	x	x			AMF
Protobothrops jerdonii	USNM 279854, 292049	China	x	x		x	AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Protobothrops jerdonii	USNM 69933, 95668	China	x	x			AMF
Protobothrops jerdonii	–	–		x			Vogel 2006
Protobothrops jerdonii	SCUM 035078	China: Shaanxi			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops jerdonii	SCUM 035028, 035029	China: Sichuan: An Co.			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops jerdonii	SCUM 035041, 035075	China: Sichuan: Huili Co.			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops jerdonii	SCUM 035081	China: Sichuan: Zoigê Co.			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops kaulbacki	CAS 224430	Myanmar: Kachin State: Putao Dist.	x	x			AMF
Protobothrops kaulbacki	–	–		x			Vogel 2006
Protobothrops mangshanensis	CIB no number, ZS 8901–8902	China: Hunan Prov.: Yizhang Co.: Pingheng Dist.	x	x			David and Tong 1997
Protobothrops mangshanensis	–	–		x			Vogel 2006
Protobothrops mangshanensis	SCUM 035024	China: Hunan: Yizhang Co.			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops maolanensis	SYS r000211	China: Guizhou: Libo Co.: Maolan Twnsp.	x	x			Yang et al. 2011
Protobothrops maolanensis	SYS r000210, r000276, r000277	China: Guizhou: Libo Co.: Maolan Twnsp.	x				Yang et al. 2011
Protobothrops mucrosquamatus	AMNH R-33212	China: Fujian Prov.			x		AMF
Protobothrops mucrosquamatus	CAS 232934	Myanmar: Kachin State: Myitkyina Dist.	x	x			AMF
Protobothrops mucrosquamatus	CAS 238906	Myanmar: Mohnyin Dist.: Mohnyin Twnsp.	x	x		x	AMF
Protobothrops mucrosquamatus	FLMNH 13256, 13257, 120355	Taiwan	x	x		x	AMF
Protobothrops mucrosquamatus	FLMNH 13260	Taiwan	x	x			AMF
Protobothrops mucrosquamatus	FMNH 140101	Taiwan			x		AMF
Protobothrops mucrosquamatus	FMNH 16255	China: Sichuan Prov.			x		AMF
Protobothrops mucrosquamatus	MVZ 22324	China: Jiangxi Prov.: Lushan Dist.			x		AMF
Protobothrops mucrosquamatus	MVZ 226628	Vietnam: Vĩnh Phúc Prov.: Tam Đao Dist.	x	x		x	AMF
Protobothrops mucrosquamatus	MVZ 23908	China: Jiangxi Prov.	x	x			AMF
Protobothrops mucrosquamatus	MVZ 241450	China: Hainan Prov.: Hainan Isl.	x	x		x	AMF
Protobothrops mucrosquamatus	–	–		x			Vogel 2006
Protobothrops mucrosquamatus	SCUM 035050	China: Sichuan: Chengdu Sub-Prov. City			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops mucrosquamatus	SCUM 035031, 035032, 035076	China: Sichuan: Hongya Co.			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops mucrosquamatus	SCUM 035026	China: Sichuan: Yibin Pref.-lvl. City			x		Guo and Zhao 2006, Guo et al. 2010
Protobothrops sieversorum	ZFMK 71262	Vietnam: Quang Binh Prov.: Phong Na Nature Reserve	x	x			Ziegler et al. 2000
Protobothrops sieversorum	–	–		x			Vogel 2006
Protobothrops sieversorum	PNNP 00220	Vietnam			x		Guo et al. 2010
Protobothrops tokarensis	FLMNH 120361–120364	Japan: Tokara Isl.	x	x			AMF
Protobothrops tokarensis	FMNH 218975, 218976	–	x	x			AMF
Protobothrops tokarensis	ROM 22881	–	x	x			AMF
Protobothrops tokarensis	TCWC 60446, 60455, 60456	–	x	x			AMF
Protobothrops tokarensis	–	–		x			Vogel 2006
Protobothrops tokarensis	KUZ R21123	Japan			x		Guo et al. 2009, Guo et al. 2010
Protobothrops trungkhanhensis	ZISP 25351	Vietnam: Cao Bang Prov.: Trung Khanh Dist.	x	x			Orlov et al. 2009
Protobothrops trungkhanhensis	IEBR A.0901	Vietnam: Cao Bang Prov.: Trung Khanh Dist.	x	x			Orlov et al. 2009
Protobothrops xiangchengensis	CIB 725048–725055	China: Sichuan: Xiangcheng Co.	x	x			David and Tong 1997
Protobothrops xiangchengensis	–	–		x			Vogel 2006
Protobothrops xiangchengensis	CIB no number	China: Sichuan				x	Guo and Zhang 2001
Protobothrops xiangchengensis	SCUM 035042, 035043, 035046	China: Sichuan: Jiulong Co.			x		Guo and Zhao 2006, Guo et al. 2010
Rhinocerophis alternatus	AMNH R-31737	Brazil			x		AMF
Rhinocerophis alternatus	AMNH R-76209	Paraguay			x		AMF
Rhinocerophis alternatus	CAS uncataloged	–			x		AMF
Rhinocerophis alternatus	FMNH 51663	Brazil			x		AMF
Rhinocerophis alternatus	LACM 146309	Argentina: Entre Ríos Prov.	x	x			AMF
Rhinocerophis alternatus	LSUMZ 27748	Uruguay: Dept. Maldonado	x	x			AMF
Rhinocerophis alternatus	LSUMZ 55460	–			x		AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Rhinocerophis alternatus	UMMZ 62921, 62926, 62927, 79626	Brazil: São Paulo	x	x			AMF
Rhinocerophis alternatus	UMMZ 62923	Brazil: São Paulo	x	x		x	AMF
Rhinocerophis alternatus	UTA R-32427	Brazil: Rio Grande do Sul	x	x			AMF
Rhinocerophis alternatus	UTA R-37709	Brazil: Minas Gerais: Munic. Frutal	x	x		x	AMF
Rhinocerophis alternatus	UTA R-38293	Brazil: São Paulo	x	x		x	AMF
Rhinocerophis alternatus	UTA R-38294	Brazil: São Paulo	x	x			AMF
Rhinocerophis alternatus	UTA R-5602	Paraguay				x	AMF
Rhinocerophis alternatus	–	–		x			Campbell and Lamar 2004
Rhinocerophis ammodytoides	CM 147885	Argentina: Catamarca Prov.	x	x			AMF
Rhinocerophis ammodytoides	LACM 146317	Argentina: San Luis Prov.	x	x			AMF
Rhinocerophis ammodytoides	MVZ 127512	Argentina: Mendoza Prov.: Dept. Las Heras	x	x		x	AMF
Rhinocerophis ammodytoides	MVZ 127513	Argentina: Mendoza Prov.: Dept. Malargüe	x	x			AMF
Rhinocerophis ammodytoides	MVZ 127514	Argentina: Mendoza Prov.: Dept. Malargüe	x	x		x	AMF
Rhinocerophis ammodytoides	MVZ 127518	Argentina: Neuquén Prov., Dept. Zapala	x	x			AMF
Rhinocerophis ammodytoides	MVZ 134149	Argentina: San Luis Prov.	x	x			AMF
Rhinocerophis ammodytoides	TNHC 44803	Argentina: Catamarca Prov.	x	x		x	AMF
Rhinocerophis ammodytoides	UTA R-16334	Argentina: San Luis Prov.	x	x		x	AMF
Rhinocerophis ammodytoides	MACN 32893, 39068	–		x			Carrasco et al. 2010
Rhinocerophis ammodytoides	–	–		x			Campbell and Lamar 2004
Rhinocerophis ammodytoides	MLP-JW 20	–		x			Carrasco et al. 2010
Rhinocerophis ammodytoides	–	–		various inds.			Carrasco et al. 2010
Rhinocerophis cotiara	CM R 364	Brazil: Minas Gerais	x	x			AMF
Rhinocerophis cotiara	FLMNH 39811	Brazil: Santa Catarina	x	x			AMF
Rhinocerophis cotiara	FLMNH 39812	Brazil: São Paulo	x	x			AMF
Rhinocerophis cotiara	FMNH 51662	Brazil			x		AMF
Rhinocerophis cotiara	KU 124648, 124650	Brasil: Santa Catarina	x	x			AMF
Rhinocerophis cotiara	MVZ 200831	Brazil: São Paulo	x	x			AMF
Rhinocerophis cotiara	USNM 100695	Brazil: Santa Catarina	x	x			AMF
Rhinocerophis cotiara	USNM 76317, 100750, 165443	Brazil	x	x			AMF
Rhinocerophis cotiara	–	–		x			Campbell and Lamar 2004
Rhinocerophis cotiara	–	–			2 inds.		Brattstrom 1964
Rhinocerophis fonsecai	CAS 116332	Brazil, São Paulo	x	x			AMF
Rhinocerophis fonsecai	FMNH 171285, 171288	Brazil	x	x			AMF
Rhinocerophis fonsecai	KU 125379	Brasil: São Paulo	x	x			AMF
Rhinocerophis fonsecai	MCZ 20893	Brazil, São Paulo	x	x			AMF
Rhinocerophis fonsecai	UMMZ 129625, 204214	Brazil: São Paulo	x	x			AMF
Rhinocerophis fonsecai	USNM 165449	Brazil	x	x			AMF
Rhinocerophis fonsecai	UTA R-38291, R-38292	Brazil: Minas Gerais	x	x			AMF
Rhinocerophis fonsecai	–	–		x			Campbell and Lamar 2004
Rhinocerophis itapetiningae	FMNH 10815	Brazil: Matto Grosso	x	x	x		AMF
Rhinocerophis itapetiningae	FMNH 2619	Brazil: São Paulo	x	x			AMF
Rhinocerophis itapetiningae	MCZ 20904, 20908, 20910	Brazil: São Paulo	x	x			AMF
Rhinocerophis itapetiningae	UMMZ 62913, 62914	Brazil: São Paulo	x	x			AMF
Rhinocerophis itapetiningae	USNM 38187, 39059, 76320, 165514–165516	Brazil	x	x			AMF
Rhinocerophis itapetiningae	–	–		x			Campbell and Lamar 2004
Rhinocerophis jonathani	UTA R-34564	Bolivia: Cochabamba	x	x			AMF
Rhinocerophis jonathani	MNK R-1000	Bolivia: Dept. Cochabamba: Carrasco Prov.	x	x			Harvey 1994
Rhinocerophis jonathani	MNKR 718, 1618	–			x	x	Carrasco et al. 2009
Rhinocerophis jonathani	CBF 2319	–			x		Carrasco et al. 2009
Rhinocerophis jonathani	–	–		x			Campbell and Lamar 2004
Rhinocerophis jonathani	–	–					Harvey 2005
Rhinocerophis jonathani	–	–	var. inds.	x			Carrasco et al. 2009
Rhinocerophis jonathani	CBF 2318	Bolivia: Dept. Tarija: José María Aviles Prov.	x				Carrasco et al. 2009
Sinovipera sichuanensis	YBU 030116, 071077	China: Sichuan: Hejiang Co.	x	x			Guo and Wang 2011
Sistrurus catenatus	AMNH R-64925	USA: Illinois: Lake Co.				x	AMF/KMD
Sistrurus catenatus	AMNH R-74841, R-75282	–			x		AMF/KMD
Sistrurus catenatus	AMNH R-87494	USA: Kansas: McPherson Co.			x		AMF/KMD

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Sistrurus catenatus	FMNH 11034	USA: Indiana			x		AMF/KMD
Sistrurus catenatus	UCF 2341	USA: Texas: Throckmorton Co.	x	x			AMF/KMD
Sistrurus catenatus	UTA R-11290, R-21924	USA: Texas: Tarrant Co.				x	AMF/KMD
Sistrurus catenatus	UTA R-33955	USA: Texas: Wise Co.				x	AMF/KMD
Sistrurus catenatus	–	–		x			Campbell and Lamar 2004
Sistrurus catenatus	UTA R-21923	USA: Texas: Tarrant Co.		x			Campbell and Lamar 2004
Sistrurus miliarius	AMNH R-140812	–			x		AMF/KMD
Sistrurus miliarius	AMNH R-140854	USA: North Carolina			x		AMF/KMD
Sistrurus miliarius	AMNH R-63825, R-63827	USA: Louisiana				x	AMF/KMD
Sistrurus miliarius	AMNH R-79049	–			x		AMF/KMD
Sistrurus miliarius	FLMNH 143944	USA: Florida: Hamilton Co.			x		AMF/KMD
Sistrurus miliarius	FMNH 21761	USA: Florida			x		AMF/KMD
Sistrurus miliarius	FMNH 98899	USA: North Carolina: Hyde Co.			x		AMF/KMD
Sistrurus miliarius	UCF 2364	USA: Florida: Orange Co.	x	x			AMF/KMD
Sistrurus miliarius	UCF 2367	USA: Florida: Osceola Co.	x	x			AMF/KMD
Sistrurus miliarius	UCF CLP210	–	x	x		x	AMF/KMD
Sistrurus miliarius	UCF CLP212, CLP214	–	x	x			AMF/KMD
Sistrurus miliarius	UCF CLP901	USA: Florida	x	x			AMF/KMD
Sistrurus miliarius	UCF CLP941	USA: Florida: Orange Co.	x	x		x	AMF/KMD
Sistrurus miliarius	UTA R-18364	USA: Florida: Dade Co.				x	AMF/KMD
Sistrurus miliarius	–	–		x			Campbell and Lamar 2004
Sistrurus miliarius	UTA R-19315	USA: Texas: Montague Co.		x			Campbell and Lamar 2004
Trimeresurus andalasensis	SMF 22429	–	x	x			David et al. 2006
Trimeresurus andalasensis	PSGV 548	–	x				David et al. 2006
Trimeresurus andalasensis	ANSP 21536	–	x				David et al. 2006
Trimeresurus andalasensis	ZMB 29641	–	x				David et al. 2006
Trimeresurus andalasensis	NMBE 1018070, 1018071	–	x				David et al. 2006
Trimeresurus andalasensis	–	–		x			Vogel 2006
Trimeresurus andalasensis	ZSM 17/1927	–	x				David et al. 2006
Trimeresurus borneensis	CAS 16860	Malaysia: Borneo: Sarawak	x	x			AMF
Trimeresurus borneensis	FMNH 131847	Malaysia: Borneo: Sarawak			x		AMF
Trimeresurus borneensis	TCWC 81406–81410	Borneo	x	x			AMF
Trimeresurus borneensis	USNM 36277	Malaysia: Borneo: West Kalimantan Prov.	x	x			AMF
Trimeresurus borneensis	–	–		x			Vogel 2006
Trimeresurus borneensis	–	–		x			David et al. 2006
Trimeresurus borneensis	–	–				x	Malhotra and Thorpe 2004
Trimeresurus brongersmai	USNM 104340	Indonesia: Sumatra: North Sumatra	x	x			AMF
Trimeresurus brongersmai	RMNH 5654A	–					David et al. 2006
Trimeresurus brongersmai	–	–		x			Vogel 2006
Trimeresurus brongersmai	–	–					David et al. 2006
Trimeresurus gracilis	MVZ 23905	Taiwan: Chiayi County	x	x			AMF
Trimeresurus gracilis	UMMZ 198961–198965	Taiwan: Nantou County	x	x			AMF
Trimeresurus gracilis	USNM 134034	Taiwan			x		AMF
Trimeresurus gracilis	USNM 152453	Taiwan: Tainan County	x	x			AMF
Trimeresurus gracilis	–	–		x			Vogel 2006
Trimeresurus gracilis	USNM 134034	China: Taiwan					Guo et al. 2009, Guo et al. 2010
Trimeresurus gramineus	AMNH R-57963, R-57964	India: Khandala	x	x			AMF
Trimeresurus gramineus	CAS 17272	Myanmar: Kachin: Putao Dist.	x	x			AMF
Trimeresurus gramineus	FLMNH 20112	India: Kerala	x	x			AMF
Trimeresurus gramineus	FLMNH 21365	India: Maharashtra	x	x			AMF
Trimeresurus gramineus	–	–		x			Vogel 2006
Trimeresurus gramineus	–	–				x	Malhotra and Thorpe 2004
Trimeresurus malabaricus	CAS 104089	India: Tamil Nadu: Kanyakumari Dist.	x	x			AMF
Trimeresurus malabaricus	CAS 125400	India: Kerala	x	x			AMF
Trimeresurus malabaricus	CAS 17273	India: Kerala	x	x		x	AMF
Trimeresurus malabaricus	CAS 17274	India	x	x			AMF
Trimeresurus malabaricus	CM 115132, 115195, 122112, 122113	India: Kerala	x	x			AMF
Trimeresurus malabaricus	MCZ 119447	India: Kerala	x	x			AMF
Trimeresurus malabaricus	MCZ 3845, 3846, 3851, 3883	India: Tamil Nadu	x	x			AMF
Trimeresurus malabaricus	–	–		x			Vogel 2006
Trimeresurus malabaricus	–	–				x	Malhotra and Thorpe 2004
Trimeresurus malabaricus	AFS 06.27	India			x		Guo et al. 2009, Guo et al. 2010
Trimeresurus malabaricus	AM 08, 09	India			x		Guo et al. 2010
Trimeresurus puniceus	LSUMZ 81719	Indonesia: Java: West Java Prov.	x	x			AMF
Trimeresurus puniceus	LSUMZ 81720	Indonesia: Java: West Java Prov.	x	x		x	AMF
Trimeresurus puniceus	MCZ 37799	Indonesia: Sumatra: North Sumatra: Langkat Regency	x	x			AMF
Trimeresurus puniceus	MCZ 8018, 8019	Indonesia: Java: West Java Prov.	x	x			AMF
Trimeresurus puniceus	UMMZ 227772	Indonesia: Java	x	x			AMF
Trimeresurus puniceus	USNM 26544	Indonesia	x	x			AMF

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Trimeresurus puniceus	RMNH 1557	Thailand: Nakhon Si Thammarat Prov.		x			David et al. 2006
Trimeresurus puniceus	–	–			2 inds.		Brattstrom 1964
Trimeresurus puniceus	–	–				x	Malhotra and Thorpe 2004
Trimeresurus puniceus	AFS 06.45	Indonesia			x		Guo et al. 2009, Guo et al. 2010
Trimeresurus puniceus	AM 02, 05	Indonesia			x		Guo et al. 2010
Trimeresurus puniceus	–	Indonesia: Java		5 inds.			Vogel 2006
Trimeresurus puniceus	–	Indonesia: Sumatra		2 inds.			Vogel 2006
Trimeresurus puniceus	–	Indonesia: Java and South Sumatra		x			David et al. 2006
Trimeresurus strigatus	CAS 17271	India: Orissa	x	x		x	AMF
Trimeresurus strigatus	–	–		x			Vogel 2006
Trimeresurus strigatus	–	–				x	Malhotra and Thorpe 2004
Trimeresurus trigonocephalus	CM 67657, 67660, 67714, 68000, 68001	Sri Lanka: Central Prov: Kandy Dist.	x	x			AMF
Trimeresurus trigonocephalus	UMMZ 225453, 225454	–	x	x	x		AMF
Trimeresurus trigonocephalus	UTA R-25103, R-32124	Sri Lanka	x	x			AMF
Trimeresurus trigonocephalus	UTA R-7292, R-8191, R-40461	Sri Lanka	x	x		x	AMF
Trimeresurus trigonocephalus	UTA R-45032	–			x		AMF
Trimeresurus trigonocephalus	–	–		x			Vogel 2006
Trimeresurus trigonocephalus	AFS 06.36, 06.37, 06.47	Sri Lanka					Guo et al. 2010
Trimeresurus wiroti	UTA R-16428	Thailand	x	x		x	AMF
Trimeresurus wiroti	UTA R-31829	Thailand	x	x			AMF
Trimeresurus wiroti	UTA R-31940	Thailand	x	x			AMF
Trimeresurus wiroti	UTA R-38540	Thailand	x	x		x	AMF
Trimeresurus wiroti	UTA R-50567	Thailand	x	x			AMF
Trimeresurus wiroti	UTA R-50574	Thailand	x	x			AMF
Trimeresurus wiroti	SMF 69695	Thailand: Nakhon Si Thammarat Prov.: Chawang Co.	x	x			David et al. 2006
Trimeresurus wiroti	–	–		x			David et al. 2006
Trimeresurus wiroti	–	South Thailand		3 inds.			Vogel 2006
Trimeresurus wiroti	–	Thailand: Trang Prov.		x			Vogel 2006
Tropidolaemus huttoni	BMNH 1948.1.8.75	India: Punjab: Malwa Dist.	x	x			David and Vogel 1998, Vogel 2006
Tropidolaemus huttoni	BMNH 2658	India: Tamil Nadu	x				David and Vogel 1998
Tropidolaemus laticinctus	BMNH 96.12.9.80	Indonesia: Sulawesi: Central Sulawesi Prov.	x	x			Kuch et al. 2007
Tropidolaemus laticinctus	NMW 27963:2	Indonesia: Sulawesi: South Sulawesi Prov.		x			Kuch et al. 2007
Tropidolaemus laticinctus	ZMB 34317	Indonesia: Sulawesi: Central Sulawesi Prov.	x	x			Kuch et al. 2007
Tropidolaemus laticinctus	ZMB 34318	Indonesia: Sulawesi: North Sulawesi Prov.: Subdist. Paleleh		x			Kuch et al. 2007
Tropidolaemus laticinctus	ZMB 47809	no data		x			Kuch et al. 2007
Tropidolaemus laticinctus	–	–	var. inds.				Kuch et al. 2007
Tropidolaemus philippensis	CM R2307, R2314, R2316, S6376	Philippines	x	x			AMF
Tropidolaemus philippensis	FMNH 15017, 53568	Philippine Isls.: Mindanao Isl.	x	x			AMF
Tropidolaemus philippensis	MNHN 4064	Philippines		x			Vogel et al. 2007
Tropidolaemus philippensis	–	–		x			Vogel 2006
Tropidolaemus philippensis	BMNH 1946.1.17.7	Philippines: Mindanao Isl.		x			Vogel et al. 2007
Tropidolaemus subannulatus	CM 147768	Indonesia	x	x			AMF
Tropidolaemus subannulatus	CM R2163	Philippines: Palawan Prov.: Balabac Isl.	x	x			AMF
Tropidolaemus subannulatus	FLMNH 120365	Malaysia: Borneo: Sabah	x	x			AMF
Tropidolaemus subannulatus	FLMNH 50894, 54656	Philippines: Luzon Isls.: Luzon: Camarines Sur Prov.	x	x			AMF
Tropidolaemus subannulatus	FLMNH 67912, 67913	Philippines: Palawan Prov.: Palawan Isl.	x	x		x	AMF
Tropidolaemus subannulatus	FLMNH 79805	Philippines: Luzon Isls.: Luzon: Camarines Sur Prov.	x	x		x	AMF
Tropidolaemus subannulatus	FMNH 71640, 129468	Malaysia: Borneo: Sarawak			x		AMF
Tropidolaemus subannulatus	FMNH 158669, 188496	Malaysia: Borneo: Sarawak	x	x		x	AMF
Tropidolaemus subannulatus	KU 303036	Philippines: Antique Prov.: Munic. Pandan	x	x			AMF
Tropidolaemus subannulatus	KU 303037	Philippines: Negros Oriental Prov: Munic. Valencia	x	x		x	AMF
Tropidolaemus subannulatus	KU 306592, 310176	Philippines: Dinagat Isls. Prov.: Munic. Loreto	x	x			AMF
Tropidolaemus subannulatus	KU 307696	Philippines: Quezon Prov.: Munic. Polillo	x	x			AMF

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Tropidolaemus subannulatus	KU 310863	Philippines: Eastern Samar Prov.: Munic. Taft	x	x		x	AMF
Tropidolaemus subannulatus	KU 311289, 311292	Philippines: Leyte Prov.: Municip. Baybay	x	x			AMF
Tropidolaemus subannulatus	BMNH 1946.1.19.32	–		x			Vogel et al. 2007
Tropidolaemus subannulatus	–	Malaysia: Borneo: Sarawak		2 inds.			Vogel 2006
Tropidolaemus subannulatus	–	Philippines		x			Vogel 2006
Tropidolaemus subannulatus	–	Sulawesi		2 inds.			Vogel 2006
Tropidolaemus wagleri	CAS 16781, 16782	Singapore	x	x			AMF
Tropidolaemus wagleri	CAS SU8317	Singapore: Singapore Isl.	x	x			AMF
Tropidolaemus wagleri	CM 147741	Indonesia: Sumatra	x	x	x		AMF
Tropidolaemus wagleri	FLMNH 88587	Thailand	x	x			AMF
Tropidolaemus wagleri	FMNH 11132, 11133	Singapore	x	x			AMF
Tropidolaemus wagleri	FMNH 179121	Thailand	x	x			AMF
Tropidolaemus wagleri	FMNH 183789–183791	Malaysia	x	x			AMF
Tropidolaemus wagleri	UTA R-45037	Thailand		x	x		AMF
Tropidolaemus wagleri	MNHN 1879.0708	Sumatra: West Sumatra	x	x			Vogel et al. 2007
Tropidolaemus wagleri	–	Indonesia: Sumatra		2 inds.			Vogel 2006
Tropidolaemus wagleri	–	Indonesia: Sumatra: Aceh Prov.: Subdist. Ketambe		x			Vogel 2006
Tropidolaemus wagleri	–	West Malaysia: Cameron Highlands		x			Vogel 2006
Tropidolaemus wagleri	–	West Malaysia: Templer Park		x			Vogel 2006
Vipera ammodytes	UTA R-18216, R-18217	Austria	x	x			AMF
Vipera ammodytes	UTA R-34195	–	x	x		x	AMF
Vipera ammodytes	UTA R-8003, R-8004	Croatia	x	x			AMF
Viridovipera gumprechti	AMNH R-147163	Vietnam: Hà Tính Prov.: Huong Son Dist.	x	x		x	AMF
Viridovipera gumprechti	CAS 230233	Myanmar: Chin State	x	x			AMF
Viridovipera gumprechti	CAS 234873	Myanmar: Chin State	x	x		x	AMF
Viridovipera gumprechti	CAS 235959	Myanmar: Chin State: Phalum Dist.	x	x			AMF
Viridovipera gumprechti	MVZ 226641	Vietnam: Vĩnh Phúc Prov.: Tam Dao Ntl. Park	x	x		x	AMF
Viridovipera gumprechti	ROM 25814	Vietnam: Nghệ An Prov.: Con Cuông Dist.	x	x		x	AMF
Viridovipera gumprechti	ROM 35321	Vietnam: Cao Bắng Prov.	x	x		x	AMF
Viridovipera gumprechti	USNM 70353	Thailand	x	x			AMF
Viridovipera gumprechti	MNHN 1999.9072	Thailand: Loei Prov.	x	x			David et al. 2002
Viridovipera gumprechti	PSUAA 0047	–	x	x			David et al. 2002
Viridovipera gumprechti	RFI 1345	–	x	x			David et al. 2002
Viridovipera gumprechti	MNHN 1999.9073	–	x	x			David et al. 2002
Viridovipera gumprechti	ZFMK 75797	–	x	x			David et al. 2002
Viridovipera gumprechti	–	–				x	Malhotra and Thorpe 2004
Viridovipera gumprechti	AM 07, 09	Thailand: Loei Prov.			x		Guo et al. 2010
Viridovipera gumprechti	RTV 10	Thailand: Loei Prov.			x		Guo et al. 2009, Guo et al. 2010
Viridovipera gumprechti	–	Thailand: Loei Prov.		2 inds.			Vogel 2006
Viridovipera gumprechti	–	Vietnam: Lao Cai Prov.		x			Vogel 2006
Viridovipera medoensis	AMNH R-58532	Myanmar: Kachin State: Myitkyina Dist.	x	x			AMF
Viridovipera medoensis	CAS 221528	Myanmar: Kachin State: Putao Dist.	x	x			AMF
Viridovipera medoensis	CIB no number	China: Tibet					Guo and Zhang 2001
Viridovipera medoensis	CIB 73 II 5208, 73 II 5209	China: Tibet Aut. Region: Mêdog Co.	x	x			David and Tong 1997
Viridovipera medoensis	–	–		x			Vogel 2006
Viridovipera stejnegeri	AMNH R-33769	China: Fujian Prov.			x		AMF
Viridovipera stejnegeri	FLMNH 13262–13264	Taiwan: Taichung Co.	x	x			AMF
Viridovipera stejnegeri	FLMNH 13265, 13267	Taiwan: Pingtung Co.	x	x			AMF
Viridovipera stejnegeri	FLMNH 13266	Taiwan: Yangmingshan Ntl. Park	x	x			AMF
Viridovipera stejnegeri	FMNH 127229, 127233	Taiwan			x		AMF
Viridovipera stejnegeri	FMNH 127238	Taiwan: Taichung Co.			x		AMF
Viridovipera stejnegeri	FMNH 170642	China: Sichuan Prov.	x	x		x	AMF
Viridovipera stejnegeri	FMNH 25195	China: Fujian Prov.			x		AMF
Viridovipera stejnegeri	FMNH 7134	China: Anhui Prov.	x	x			AMF
Viridovipera stejnegeri	MVZ 22326	China: Jiangxi Prov.: Jiujiang City: Lushan Dist.			x		AMF
Viridovipera stejnegeri	UMMZ 71247a-b	China: Jiangsu Prov.: Nanjing City	x	x			AMF
Viridovipera stejnegeri	–	–		x			Vogel 2006
Viridovipera stejnegeri	–	China		x			Vogel 2006
Viridovipera stejnegeri	CIB no number	China: Fujian					Guo and Zhang 2001
Viridovipera stejnegeri	–	China: Guangdong		x			Vogel 2006
Viridovipera stejnegeri	–	China: Hainan		x			Vogel 2006
Viridovipera stejnegeri	SCUM 035079	China: Guangdong			x		Guo and Zhao 2006, Guo et al. 2010
Viridovipera stejnegeri	AM 07	China: Hainan			x		Guo and Zhao 2006, Guo et al. 2010
Viridovipera stejnegeri	RTV 10	China: Hainan			x		Guo and Zhao 2006, Guo et al. 2010

Species	Voucher	Locality	Scales	Color	Bones	Hemipenes	Examiner or Publication
Viridovipera stejnegeri	–	Vietnam: Tam Dao		x			Vogel 2006
Viridovipera stejnegeri	SCUM 035053	China: Sichuan: Hejiang Co.			x		Guo and Zhao 2006, Guo et al. 2010
Viridovipera truongsonensis	ZISP 22931, 22932	Vietnam: Quảng Binh Prov.	x	x			Orlov et al. 2004
Viridovipera truongsonensis	ZISP 22933, 22934	Vietnam: Quảng Binh Prov.	x				Orlov et al. 2004
Viridovipera truongsonensis	VNUH 190606	–	x				Dawson et al. 2008
Viridovipera truongsonensis	–	–		x			Vogel 2006
Viridovipera vogeli	FMNH 180256	Thailand	x	x	x	x	AMF
Viridovipera vogeli	FMNH 180258	Thailand	x	x	x		AMF
Viridovipera vogeli	FMNH 180260, 180269, 180273	Thailand	x	x		x	AMF
Viridovipera vogeli	FMNH 180261	Thailand	x	x	x		AMF
Viridovipera vogeli	FMNH 180263, 180274	Thailand				x	AMF
Viridovipera vogeli	FMNH 258941	Laos	x	x			AMF
Viridovipera vogeli	FMNH 258945, 258946, 258953	Laos	x	x		x	AMF
Viridovipera vogeli	–	–		x			Vogel 2006
Viridovipera vogeli	FMNH 180269	Thailand: Nakhon Ratchasima Prov.					Guo et al. 2010
Viridovipera vogeli	AM 07	Thailand: Nakhon Ratchasima Prov.					Guo et al. 2010
Viridovipera vogeli	RTV 10	Thailand: Nakhon Ratchasima Prov.					Guo et al. 2009, Guo et al. 2010
Viridovipera yunnanensis	AMNH R-21057	China: Yunnan Prov.: Baoshan Pref.: Tengchong Co.	x	x			AMF
Viridovipera yunnanensis	CAS 215141	China: Yunnan Prov.: Nujiang Pref.: Fugong Co.	x	x	x	x	AMF
Viridovipera yunnanensis	CAS 230260	Myanmar: Kachin State	x	x			AMF
Viridovipera yunnanensis	CAS 234261	China: Yunnan Prov.: Baoshan Pref.: Longling Co.	x	x			AMF
Viridovipera yunnanensis	FLMNH 63903	China: Yunnan Prov.	x	x			AMF
Viridovipera yunnanensis	FMNH 7064, 7065	China: Yunnan Prov.	x	x			AMF
Viridovipera yunnanensis	MCZ 14671	China: Yunnan Prov.	x	x			AMF
Viridovipera yunnanensis	–	–		x			Vogel 2006
Viridovipera yunnanensis	SCU M035108, M035114	China: Sichuan			2 inds.		Guo et al. 2006
Viridovipera yunnanensis	SCUM 035037, 035045, 035114	China: Sichuan: Huili Co.					Guo and Zhao 2006, Guo et al. 2010
Viridovipera yunnanensis	SCUM 035077	China: Yunnan: Kunming					Guo and Zhao 2006, Guo et al. 2010

APPENDIX C:
MOLECULAR DATA COLLECTED FOR PHYLOGENY OF CROTALINAE

Species used, voucher data, collecting locality, and GenBank accession numbers for each species analyzed in pitviper phylogeny. Accession numbers labeled TBD are sequences original to this study. Institutional abbreviations are listed in Leviton, Gibbs, Heal & Dawson (1985).

Species	Field ID	Museum ID	Locality	12S	16S	cyt-*b*	ND4	Rag1
Crotalinae								
Agkistrodon bilineatus	Lamar 2		Costa Rica: Guanacaste Prov.	AF156593	AF156572	AY223613	AY156585	TBD
Agkistrodon contortrix	M338		USA: Ohio	AF057229	AF057276	AY223612	AF156576	TBD
Agkistrodon piscivorous	CLP 30 (mtDNA), CLP 74 (Rag1)		USA: South Carolina (mtDNA), USA: Florida (Rag1)	AF057231	AF057278	AY223615	AF156578	TBD
Agkistrodon taylori	CLP 140		Mexico: Tamaulipas	AF057230	AF057230	AY223614	AF156580	TBD
Atropoides indomitus	ENS 10630		Honduras: Dept. Olancho	TBD		DQ061194	DQ061219	
Atropoides mexicanus	CLP 168 (mtDNA), ENS 10512 (Rag1)		Costa Rica: San José Prov. (mtDNA), Mexico: Chiapas (Rag1)	AF057207	AF057254	AY223584	U41871	TBD
Atropoides nummifer	ENS 10515		Mexico: Puebla	DQ305422	DQ305445	EU684273	EU684290	TBD
Atropoides occiduus	ENS 4584 (Rag1)	UTA R-29680 (mtDNA), UTA R-41219 (Rag1)	Guatemala: Dept. Escuintla (mtDNA), unknown (Rag1)	DQ305423	DQ305446	AY220315	AY220338	TBD
Atropoides olmec	JAC 16021 (mtDNA)	UTA R-25113 (mtDNA), UTA R-34158 (Rag1)	Mexico: Veracruz (mtDNA), Guatemala: Dept. Baja Verapaz (Rag1)	AY223656	AY223669	AY223585	AY223632	TBD
Atropoides picadoi	CLP 45 (12S, 16S, cyt-b, Rag1)	MZUCR 11156 (12S, 16S, cyt-b, Rag1), UMMZ 177000 (ND4)	Costa Rica: Alajuela Prov. (12S, 16S, cyt-b, Rag1), Costa Rica: Heredia Prov. (ND4)	AF057208	AF057255	AY223593	U41872	TBD
Bothriechis aurifer	DPL 2984	UTA R-35031	Guatemala	DQ305425	DQ305448	DQ305466	DQ305483	TBD
Bothriechis bicolor	ENS 10507 (mtDNA), DPL 2899 (Rag1)	UTA R-34156 (mtDNA)	Mexico: Chiapas (mtDNA), unknown (Rag1)	DQ305426	DQ305449	DQ305467	DQ305484	TBD

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Bothriechis lateralis	CLP 48	MZUCR 11155	Costa Rica: San José Prov.	AF057211	AF057258	AY223588	U41873	TBD
Bothriechis marchi	San Antonio Zoo 5 (Rag1)	UTA R-52959 (mtDNA)	Guatemala: Dept. Zacapa (mtDNA), unknown (Rag1)	DQ305428	DQ305451	DQ305469	DQ305486	TBD
Bothriechis nigroviridis	CLP 49 (mtDNA), ICP 1068 (Rag1)	MZUCR 11151 (mtDNA)	Costa Rica: San José Prov.	AF057212	AF057259	AY223589	AY223635	TBD
Bothriechis rowleyi	JAC 13295	UTA R-22243	Mexico: Oaxaca	DQ305427	DQ305450	DQ305468	DQ305485	TBD
Bothriechis schlegelii	CLP 51 (mtDNA)	MZUCR 11149 (mtDNA)	Costa Rica: Cariblanco de Sarapiqui (mtDNA), unknown (Rag1)	AF0572113	AF057260	AY223590	AY223636	TBD
Bothriechis supraciliaris	San Vito 5		Costa Rica: Puntarenas Prov.	DQ305429	DQ305452	DQ305470	DQ305487	TBD
Bothriechis thalassinus	ENS 9416 (Rag1)	UTA R-52958 (mtDNA), UTA R-46526 (Rag1)	Guatemala: Dept. Zacapa (mtDNA), Guatemala: Dept. Izabal (Rag1)	DQ305424	DQ305447	DQ305465	DQ305482	TBD
Bothriopsis bilineata	S.2		Brazil: São Paulo	TBD	TBD	TBD	TBD	TBD
Bothriopsis chloromelas		LSUMZ 41037	Peru: Pasco Region	DQ305430	DQ305453	DQ305471	DQ305488	
Bothriopsis oligolepis	WW 2957		Peru: Cuzco Region			TBD	TBD	
Bothriopsis pulchra	JM 78		Ecuador	JN870179		TBD	TBD	
Bothriopsis taeniata	–		Suriname	AF057215	AF057262	AY233592	AY223637	TBD
Bothrocophias campbelli	INHMT, uncataloged		Ecuador: Chimborazo Prov.			AF292584	AF292622	
Bothrocophias hyoprora	unknown (mtDNA), WED 59884 (Rag1)		Colombia: Dept. Amazonas (mtDNA), Peru: Loreto Region (Rag1)	AF057206	AF057253	AY223593	U41886	TBD
Bothrocophias microphthalmus		LSUMZ H9372	Peru: Pasco Region	AY223657	AY223670	AY223594	AY223638	TBD
Bothrocophias myersi			–					

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Bothropoides alcatraz	CBGM baz001		Brazil: São Paulo: Ilha de Alcatrazes			AY865820		
Bothropoides diporus	PT 3404		Argentina: La Rioja Prov.	DQ305431	DQ305454	DQ305472	DQ305489	TBD
Bothropoides erythromelas	RG 829		Brazil: Algoas	AF057219	AF057266	AY223600	U41877	TBD
Bothropoides insularis	WW		Brazil: São Paulo: Ilha Queimada Grande	AF057216	AF057263	AY223596	AY223641	
Bothropoides jararaca	(19)6		Brazil: São Paulo	EU867254	EU867266	EU867278	EU867290	
Bothropoides lutzi			–					
Bothropoides marmoratus			–					
Bothropoides mattogrossensis			–					
Bothropoides neuwiedi		IB 5555	Brazil: São Paulo			AF292585	AF292623	
Bothropoides pauloensis	CLP 3 (mtDNA), B941 (Rag1)		unknown (mtDNA), Brazil: São Paulo (Rag1)	EU867260	EU867272	EU867284	EU867296	TBD
Bothropoides pubescens	SC N132 (mtDNA), SC N331 (Rag1)		Uruguay: Dept. Rocha (mtDNA), Uruguay: Dept. Canelones (Rag1)	JN870180	JN870192	JN870200	TBD	TBD
Bothrops andianus		Corbidi 8355	–	TBD	TBD	TBD	TBD	
Bothrops asper	CLP 50	MZUCR 11152	Costa Rica: Puntarenas Prov.	AF057218	AF057265	AY223599	U41876	TBD, EU402838 in part
Bothrops atrox	WW 743		–	AY223659	AY223672	AY223598	AY223641	TBD
Bothrops barnetti	WW 2060		Peru	TBD	TBD	TBD	TBD	
Bothrops brazili		RWM 17831 (from USNM)	Venezuela: Amazonas	EU867252	EU867264	EU867276	EU867288	TBD

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Bothrops caribbaeus	released after sampling		Saint Lucia			AF292598	AF292636	
Bothrops jararacussu	DPL 104		–	AY223661	AY223674	AY223602	AY223643	TBD
Bothrops lanceolatus	unknown		Martinique			AF292599	AF292637	
Bothrops leucurus	CLP 195		–	EU867255	EU867267	EU867279	EU867291	TBD
Bothrops marajoensis	unknown		–			AF292605	AF292643	
Bothrops moojeni	ITS 418		Brazil: São Paulo	EU867257	EU867269	EU867281	EU867293	TBD
Bothrops osbornei	FHGO live 2166		Ecuador: Pichincha Prov.			AF292595	AF292633	
Bothrops pictus	WW 2471	Corbidi 2066	–		TBD	TBD	TBD	
Bothrops punctatus	FHGO live 2452		–			AF292594	AF292632	
Bothrops roedingeri	WW 2479		–				TBD	
Calloselasma rhodostoma		UTA R-22247	–	AF057190	AF057237	AY223562	U1878	TBD
Cerrophidion godmani	ENS 5857 (mtDNA), ENS 7005 (Rag1)	UTA R-40008 (mtDNA), UTA R-39567 (Rag1)	Guatemala: Dept. Baja Verapaz (mtDNA), Guatemala: Dept. Guatemala (Rag1)	DQ305419	DQ305442	AY220325	AY220348	TBD
Cerrophidion petlalcalensis	ENS 10528		Mexico: Veracruz	DQ305420	DQ305443	DQ061202	DQ061227	TBD
Cerrophidion sasai	CLP 46	MZUCR 11153	Costa Rica: San José Prov.	AF057203	AF057250	AY223578	U41879	TBD
Cerrophidion tzotzilorum	ENS 10529 (mtDNA), ENS 10530 (Rag1)		Mexico: Chiapas	JN870182	JN870193	DQ061203	DQ061228	TBD
Cerrophidion wilsoni	ENS 10632		Honduras: Dept. Francisco Morazán			EU684286	EU684301	
Crotalus adamanteus	CLP 4		USA: Florida	AF057222	AF057269	AY223605	U41880	TBD

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Crotalus aquilus		ROM 18114 (12S, 16S, cyt-b), ROM 42394 (ND4)	Mexico: Distrito Federal (12S, 16S, cyt-b), Mexico: Aguascalientes (ND4)	AF259231	AF259124	AF259161	HQ257762	
Crotalus atrox	CLP 64		USA: Texas	AF0572225	AF057272	AY223608	AY223646	TBD
Crotalus basiliscus		ROM 18188 (12S, 16S, cyt-b), unknown (ND4)	Mexico: Nayarit	AF259244	AF259136	AF259174	AY704894	
Crotalus catalinensis		ROM 18250, BYU 34641-42	Mexico: Baja California Sur: Santa Catalina Isl.	AF259259	AF259151	AF259189		
Crotalus cerastes		ROM FC-2099 (12S), ROM 19745 (16S, cyt-b)	USA: California	AF259235	AF259128	AF259165		
Crotalus cerberus	CP 016		USA: Arizona			AF147859	AF194150	
Crotalus culminatus	WW 3291	ROM 18261 (mtDNA)	Mexico: Morelos	AF259247	AF259139	AY704830	AY704880	TBD
Crotalus durissus	CFLZoo (Rag1)		Venezuela (mtDNA), unknown (Rag1)			AF259177	TBD	
Crotalus enyo		ROM FC-441 (12S), ROM 13648 (16S, cyt-b)	Mexico: Baja California Sur	AF259245	AF259137	AF259175		
Crotalus horridus		UTA R-14697 (12S, 16S, cyt-b), TNHC 65471 (ND4, Rag1)	USA: Arkansas (12S, 16S, cyt-b), USA: Texas (ND4, Rag1)	AF259252	AF259144	AF259182	JN870207	TBD
Crotalus intermedius	JAC 8881	TNHC	Mexico: Oaxaca	TBD	TBD	TBD	JN870208	TBD
Crotalus lepidus		ROM 18128 (12S, 16S, cyt-b), unknown (ND4), TNHC 65409 (Rag1)	Mexico: Chihuahua (12S, 16S, cyt-b), USA: New Mexico (ND4), USA: Texas (Rag1)	AF259230	AF259123	AF259160	U41881	TBD

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Crotalus mitchelli		ROM 18178	USA: California	AF259250	AF259142	AF259180		
Crotalus molossus	CLP 66		USA: Texas	AF057224	AF057271	AY223607	AY223645	TBD
Crotalus oreganus	CP 014 (ND4)	ROM 19656 (12S, 16S, cyt-b)	USA: California (12S, 16S, cyt-b), Mexico: Baja California: Coronado Sur Isl. (ND4)	AF259253	AF259145	AF259183	AF194149	
Crotalus polystictus		ROM FC-263 or ROM 18139	Mexico: Distrito Federal	AF259236	AF259129	AF259166		
Crotalus pricei		ROM FC-2144 or ROM 18158	Mexico: Nuevo León	AF259237	AF259130	AF259167		
Crotalus pusillus		ROM FC-271 (12S, 16S, cyt-b), ROM 47056 (ND4)	Mexico: Michoacán	AF259229	AF259122	AF259159	HQ257880	
Crotalus ravus	OFV 296 (Rag1)	UTA-live (mtDNA)	Mexico: Puebla (mtDNA), unknown (Rag1)	AF057226	AF057273	AY223609	AY223647	TBD
Crotalus ruber		ROM 18197-98 or ROM 18207 (12S, 16S, cyt-b), RWV 2001-08 (ND4)	USA: California	AF259261	AF259153	AF259191	DQ679838	
Crotalus scutulatus		ROM 18210 or ROM 18218 (12S, 16S, cyt-b), UTEP CRH-153 (ND4)	USA: Arizona (12S, 16S, cyt-b), USA: New Mexico (ND4)	AF259254	AF259146	AF259184	AF194167	

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Crotalus simus	WW-1321 (12S, 16S), 1097 (cyt-b, ND4), MSM 192 (Rag1)		Costa Rica: Guanacaste Prov. (12S, 16S), Costa Rica: Puntarenas Prov. (cyt-b, ND4), Guatemala: Dept. Zacapa (Rag1)	EU624240	EU624274	EU624302	AY704885	TBD
Crotalus tigris	CLP 169		USA: Arizona	AF057223	AF057270	AY223606	AF156574	TBD
Crotalus totonacus	SD		Mexico: Tamaulipas			AY704837	AY704887	
Crotalus transversus	KZ shed skin		Mexico	AF259239		AF259169		
Crotalus triseriatus	YMH 47 (Rag1)	ROM 18121 (12S, 16S, cyt-b), ROM 18120 (ND4)	Mexico: Distrito Federal (12S, 16S, cyt-b), Mexico (ND4), unknown (Rag1)	AF259233	AF259126	AF259163	HQ257879	TBD
Crotalus tzabcan	255, 258-Peter Singfield live coll.		Belize: Corozal Dist.			AY704806	AY704856	
Crotalus viridis	CP 048	UTEP 17625	USA: Colorado	DQ020027		AF147866	AF194157	
Crotalus willardi	HWG 2575 (12S, 16S, cyt-b), W9306 (ND4, Rag1)	TNHC (ND4, Rag1)	USA: Arizona	AF259242	AF259134	AF259172	JN870209	TBD
Cryptelytrops albolabris	AM A165 (mtDNA)	ROM 16497 (Rag1)	Thailand: Loei Prov. (mtDNA), unknown (Rag1)	AF517169	AF517182	AF517185	AF517214	TBD
Cryptelytrops andersoni	AM A77 (12S, 16S, ND4), AM A76 (cyt-b)		India: Andaman Is.	AY352801	AY352740	AF171922	AY352835	
Cryptelytrops cantori	AM A85 (mtDNA)		India: Nicobar Is.	AY352802	AY352741	AF171889	AY352836	TBD

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Cryptelytrops erythrurus	AM B220 (mtDNA)	CAS 204989 (Rag1)	Bangladesh: Chittagong Div. (mtDNA), Myanmar: Rakhine State (Rag1)	AY352800	AY352739	AY352768	AY352634	TBD
Cryptelytrops fasciatus	AM B212		Indonesia: Tanadjampea Isl.	GQ428492	GQ428466	GQ428475	GQ428482	
Cryptelytrops insularis	AM A109		Indonesia: Java	AY352799	AY352738	AY352767	AY352833	
Cryptelytrops kanburiensis	AM B522		Thailand	AY289219	AY352737	AY289225	AY289231	
Cryptelytrops macrops	AM B27 (mtDNA), AM B72 (Rag1)		Thailand: Bangkok (mtDNA), unknown (Rag1)	AF517163	AF517176	AF517184	AF517219	TBD
Cryptelytrops pupureomaculatus	AM B418 (mtDNA)	CAS 212246 (mtDNA), CAS 206604 (Rag1)	Myanmar: Ayeyarwade Region	AY352807	AY352746	AY352772	AY352841	TBD
Cryptelytrops septentrionalis	AM A100		Nepal: Central Region: Janakpur Zone	AY059543	AY059559	AF171909	AY059592	
Cryptelytrops venustus	AM A241		Thailand: Nakhon Si Thammarat Prov.	AY293931	AY352723	AF171914	AY293930	
Deinagkistrodon acutus	CLP 28		China	AF057188	AF057235	AY223560	U41883	TBD
Garthius chaseni	AM B306		Malaysia: Sabah	AY352791	AY352729	AY352760	AY352825	
Gloydius blomhoffii	CLP 44		–	TBD	TBD	TBD	TBD	TBD
Gloydius brevicaudus	AM B525		China	AY352781	AY352720	AY352752	AY352815	
Gloydius halys caraganus	–		Kazakhstan	AF057191	AF057238	AY223564	AY223621	
Gloydius intermedius	unknown (12S, 16S, cyt-b), NNU 95050 (ND4)		Japan (12S, 16S, cyt-b), Mongolia (ND4)	JN870184	JN870194	JN870201	EF012788	
Gloydius monticola	Zhou, J., Zhang, Y. and Huang, M., unpub.		–			AF182530		
Gloydius saxatilis	60588-2, Alec		–	JN870185	JN870195	JN870202	JN870210	TBD

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Gloydius shedaoensis		ROM 20468	China: Liaoning Prov.	AF057194	AF057241	AY223566	AY223623	TBD
Gloydius strauchi		ROM 20473 (mtDNA), MVZ 216826 (Rag1)	China: Sichuan Prov.	AF057192	AF057239	AY223563	AY223620	AY662614
Gloydius tsushimaensis	–		–	JN870186	JN870196	JN870203	JN870211	
Gloydius ussuriensis		ROM 20452	China: Jilin Prov.	AF057193	AF057240	AY223565	AY223622	TBD
Himalayophis tibetanus	AM B258	ZMB 65641	Nepal: Helambu	AY352776	AY352715	AY352749	AY352810	
Hypnale hypnale	CLP 164		Sri Lanka: Western Prov.	AF057189	AF057236	AY223561	U41884	TBD
Lachesis acrochorda	CLP 319		Colombia	JN870187	JN870197	JN870197	JN870212	TBD
Lachesis melanocephala	–		Costa Rica: Peninsula de Oro			U96018	U96028	
Lachesis muta	Cadle 135		Peru	AF057221	AF057268	AY223604	AY223644	TBD
Lachesis stenophrys	–		Costa Rica: Limón Prov.	AF057220	AF057267	AY223603	U41885	TBD
Mixcoatlus barbouri		MZFC 21432	Mexico: Guerrero	HM363639	HM363640	HM363641	HM363642	
Mixcoatlus browni		MZFC 21431	Mexico: Guerrero	HM363643	HM363644	HM363645	HM363646	
Mixcoatlus melanurus	RLG 1086	UTA R-34605	Mexico	AF057210	AF057257	AY223587	AY223634	TBD
Ophryacus undulatus	CLP 73		Mexico	AF057209	AF057256	AY223586	AY223633	TBD
Ovophis monticola	JBS 16330	CAS 215050	China: Yunnan Prov.	DQ305416	DQ305439	DQ305462	DQ305480	TBD
Ovophis okinavensis	CLP 162		USA: Louisiana	AF057199	AF057246	AY223573	AY223627	TBD
Parias flavomaculatus	AM B3		Philippines: Luzon	AY059535	AY059551	AF171916	AY059584	
Parias hageni	AM B33		Thailand: Songhkla Prov.	AY059536	AY059552	AY059567	AY059585	
Parias malcolmi	AM B295		Malaysia: Sabah	AY371758	AY371793	AY371822	AY371860	
Parias schultzei	AM B210		Philippines: Palawan	AY352785	AY352725	AY352756	AY352819	
Parias sumatranus	AM B367		Indonesia: Sumatra: Bengkulu Prov.	AY371765	AY371791	AY371824	AY371864	

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Popeia barati	AM B361		Indonesia: Sumatra: Bengkulu Prov.	AY371753	AY371769	AY371801	AY371837	
Popeia buniana	AM B519		Malaysia: Pahang: Tioman Isl.	AY371752	AY371778	AY371818	AY371853	
Popeia fucata	AM A203		Thailand: Nakhon Si Thammarat Prov.	AY059537	AY059553	AY371796	AY059588	
Popeia nebularis	AM A197		Malaysia: Cameron Highlands	AY371746	AY371773	AY371808	AY371846	
Popeia popeiorum	AM B34		Thailand: Phetchaburi Prov.	AY059542	AY059558	AY059572	AY059591	
Popeia sabahi	AM B338		Malaysia: Sabah	AY371733	AY371785	AY371798	AY371835	
Porthidium arcosae	WW 750		Ecuador	AY223655	AY223668	AY223582	AY223631	TBD
Porthidium dunni	ENS 9705		Mexico: Oaxaca	AY223654	AY223667	AY223581	AY223630	
Porthidium hespere	UOGV 726		–			EU017534	EU016099	
Porthidium lansbergii	WW 787		Venezuela: Falcón	EU624242	EU624276	AY713375	AF393623	
Porthidium nasutum	CLP 52 (mtDNA), WWL (Rag1)	MZUCR 11150 (mtDNA)	Costa Rica: Limón Prov. (mtDNA), Costa Rica: Puntarenas Prov. (Rag1)	AF057204	AF057251	AY223579	U41887	TBD
Porthidium ophryomegas	MSM 23 (Rag1)	UMMZ 210276 (mtDNA)	Costa Rica: Guanacaste Prov. (mtDNA), Guatemala: Dept. Zacapa (Rag1)	AF057205	AF057252	AY223580	U41888	TBD
Porthidium porrasi	MSM		Costa Rica: Puntarenas Prov.	DQ305421	DQ305444	DQ061214	DQ061239	
Porthidium yucatanicum	JAC 24438		Mexico: Yucatán	JN870189	JN870198	DQ061215	DQ061244	TBD
Protobothrops cornutus	AM B350	ZMFK 75067	Vietnam: Phong Nha-Kẻ Ntl. Park	AY294276	AY294267	AY294272	AY294262	
Protobothrops elegans		UMMZ 199970	Japan: Ryukyu Isls.: Ishigaki Isl.	AF057201	AF057248	AY223575	U41893	

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Protobothrops flavoviridis		UMMZ 199973	Japan: Ryukyu Isls.: Tokunoshima Isl.	AF057200	AF057247	AY223574	U41894	
Protobothrops jerdonii		CAS 215051	China: Yunnan Prov.	AY294278	AY294269	AY294274	AY294264	
Protobothrops kaulbacki	SYNU 0400II30		China	DQ666056	DQ666055	DQ666060	DQ666057	
Protobothrops mangshanensis	AM B300		China: Hunan Prov.	AY352787	AY352726	AY352758	AY352821	
Protobothrops mucrosquamatus	AM B106 (mtDNA), HWG (Rag1)		Vietnam: Vĩnh Phúc Prov. (mtDNA), unknown (Rag1)	AY294280	AY294271	AY294275	AY294266	TBD
Protobothrops sieversorum	AM B162		Central Vietnam	AY352782	AY352721	AY352753	AY352816	
Protobothrops tokarensis	FK 1997 (mtDNA)	ROM 22881 (Rag1)	Japan: Ryukyu Isls.: Takarajima (mtDNA), unknown (Rag1)	AF057202	AF057249	AY223576	AY223628	TBD
Protobothrops xiangchengensis	SCUM 035046		–	AY763189	AY763208	DQ666062	DQ666059	
Rhinocerophis alternatus	DPL 2879		–	AY223660	AY223673	AY223601	AY223642	TBD
Rhinocerophis ammodytoides	REE 206 (Rag1)	MVZ 223514 (mtDNA)	Argentina: Neuquén Prov. (mtDNA), Argentina: Catamarca Prov. (Rag1)	AY223658	AY223671	AY223595	AY223639	TBD
Rhinocerophis cotiara	WW (mtDNA), CLP 444 (Rag1)		Brazil (mtDNA), Brazil: São Paulo (Rag1)	AF057217	AF057264	AY223597	AY223640	TBD
Rhinocerophis fonsecai	IB 55543		Brazil: São Paulo			AF292580	AF292618	
Rhinocerophis itapetiningae	ITS 427 (mtDNA), 83E (Rag1)		Brazil: São Paulo	EU867253	EU867265	EU867277	EU867289	TBD
Sinovipera sichuanensis	GP7	YBU 030116	China: Sichuan Prov.	HQ850445	HQ850446	HQ850447	HQ850449	
Sistrurus catenatus	M502		USA: Texas	AF057227	AF057274	AY223610	AY223648	TBD

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Sistrurus miliarius	M504 (Rag1)	UTA-live (mtDNA)	USA: Florida (mtDNA), unknown (Rag1)	AF057228	AF057275	AY223611	U41889	TBD
Trimeresurus borneensis	AM B301		Malaysia: Sabah	AY352783	AY352722	AY352754	AY352817	
Trimeresurus gracilis	NTNUB 200515		Taiwan	DQ305415	DQ305438	DQ305460	DQ305478	TBD
Trimeresurus gramineus	AM A220		India: Tamil Nadu	AY352793	AY352731	AY352761	AY352827	
Trimeresurus malabaricus	AM A218		India: Tamil Nadu	AY059548	AY059564	AY059569	AY059587	
Trimeresurus puniceus	AM B213		Indonesia	AF517164	AF517177	AF517192	AF517220	
Trimeresurus trigonocephalus	AM A58		Sri Lanka: Sabaragamuwa Prov.	AY059549	AY059565	AF171890	AY059597	
Trimeresurus wiroti			Thailand: Nakhon Si Thammarat Prov.			DQ646788		
Tropidolaemus subannulatus	CLP141		Indonesia: Borneo: West Kalimantan Prov.	AF057198	AF057245	AY223571	AY223625	TBD
Tropidolaemus wagleri	AM-B132		Malaysia: Perak	AF517167	AF517180	GQ428472	AF517223	
Viridovipera gumprechti	AM-A164		Thailand: Loei Prov.	AF517168	AF517181	AY352766	AF157224	
Viridovipera medoensis	AM-B416	CAS221528	Myanmar: Kachin State	AY352797	AY352735	AY352765	AY352831	
Viridovipera stejnegeri	AM-A160		Taiwan: Taipei	AY059539	AY059555	AF171896	AY059593	
Viridovipera truongsonensis	AM-B659	VNUH 190606	Vietnam: Quảng Bình Prov.	EU443817	EU443818	EU443815	EU443816	
Viridovipera vogeli	AM-B97		Thailand: Nakhon Ratchasima Prov.	AY059546	AY059562	AY059574	AY059596	
Viridovipera yunnanensis	GP37		China: Sichuan Prov.	EU443811	EU443812	EF597522	EF597527	
Azemiopinae								
Azemiops feae	CLP157		China	AF057187	AF057234	AY223559	U41865	TBD, EU402836 in part

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Viperinae outgroups								
Atheris ceratophora	Unknown (mtDNA), CLP 920 (Rag1)		–	DQ305410	DQ305433	DQ305456	DQ305474	TBD
Atheris nitschei		CAS 201653 (mtDNA), R-970152 (Rag1)	Uganda: Kabale Dist. (mtDNA), unknown (Rag1)	AY223650	AY223663	AY223557	AY223618	TBD
Atheris squamigera		CAS 207866	Equatorial Guinea: Bioko Sur Prov.	TBD	TBD	TBD	TBD	TBD
Bitis arietans			Togo	AF057185	AF57232	AY223558	AY223619	TBD
Bitis nasicornis		CAS 207874	Equatorial Guinea: Bioko Sur Prov.	DQ305411	DQ305434	DQ305457	DQ305475	TBD
Bitis peringueyi		CAS 193863	South Africa: Cape Prov.	DQ305412	DQ305435	DQ305458	DQ305476	TBD
Causus defilippi	CLP 154		Tanzania	AF057186	AF057233	AY223556	AY223617	TBD
Causus resimus	CLP 79		Africa	AY223649	AY223662	AY223555	AY223616	TBD
Causus rhombeatus	Unknown		Africa	DQ305409	DQ305432	DQ305455	DQ305473	TBD
Cerastes cerastes	WW 1640	Latoxan, live coll. 0504-2	Egypt	EU624254	EU624288	EU624308	EU624222	EU852329
Cerastes gasperettii	CLP 910 (12S), HLMD RA-1593 (16S, cyt-b)		–	JN870181	AJ275756	AJ275704		
Daboia russelli	HLMD RA-2899		Pakistan		AJ275776	AJ275723		
Daboia siamensis	JBS 1019, MS 205253	CAS 205253	Myanmar: Mandalay	DQ305413	DQ305436	DQ305459	DQ305477	TBD
Echis carinatus	Latoxan, live coll. 0012-74 (mtDNA), WW 1668 (Rag1)		Pakistan (mtDNA), United Arab Emirates (Rag1)	EU624255	EU624289	EU624309	EU624223	EU852325
Echis pyramidum	WW 1611 (mtDNA), WW 1521 (Rag1)		Egypt (mtDNA), Kenya (Rag1)	EU624258	EU624292	EU624312	EU624226	EU852326

Species	Field ID	Museum ID	Locality	12S	16S	cyt-b	ND4	Rag1
Macrovipera lebetina	Latoxan live coll. 0413-2 (12S, 16S, ND4), G. Nilson private coll. (cyt-b)		Turkmenistan : Kopet Dag (12S, 16S, ND4), Uzbekistan: Nuratau Biosphere Reserve (cyt-b)	EU624260	EU624294	AJ275713	EU624228	
Vipera ammodytes	Liverpool School of Tropical Medicine, live coll., Va1		–	EU624266	EU624297	EU624314	EU624232	

APPENDIX D:
SUPPLEMENTAL PHYLOGRAMS SUPPORTING BOTHROPOID TAXONOMY

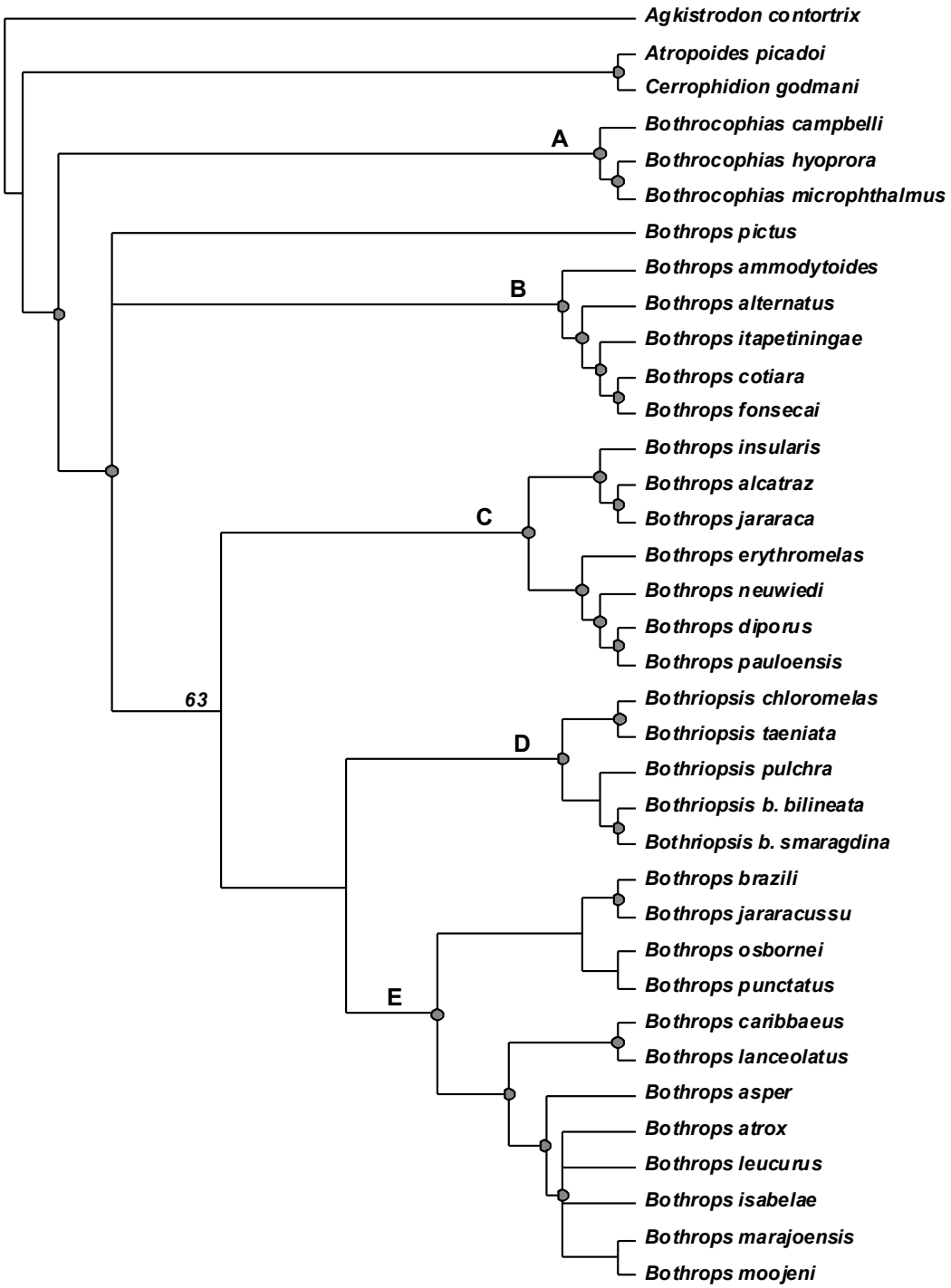

Fig. S-1. Majority-rule consensus cladogram of six most parsimonious trees from analysis excluding taxa with morphological data only (analysis 10). Cladogram derived from analysis of 2343 bp of mitochondrial DNA and 85 gap weighted or majority coded morphological characters (3083 steps, CI = 0.399 RI = 0.533). Bootstrap support above 50% shown above nodes. Gray circles indicate bootstrap values of 70 or greater. Bootstrap values 56 for sister relationship of *Bothrops pictus* to lineage B and 57 for clade containing *B. osbornei, B. punctatus, B. caribbaeus, B. lanceolatus, B. asper, B. atrox, B. leucurus, B. isabelae, B. marajoensis,* and *B. moojeni*; these relationships were not found in the consensus of shortest trees. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

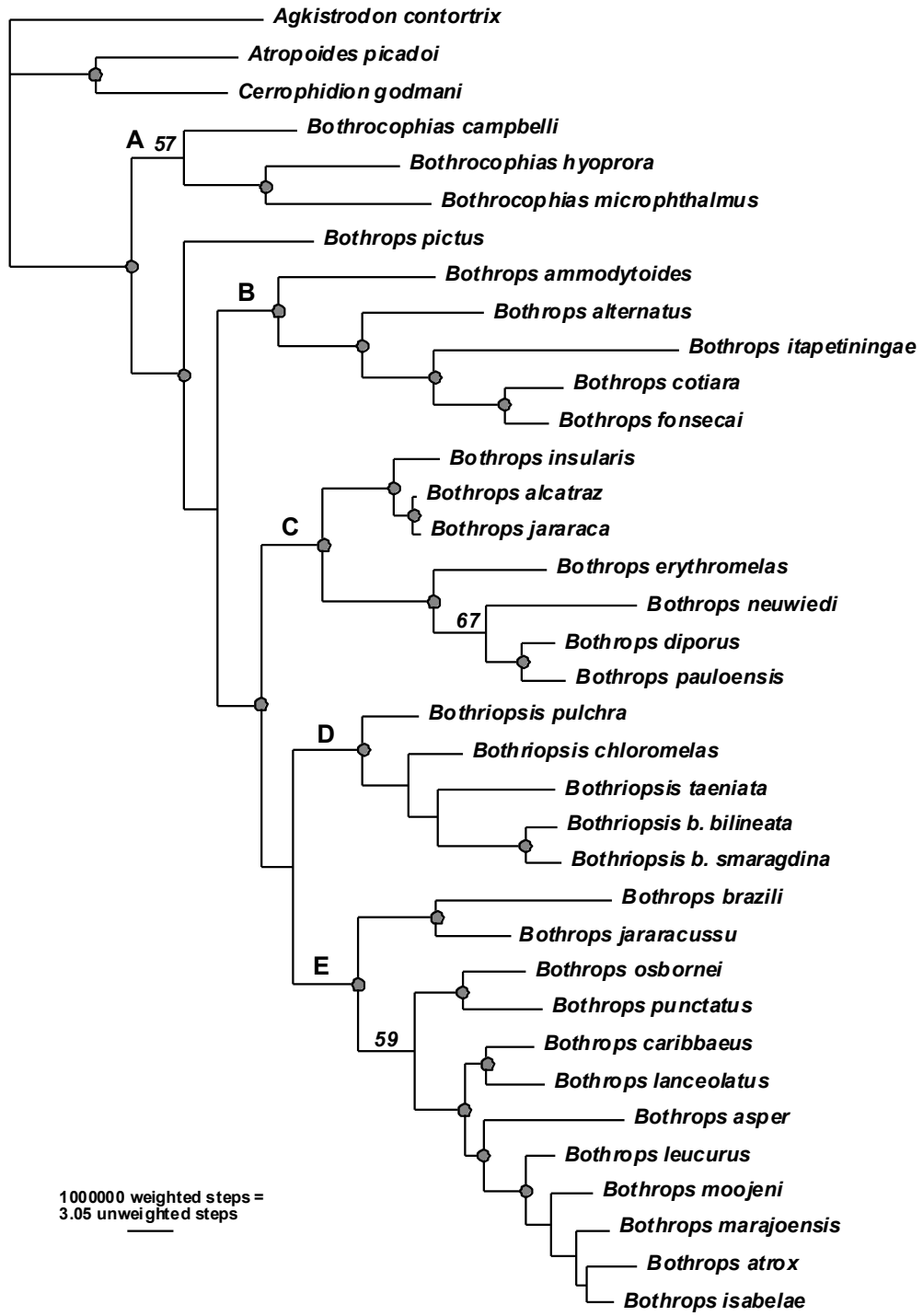

Fig. S-2. Phylogram of single most parsimonious tree from analysis excluding taxa with morpholgical data only (analysis 9). Phylogram derived from analysis of 2343 bp of mitochondrial DNA and 85 generalized frequency coded morphological characters (109,284,371 weighted steps = 3335 unweighted steps, CI = 0.468, RI = 0.520). Bootstrap support above 50% shown above nodes. Gray circles indicate bootstrap values of 70 or greater. Bootstrap value 69 for sister relationship of *Bothriopsis chloromelas* and *B. taeniata*; this relationship was not found in the shortest tree. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

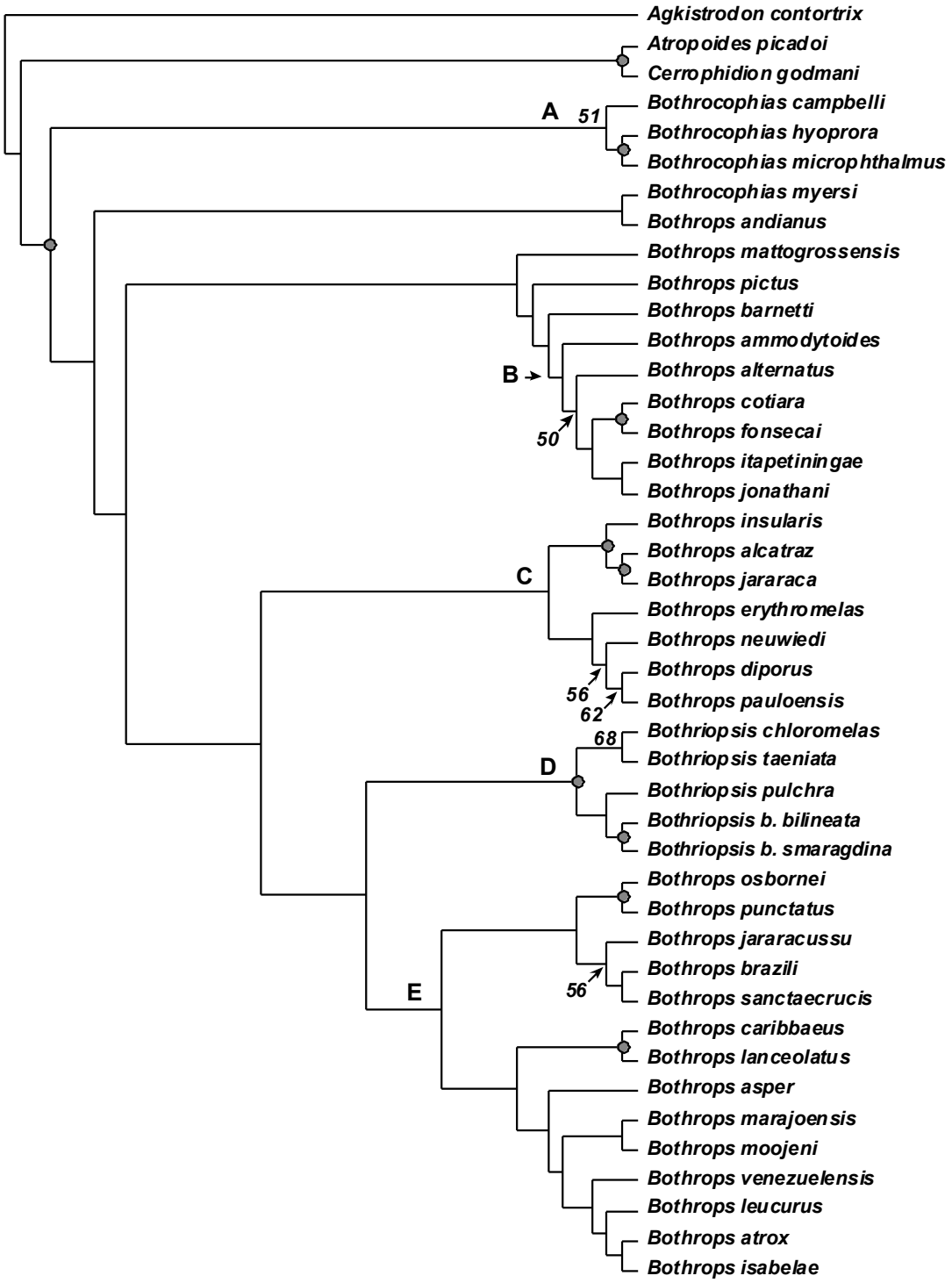

Fig. S-3. Majority rule consensus cladogram of ten most parsimonious trees from analysis including taxa with morphological data only (analysis 7). Cladogram derived from analysis of 2343 bp of mitochondrial DNA and 85 gap weighted or majority coded morphological characters (3164 steps, CI = 0.390, RI = 0.531). Bootstrap support above 50% shown above nodes. Gray circles indicate bootstrap values of 70 or greater. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

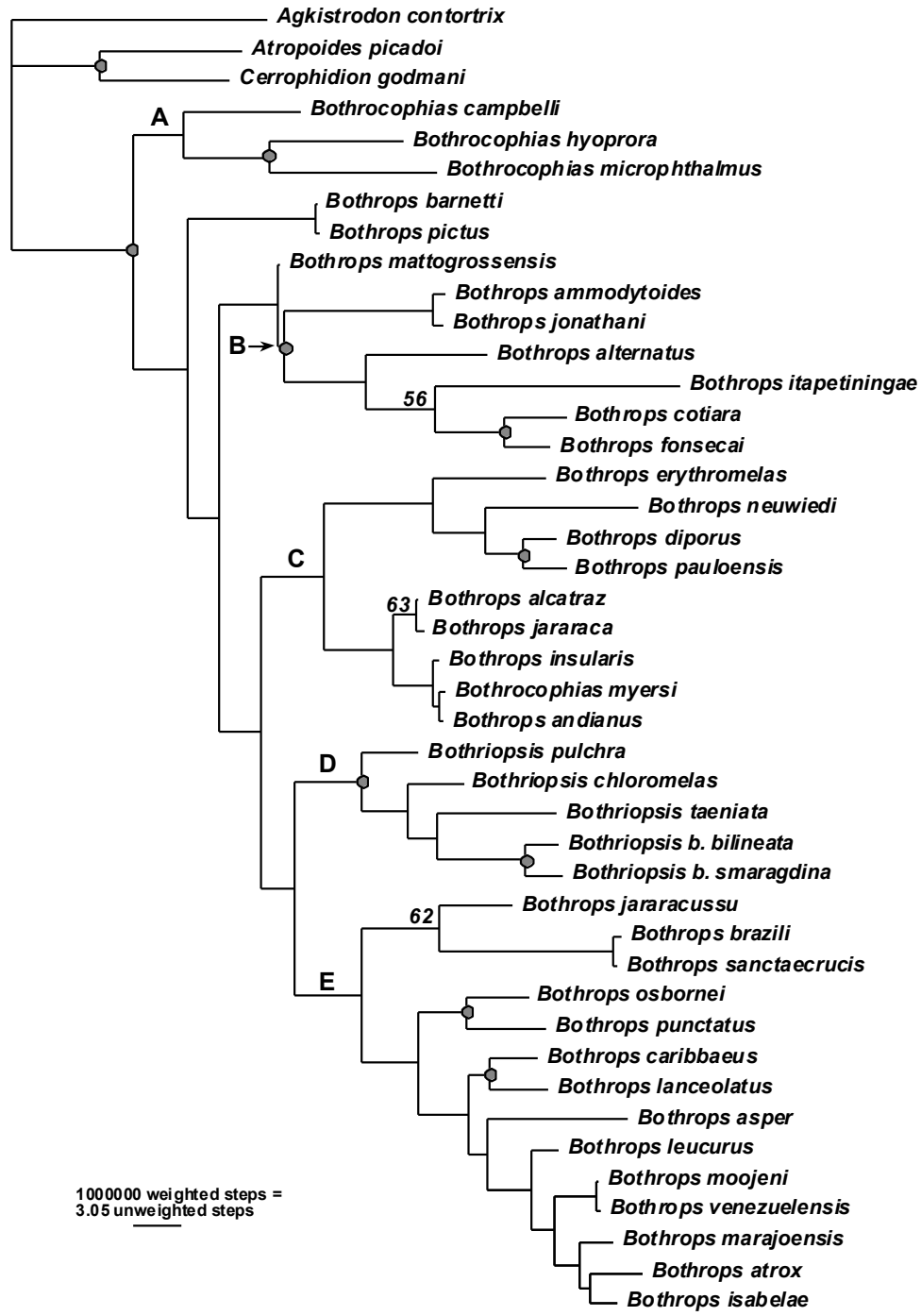

Fig. S-4. Phylogram of single most parsimonious tree from analysis including taxa with morphological data only (analysis 6). Phylogram derived from analysis of 2343 bp of mitochondrial DNA and 85 generalized frequency coded morphological characters (110,255,413 steps = 3364 unweighted steps, CI = 0.464, RI = 0.518). Bootstrap support above 50% shown above nodes. Gray circles indicate bootstrap values of 70 or greater. Bootstrap values 64 for clade of *Bothrops alcatraz, B. jararaca*, and *B. insularis*, 66 for sister relationship of *Bothriopsis pulchra* and *Bothriopsis chloromelas*, and 61 for *Bothrops asper, B. leucurus, B. moojeni, B. marajoensis, B. atrox*, and *B. isabelae*; these relationships were not found in the shortest tree. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

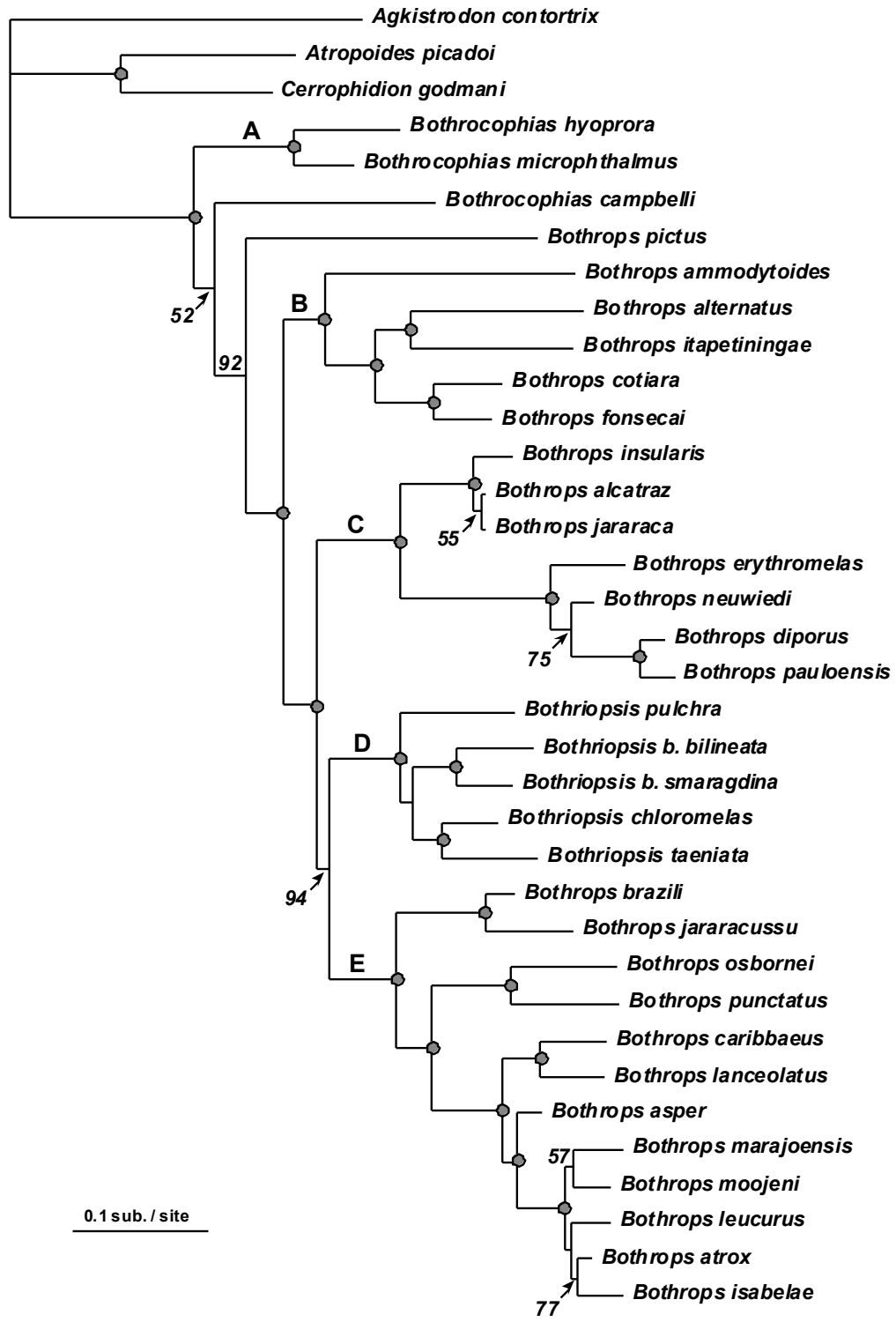

Fig. S-5. Bayesian MCMC 50% majority-rule consensus phylogram derived from analysis of 2343 bp of mitochondrial DNA (analysis 5). Posterior probability support above 50% shown above nodes. Gray circles indicate posterior probabilities of 95 or greater. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

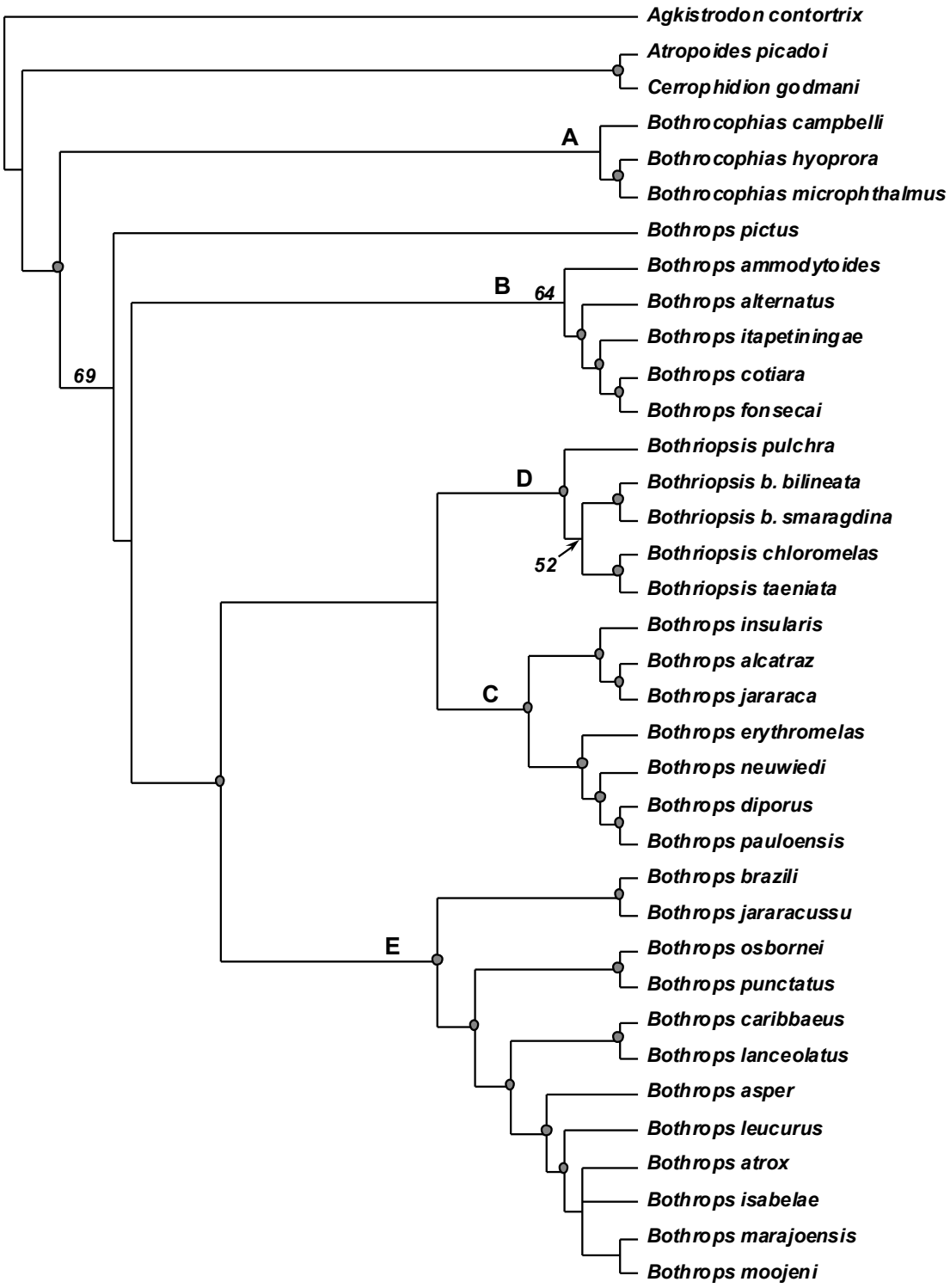

Fig. S-6. Majority-rule consensus cladogram of 11 most parsimonious trees derived from analysis of 2343 bp of mitochondrial DNA (analysis 4, 2475 steps, CI = 0.423, RI = 0.563). Bootstrap values shown above nodes. Gray circles indicate bootstrap values of 70 or greater. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

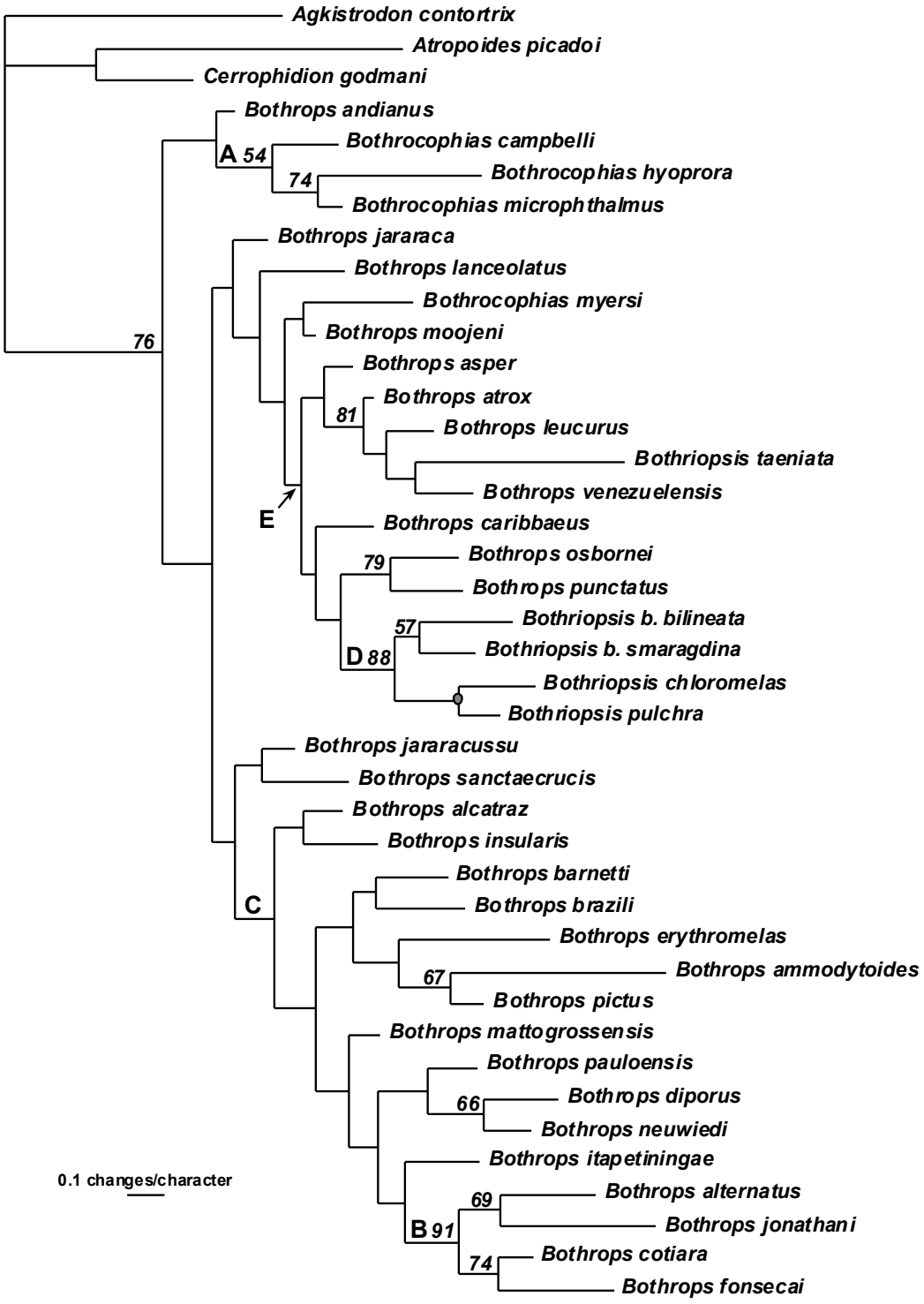

Fig. S-7. Bayesian MCMC 50% majority-rule consensus phylogram derived from analysis of 85 gap weighted or majority coded morphological characters (analysis 3). Posterior probability support above 50% shown above nodes. Gray circles indicate posterior probabilities of 95 or greater. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

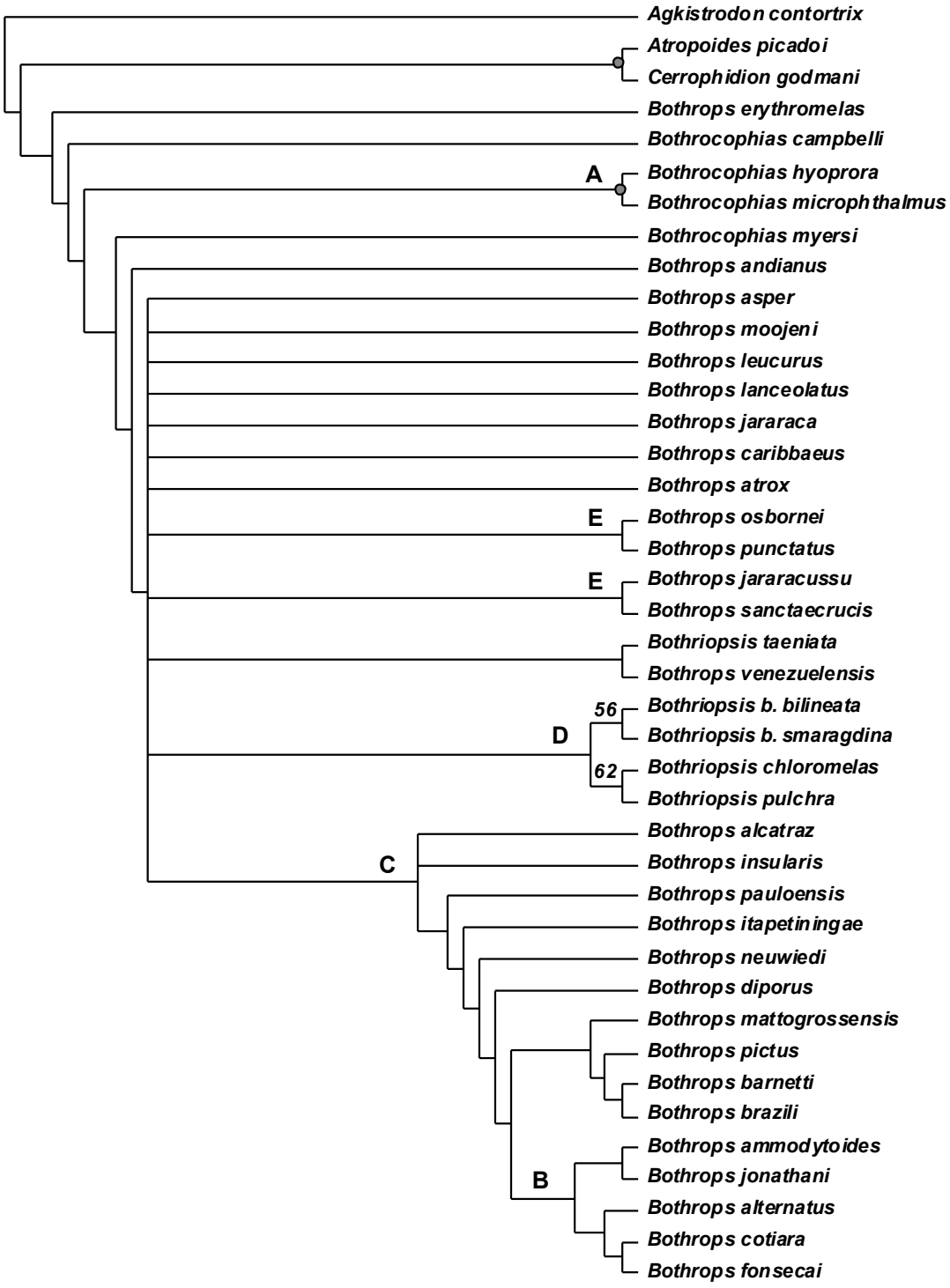

Fig. S-8. Parsimony 50% majority-rule consensus cladogram of 107 shortest trees derived from analysis of 85 gap weighted or majority coded morphological characters (analysis 2, 640 unweighted steps, CI = 0.295 RI = 0.464. Bootstrap support above 50% shown above nodes. Gray circles indicate bootstrap values of 70 or greater. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi + B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

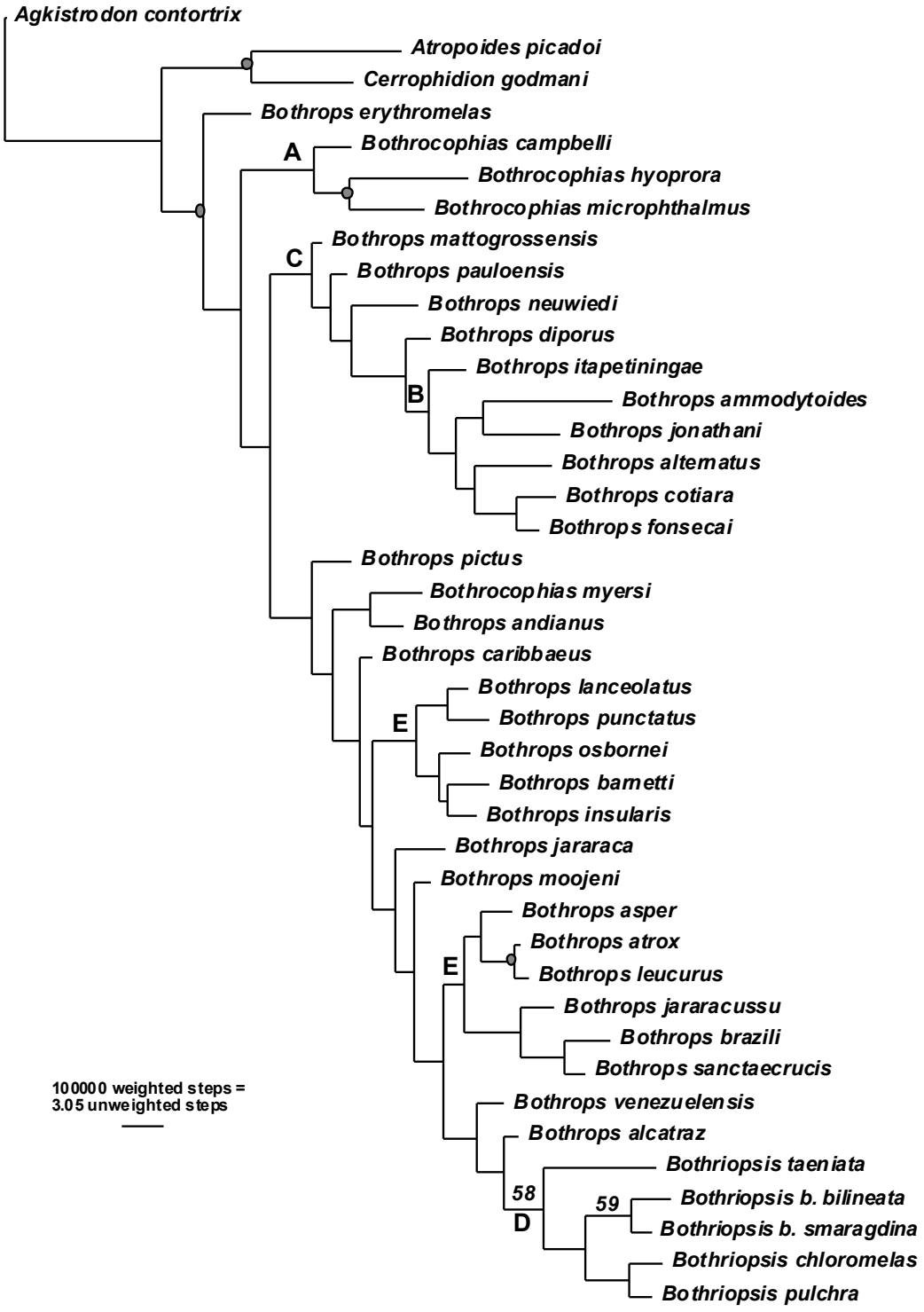

Fig. S-9. Phylogram of single most parsimonious tree derived from analysis of 85 generalized frequency coded morphological characters (analysis 1, 7,920,556 weighted steps = 242 unweighted steps, CI = 0.309, RI = 0.447). Bootstrap support above 50% shown above nodes. Gray circles indicate bootstrap values of 70 or greater. Letters correspond to major lineages: *Bothrocophias* clade (A), *Bothrops alternatus* clade (B), *Bothrops neuwiedi* + *B. jararaca* clade (C), *Bothriopsis* clade (D), and *Bothrops atrox* clade (E).

APPENDIX E:
SPECIMENS EXAMINED FOR BOTHROPOID TAXONOMY

Institutional abbreviations, except UTT (University of Texas at Tyler), are listed in Leviton et al. (1985).

Agkistrodon contortrix USA: *Arkansas*: Colombia Co. (UTA R-38098 [skeleton]). *Oklahoma*: LeFlore Co. (UTA R-40961 [skeleton]). *Texas*: Freestone Co. (UTA TBD [skeleton]), Henderson Co. (UTT 516), Smith Co. (UTT 102, 104, 113, 154, 245-246, 262, 529). NO DATA (UTT 587).

Bothriopsis b. bilineata SURINAME (UTA R-19490, R-16084), southern, captive born (FLMNH 78036), Lely Mountains (MCZ 149525). *Marowinje*: Tepoe (UTA R-15645, R-15647, R-15650).

Bothriopsis bilineata smaragdina COLOMBIA: *Vaupes*: Wacara (UTA R-3588). ECUADOR (UTA R-22581). *Napo* (LACM 73359), Rio Yasuni (FLMNH 83837). PERU (UTA R-34144). *Loreto* (ANSP 7015), near Iquitos (UTA R-2468). *Pasco* (LACM 76790). *Iquitos*: Amagou Basin (LACM 104360). NO DATA (UTA R-34145).

Bothriopsis choromelas PERU: *Junin*: Chanehamayo, Pulcalpa (FMNH 59205). *Loreto* (CM R-373). *Pasco*: Santa Cruz (LSUMZ, 41037).

Bothriopsis oligolepis PERU (USNM 119020). *Tambopato*: San Juan (FMNH 68597).

Bothriopsis pulchra ECUADOR (USNM 165183-165185, 165388, FLMNH 68161). *Tungurahua* (KU 121347-121348). PERU: *Amazonas* (LSUMZ 39316 [skeleton]). NO DATA (UMMZ 82900, 105894).

Bothriopsis taeniata BRAZIL: *Pará*: IPEAN, 3km E Belém (KU 128263). *Rondonia*: Rio Jamari (UTA R-29687). SURINAME: *Marowinje*: Tepoe (UTA R-15618). *Sipaliwini* (UTA R-10501, R-10502), within 5mi of Tepoe (UTA R-30817). NO DATA (UTA R-32087 [body + skull], R-32088).

Bothrocophias campbelli ECUADOR: *Pichincha*: Mindo (USNM 165340), Pacto (USNM 165322).

Bothrocophias hyoprora ECUADOR (USNM 165297-165299, 165301-165302, 165304-165307, 165309-165310). *Cuyabueno* (MCZ R-163236). PERU: *Loreto*: San Jacinto (KU 222208), 1.5km N Teniente Lopez (KU 222209).

Bothrocophias microphthalmus ECUADOR (USNM 165303). PERU (FMNH 63740 [skeleton]). *Buena Vista*: Valley of the Chimchao (FMNH 40242). *Loreto* (MCZ 45920), 4mi NE Iquitos along Amazon River (FLMNH 38922). *Pasco* (LSUMZ 43286). *San Martin*: 20km NE Tarapato (KU 211621). NO DATA (LACM 76791).

Bothrocophias myersi COLOMBIA: *Valle*: camp “Carton de Colombia” (FMNH 165587, 165589, 165593 [skin + skeleton]), Rio Calima, 7km from lumber camp (FMNH 165594-165595), Caimancito (UTA R-21689). NO DATA (FMNH 165586, 165588, 165590-165592, 165596).

Bothrops alternatus ARGENTINA: *Gualeguaychu*: Entre Rios (LACM 146309). BRAZIL (FMNH 51663 [skeleton]). *Minas Gerais*: Frutal (UTA R-37709). *Rio Grande do Sul*: Sao Sebastiano do Ta (UTA R-32427). *Sao Paulo*: Americo Brasiliense (UTA R-38294), Morro abudo (UTA R-38293). PARAGUAY: near Asunción (UTA R-5602 [hemipene prep]).

URUGUAY: *Maldonado*: Laguna Sance (LSUMZ 27748). NO DATA (UMMZ 62921, 62923, 62926-62927, 79626, 225041 [skeleton], LSUMZ 55460 [skeleton]).

Bothrops ammodytoides ARGENTINA: *Catamarca* (TNHC 44803), Angdalgala (CM 147885). *Mendoza*: Las Heras (MVZ 127512), Malargue (MVZ 127513, 127514). *Neuquea*: Zapata (MVZ 127518). *San Luis*: Union (MVZ 134149, UTA R-16334). NO DATA (LACM 146317).

Bothrops andianus BOLIVIA: *La Paz*: Sur Yungas (UTA R-39107). *Santa Cruz*: Florida, Yungas (UTA R-39104). PERU: *Cuzco* (KU 135212, FMNH 62943), Machu Picho (MCZ 12415). *Puño* (UTA R-26719), 11km NNE (airline) Ollachea (USNM 267836-267837). NO DATA (FLMNH 83845).

Bothrops asper BELIZE (FMNH 3480 [skull]). COLOMBIA: possibly from Chocó region (UTA R-6770). COSTA RICA (USNM 220377 [skull], UTA R-34157). *Cartago*: Parones de Turrialba (UTA R-14507-14510), Texeira de Freitas (UTA R-12932, R-12936). *Limón*: Linda Vista de Siquirres (UTA R-12920, R-12996). *Puntavenas*: Rio Peñas Blancas (UTA R-32494). GUATEMALA: *Izabal*: Morales (UTA R-40321), Puerto Barrios (UTA R-40320). HONDURAS: *Gracias a Dios*: Mocoron (UTA R-52545). *Tela* (FMNH 20641 [skull]). MEXICO: *Quintana Roo*: between Tulúm and Coba (UTA R-17095 [hemipene prep]). *Veracruz*: 20 km S Jesus Carranza (KU 23915), 60km SW Jesus Carranza (KU 23995). NICARAGUA: *Zelaya*: El Recreo, S side Rio Mico (KU 112957-112958). PANAMA: *Chiriquí*: Dolega, Central American Mission (UTA R-41026). TRINIDAD: Aripo River (UTA R-17862), St. George, Simla Research Station (UTA R-22345). NO DATA (UTA R-16961 [skull]).

Bothrops atrox BRAZIL (FMNH 51658 [skull]). *Bahía* (MCZ 1189). *Pará*: Obídos (MCZ 1211). COLOMBIA (UTA R-9328). *Meta*: 21.5mi E Puerto Gaitan (UTA R-3378), Lomalinda (UTA R- 3590, R-3610, R-3771-3772, R-3852, R-5219, R-5848, R-5850, R-5862), Serrania de la Macarena (UTA R-3377). *Vaupés*: Lomalinda (UTA R-5853). *Vichada*: Corocito (UTA R-9345). GUYANA: *Rupununi*: road between Moses and Levi's (UTA R-52552), Maca-maca (UTA R-52553), near Chinese camp (UTA R-52554). PANAMA (SDNHM 59573 [skull]). PERU: *Amazonas* (LSUMZ 39317 [skull]). *Junín*: La Mercad (MCZ 45911, 54638). *Loreto*: near Iquitos (UTA R-7196). VENEZUELA: *Amazonas*: Puerto Ayacucho (UTA R-30826). NO DATA (CM 91926 [skull], SDNHM 59509 [zoo specimen, skeleton], 59589 [skeleton]).

Bothrops barnetti PERU (LSUMZ 39318). Sechura Desert (CAS 92343). *Quebrada Parinas*: near Negritos (FMNH 11013), N of Negritos (FMNH 9777-9778, 9787-9789). *Piura*: Parinas Valley (FMNH 41603). *Tumbes*: Grau Tombes (CAS 14570).

Bothrops brazili COLOMBIA (FMNH 165563 [skull]). *Vaupés*: Timbo (UTA R-3764). PERU: *Amazonas* (MVZ 163340, 163342-163343), vicinity of Huampani, Rio Cenepa (MVZ 163341 [skeleton]), vicinity of San Rio Cenepa (MVZ 163344 [skeleton]), vicinity of Kush, Rio Cenepa (MVZ 163346 [skeleton]), Rio Cenepa (MVZ 163345). *Loreto* (KU 222206), Rio Alto Purus, San Bernardo (LSUMZ 26851 [skeleton]). SURINAM: *Sipaliwini* (UTA R-29977).

Bothrops caribbaeus WEST INDIES: *St. Lucia* (UTA R-3850, R-7304, R-8351-8353), Anse-la-Raye (KU 268957), Fond Citron, Grande Anse (MCZ 70194, 70196, 70200). NO DATA (UTA R-16311).

Bothrops cotiara BRAZIL (FMNH 51662 [skull]). *Minas Gerais*: Sao Jao del Rei (CM R-364). *Santa Catarina* (KU 124648, 124650), Ibicare City (FLMNH 39811). *Sao Paulo*: Ibicare City (FLMNH 39812), Instituto Piulueiros (MVZ 200831).

Bothrops diporus ARGENTINA: *Catamarca*: Route 1 (TNHC 44863, 44877, 44989). *Chaco*: Corzuela (MVZ 134155). *Cordoba*: La Posta (MVZ 134156). *La Rioja*: Chamical (TNHC 46875-46876). *Vermejo*: La Plata (ANSP 7013). *Jujuy*: Ledesma (MVZ 127510). PARAGUAY: *Villeta*: Colonia Nueva Italia (MCZ 47029).

Bothrops erythromelas BRAZIL: *Ceara*: Limoeiro do Norte (LSUMZ 24446).

Bothrops fonsecai BRAZIL (FMNH 171285, 171288). *Minas Gerais*: Bocaina de Minas (UTA R-38291-38292). *São Paulo* (KU 125379, MCZ 20893), Campos do Jordano (CAS 116332). NO DATA (UMMZ 129625, 204214).

Bothrops insularis BRAZIL: *São Paulo*: Isla Quemada Grande (MVZ 176399, CM R-2682). NO DATA (MCZ 17620, 17622-17623, 17625-17627, UMMZ 58506-58507).

Bothrops itapetiningae BRAZIL (USNM 38187, 39059, 76320, 165514-165516). *Matto Grosso*: Descalvados (FMNH 10815). *São Paulo* (FMNH 2619, MCZ 20904, 20908, 20910). NO DATA (UMMZ 62913-62914).

Bothrops jararaca ARGENTINA: *Bahía*: Itapetingo City (FLMNH 39821). *Minas Gerais*: Juíz de Flora City (FLMNH 39817). *Misiones* (LACM 14601). BRAZIL (ANSP 7030). *Paraná* (KU 124655). *Santa Caterina* (KU 124651). *São Paulo* (FMNH 69951 [skull], KU 125036). PERU: *Iquitos* (FLMNH 39813).

Bothrops jararacussu ARGENTINA: *Misiones*: El Dorado (LACM 146081). BRAZIL (FMNH 51659-51660, UTA R-32425). *Espirito Santo* (KU 124656). *Santa Caterina*: (KU 68959), Blumenau (UTA R-38295-38296). *São Paulo*: Evangelista Souza, Camal Santos (FMNH 171283), Jacarei (UTA R-37700), Taubate (FMNH 171300). PARAGUAY: *Cazaapa* (KU 290723).

Bothrops jonathani BOLIVIA: *Cochabamba*: 97km S Cochabamba (UTA R-34564).

Bothrops lanceolatus WEST INDIES (ANSP 7016, 7017). *Martinique* (ANSP 7018, 7022, CM S-6390, KU 268958, USNM 11317). *Tobago* (USNM 10116, 10122). NO DATA (USNM 11318).

Bothrops leucurus BRAZIL: *Bahia*: Teixeira de Freitas (UTA 38290). *Espirito Santo* (KU 124659), Sao Domingos, Aguia Branca (CAS, 116342, CM 50981), Municipio de Aracruz, Barr (UTA R-19512), Nova Venecia (UTA R-38299-38301).

Bothrops lojanus ECUADOR (USNM 98927, 98935, 232519). *Loja* (KU 135213, MCZ 93587). *Zamora* (UTA R-23529).

Bothrops mattogrossensis ARGENTINA: *Salta* (KU 183007). BOLIVIA (FMNH 16558-16560). *Bení* (FMNH 104200), San Joaquin (FMNH 140199). *Santa Cruz* (MCZ 11857, 20620, 29229, 29231). PARAGUAY (MCZ 182691), mouth of Rio Aracay on Brazilian frontier (MCZ 34211-34212). *Boqueron* (KU 73475).

Bothrops moojeni BRAZIL: *Goías*: Cristianopolis (UTA R-28231). *Parana* (KU 124657), Foz do Iguaco (UTA R-35940). *São Paulo* (4 specimens of FMNH 2617), Biriqui (FMNH 171278 [skull]), Paraguacu Paulista (UTA 38298), Pirrasunuga (UTA 38297).

Bothrops neuwiedi BRAZIL (FMNH 171255). *Parana* (MCZ 20938), Arau Caria (MCZ 54645), Jaguariavia (UTA R-38284), Piraquara (UTA R-35939), Telmaco Borba (UTA R-35938). *São Paulo* (KU 12468, MCZ 20923), Analandia (UTA R-38283), São Paulo (MVZ 134157). NO DATA (AMNH 29256 [skull]).

Bothrops osbornei ECUADOR (USNM 310822). *Chimborazo*: Pallatanga (KU 218462).

Bothrops pauloensis BRAZIL (FMNH 171277), southeast (MCZ 17729, 17731). *Goias*, Goiania (UTA R-31000). *São Paulo* (MCZ 20919).

Bothrops pictus PERU (ANSP 11521, 11522, 11524, FMNH 5662, 5663, USNM 49992), Valle de Majes (FMNH 39991). *Cajmarca*: 7km W Tembladera (FLMNH 39826). *Lima* (FMNH 229982). *Madre de Diós* (FMNH 39990).

Bothrops pubescens BRAZIL: *Rio Grande do Sul* (R-41141), Porto Alegre (CAS 90737). URUGUAY (FMNH 10245, 10503).

Bothrops punctatus COLOMBIA: *Caldas*: Pueblo Rico, Santa Cecelia (FMNH 55888 [skull], 55894). *Chocó*: Cano Dorcodo (CAS 119594), Pangala (CAS 119921). *Vallé* (FMNH 165384-165386).

Bothrops sanctaecrucis BOLIVIA: *Santa Cruz* (MCZ 20618-20619). *Santa Cruz de la Sierra* (MCZ 17693, 20619). NO DATA (3 specimens of UMMZ 68027, 68028, 68031). BRAZIL (USNM 48931).

Bothrops venezuelensis VENEZUELA: *Aragua* (KU 182734). *Sucre* (KU 133536). NO DATA (USNM 129583, 259175, CBGR0027).

APPENDIX F:
DATA USED IN REPRODUCTIVE MODE ANALYSIS

Taxa and data used in analysis, with reproductive mode for each species. Asterisks denote newly generated sequences for this project. Source numbers refer to reference list following table.

Species	Locality	Voucher/ sample	DNA				Rep. mode	Source
			12S	16S	cyt-*b*	ND4		
Viperinae								
Bitis (*B. albanica, B. armata, B. heraldica, B. inornata, B. parviocula* and *B. schneideri* not in analysis)								
B. arietans (Merrem, 1820)	Togo	–	AF057185	AF57232	AY223558	AY223619	V	1, 2
B. atropos (Linnaeus, 1758)	South Africa, Western Cape, Bettys Bay (12S, 16S, ND4), South Africa, Swartburg (cyt-*b*)	WW1446 (12S, 16S, ND4), PEM (no number, cyt-*b*)	EU624246	EU624281	AJ275691	EU624214	V	1, 2
B. caudalis (Smith, 1839)	South Africa, Northern Cape, Springbok (12S, 16S, ND4), Namibia, Swakopmund (cyt-*b*)	WW1555 (12S, 16S, ND4), ZMFK 65212 (cyt-*b*)	EU624247	EU624282	AJ275693	EU624215	V	1, 2
B. cornuta (Daudin, 1803)	near South Africa, Northern Cape, Springbok	WW1554 (12S, ND4), WW1589 (16S, cyt-*b*)	EU624248	EU624283	EU624305	EU624216	V	1, 2
B. gabonica (Duméril, Bibron, and Duméril, 1854)	South Africa, Kwazulu Natal, St. Lucia (12S, 16S, ND4), DRC, Kivu (cyt-*b*)	WW1330 (12S, 16S, ND4), ZMFK 64335 (cyt-*b*)	EU624249	EU624284	AJ275695	EU624217	V	1, 2
B. nasicornis (Shaw, 1802)	Equatorial Guinea, Bioko	CAS207874	DQ305411	DQ305434	DQ305457	DQ305475	V	1, 2
B. peringueyi (Boulenger, 1888)	Namibia, Swakopmund	CAS193863	DQ305412	DQ305435	DQ305458	DQ305476	V	1, 2
B. rhinoceros (Schlegel, 1855)	Ghana (12S, 16S, ND4), Togo (cyt-*b*)	Liverpool School of Tropical Medicine, live coll. (12S, 16S, ND4), HLMD RA-2909 (cyt *b*)	EU624250	EU624285	AJ275696	EU624218	V	1, 2
B. rubida (Branch, 1997)	South Africa, Ceres	WW1397	EU624251	EU624286	EU624306	EU624219	V	1, 2
B. worthingtoni (Parker, 1932)	Kenya	WW1369 (12S, ND4), no data (16S, cyt-*b*)	EU624252	AJ275745	AJ275692	EU624220	V	1, 2
B. xeropaga (Haacke, 1975)	–	WW1380	EU624253	EU624287	EU624307	EU624221	V	1, 2
Atheris (*A. acuminata, A. broadleyi, A. hirsuta, A. katangensis, A. rungweensis,* and *A. subocularis* not in analysis)								
A. barbouri (Loveridge, 1930)	Masisiwe, Tanzania	ZMK R68297	–	AJ275739	AJ275686	–	?	3, see Methods
A. ceratophora (Werner, 1896)	–	–	DQ305410	DQ305433	DQ305456	DQ305474	V	1, 2
A. chlorechis (Pel, 1851)	unknown (12S, 16S, ND4), Togo (cyt-*b*)	WW1579 (12S, 16S, ND4), HLMD RA-2892 (cyt-*b*)	EU624244	EU624278	AJ275679	EU624211	V	1, 2
A. desaixi (Ashe, 1968)	Kenya, Mt. Kenya	NHMN, no number	–	AJ275733	AJ275680	–	V	1, 2
A. hispida (Laurent, 1955)	Kenya, Kakamega	Collection Klaus Zahn, no number	–	AJ275734	AJ275681	–	V	1, 2
A. nitschei (Tornier, 1902)	Tanzania	CAS201653	AY223650	AY223663	AY223557	AY223618	V	1, 2
A. squamigera (Hallowell, 1854)	DRC (12S), unknown (16S, cyt-*b*, ND4)	no data (12S), WW1314 (16S, cyt-*b*, ND4)	AF544762	EU624279	EU624303	EU624212	V	1, 2

12S and 16S = small ribosomal RNA fragments, cyt b = cytochrome b, ND4 = NADH dehydrogenase subunit 4, tDNA = genomic or total DNA, O = oviparous, V = viviparous, OV = reproductively bimodal, ? = unknown mode

Species	Locality	Voucher/ sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
Montatheris hindii not in analysis								
Proatheris superciliaris (Peters, 1855)	unknown (12S, 16S, ND4), Malawi (cyt-b)	WW1578 (12S, 16S, ND4), HLMD RA-2880 (cyt-*b*)	EU624263	EU624296	AJ275685	EU624230	V	4
Causus (*C. bilineatus, C. lichtensteinii,* and *C. maculatus* not in analysis)								
C. defilippi (Jan, 1862)	Tanzania	CLP154	AF057186	AF057233	AY223556	AY223617	O	1, 2
C. resimus (Peters, 1862)	Africa	Moody 515	AY223649	AY223662	AY223555	AY223616	O	1, 2
C. rhombeatus (Lichtenstein, 1823)	Africa	–	DQ305409	DQ305432	DQ305455	DQ305473	O	1, 2, 5
Cerastes								
C. cerastes (Linnaeus, 1758)	Egypt	Latoxan, live coll. 0504-2	EU624254	EU624288	EU624308	EU624222	O	2
C. gasperettii (Leviton and Anderson, 1967)	unknown (12S), Israel (16S, cyt *b*)	CLP910 (12S), HLMD RA-1593 (16S, cyt *b*)	JN870181*	AJ275756	AJ275704	–	O	4
C. vipera (Linnaeus, 1758)	Tunisia, Djebil	HLMD RA-1432	–	AJ275757	AJ275705	–	V	6
Echis (*E. jogeri, E. khosatzkii,* and *E. borkini* not in analysis)								
E. carinatus (Schneider, 1801)	Pakistan	Latoxan, live coll. 0012-74	EU624255	EU624289	EU624309	EU624223	OV	2, 7
E. coloratus (Günther, 1878)	Israel	WW597	EU624256	EU624290	EU624310	EU624224	O	1, 2
E. ocellatus (Stemmler, 1970)	Togo	WW1378	EU624257	EU624291	EU624311	EU624225	O	4
E. omanensis (Babocsay, 2004)	–	E3026.8	–	EU642581	EU642590	–	O	1, 2
E. pyramidum (Geoffroy Saint-Hilaire, 1827)	Egypt	WW1611	EU624258	EU624292	EU624312	EU624226	O	4
Eristicophis macmahonii (Alcock and Finn, 1897)	unknown (12S, 16S, ND4), Pakistan (cyt-*b*)	WW1360 (12S, 16S, ND4), HLMD RA-2890 (cyt-*b*)	EU624259	EU624293	AJ275711	EU624227	O	8
Pseudocerastes (*P. urarachnoides* not in analysis)								
P. fieldi (Schmidt, 1930)	unknown (12S), Israel (16S, cyt-*b*)	WW1365 (12S), HLMD RA-1182 (16S, cyt-*b*)	EU624264	AJ275769	AJ275716	–	O	1, 7
P. persicus (Duméril, Bibron, and Duméril, 1854)	Pakistan	HLMD RA-1724	–	AJ275770	AJ275717	–	O	2, 9
Macrovipera (*M. deserti* not in analysis)								
M. lebetina (Linnaeus, 1758)	Turkmenistan, Kopet Dagh (cyt-*b*), Uzbekistan, Nuratau (12S, 16S, ND4)	Latoxan live coll. 0413-2 (12S, 16S, ND4), G. Nilson private coll. (cyt-*b*)	EU624260	EU624294	AJ275713	EU624228	O	1, 10, 11
M. schweizeri (Werner, 1935)	Greece, Milos	Latoxan live coll. 0413-2 (12S), G. Nilson private coll. (16S, cyt-*b*)	EU624262	AJ275768	AJ275715	–	O	11, 12

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
Montivipera								
M. albizona (Nilson, Andrén and Flärdh, 1990)	–	WW1377 (12S, ND4), no data (16S, cyt-*b*)	EU624265	AJ275780	AJ275727	EU624231	V	10
M. bornmuelleri (Werner, 1898)	Lebanon	–	–	AJ275779	AJ275726	–	V	2
M. latifii (Mertens, Darewsky and Klemmer, 1967)	unknown	CLP570	JN870191*	JN870199*	JN870205*	–	V	2
M. raddei (Boettger, 1890)	Ararat, Turkey	Collection Mario Schweiger, no number	–	AJ275784	AJ275730	–	V	2
M. wagneri (Nilson and Andrén, 1984)	unknown (12S, ND4), Turkey, Karakurt (16S, cyt *b*)	CLP568 (12S, ND4), Collection Mario Schweiger, no number (16S, cyt *b*)	JN870188*	AJ275778	AJ275725	JN870213*	V	2
M. xanthina (Gray, 1849)	unknown (12S, ND4), Turkey (16S, cyt-*b*)	Zoran Tadić, private coll. (12S, ND4), G. Nilson, private coll. (16S, cyt-*b*)	EU624268	AJ275777	AJ275724	EU624234	V	2
Daboia								
D. mauritanica (Duméril and Bibron, 1848)	Morocco	Latoxan live coll. 0415-3 (12S, 16S, ND4), HLMD RA-1182 (cyt-*b*)	EU624261	EU624295	EU624313	EU624229	O	4
D. palaestinae (Werner, 1938)	unknown (12S), Israel (16S, cyt *b*)	CLP905 (12S), HLMD RA-1904 (16S, cyt *b*)	JN870183*	AJ275775	AJ275722	–	O	2
D. russelii (Shaw and Nodder, 1797)	Pakistan	HLMD RA-2899	–	AJ275776	AJ275723	–	V	1, 2
D. siamensis (Smith, 1917)	Myanmar, Mandalay Div.	CAS205253	DQ305413	DQ305436	DQ305459	DQ305477	V	1, 2
Vipera (*V. darevskii, V. lotievi, V. magnifica, V. monticola, V. orlovi, V. renardi,* and *V. sachalinensis* not in analysis)								
V. ammodytes (Linnaeus, 1758)	–	Liverpool School of Tropical Medicine, live coll., Va1	EU624266	EU624297	EU624314	EU624232	V	1, 2
V. aspis (Linnaeus, 1758)	unknown (12S), Herault, France (cyt *b*)	CLP573 (12S), no number (cyt *b*)	JN870190*	–	AY321098	–	V	1, 2
V. barani (Böhme and Joger, 1983)	Turkey	–	–	–	AY321092	–	V	1, 13
V. berus (Linnaeus, 1758)	United Kingdom (12S, ND4), Sweden, Göteborg (16S, cyt-*b*)	WW 199 (12S, ND4), HLMD RA-1665 (16S, cyt-*b*)	EU624267	AJ275772	AJ275719	EU624233	V	1, 2, 5
V. dinniki (Nikolsky, 1913)	Georgia	HLMD RA-1610	–	AJ275773	AJ275720	–	V	2
V. kaznakovi (Nikolsky, 1909)	Turkey	–	–	–	AY321093	–	V	2
V. latastei (Bosca, 1878)	Spain	–	–	–	AY321094	–	V	2
V. nikolskii (Vedmederya, Grubant and Rudajewa, 1986)	–	Sar1 (12S), no data (16S, cyt-*b*)	EU543219	AJ275774	AJ275721	–	V	1, 13
V. seoanei (Lataste, 1879)	San Sebastian, Spain	HLMD RA-2875	–	AJ275782	AJ275729	–	V	2
V. ursinii (Bonaparte, 1835)	Nileke, Xinjiang Uygur Zizhiqu, China (ND4, 12s) / Vaucluse, France (cyt-b)	NNU 95045 (ND4, 12s) / no data (cyt-b)	EF012817	–	AY311383	EF012798	V	1, 2

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
Crotalinae								
Calloselasma rhodostoma (Boie, 1827)	–	UTA-R22247	AF057190	AF057237	AY223562	U41878	O	1, 5, 14
Hypnale (*H. nepa* and *H. walli* not in analysis)								
H. hypnale (Merrem, 1820)	Sri Lanka, Columbo	CLP-164	AF057189	AF057236	AY223561	U41884	V	5
Garthius chaseni (Smith, 1931)	Malaysia, Sabah	AM B306	AY352791	AY352729	AY352760	AY352825	?	
Deinagkistrodon acutus (Günther, 1888)	China	CLP-28	AF057188	AF057235	AY223560	U41883	O	1, 5, 14
Tropidolaemus (*T. huttoni, T. laticinctus* and *T. philippensis* not in analysis)								
T. subannulatus (Gray, 1842)	Indonesia, West Kalimantan	CLP-141	AF057198	AF057245	AY223571	AY223625	V	5
T. wagleri (Boie, 1827)	Malaysia, Perak	AM B132	AF517167	AF517180	AF517191	AF517223	V	5, 14
Trimeresurus (*T. andalasensis, T. brongersmai, T. strigatus,* and *T. wiroti* not in analysis)								
T. borneensis (Peters, 1872)	Malaysia, Sabah	AM B301	AY352783	AY352722	AY352754	AY352817	O	5
T. gramineus (Shaw, 1802)	India, Tamil Nadu	AM A220	AY352793	AY352731	AY352761	AY352827	V	7
T. malabaricus (Jerdon, 1854)	India, Tamil Nadu	AM A218	AY059548	AY059564	AY059569	AY059587	?	
T. puniceus (Boie, 1827)	Indonesia	AM B213	AF517164	AF517177	AF517192	AF517220	V	14
T. trigonocephalus (Latreilee, 1801)	Sri Lanka, Balangoda	AM A58	AY059549	AY059565	AF171890	AY059597	V	1, 15
Peltopelor macrolepis not in analysis		–	–	–	–	–		
Himalyophis tibetanus (Huang, 1982)	Nepal, Helambu Prov.	ZMB-65641	AY352776	AY352715	AY352749	AY352810	V	14
Popeia								
P. barati (Regenass and Kramer, 1981)	Sumatra, Bengkulu Prov.	AM-B361	AY371753	AY371769	AY371801	AY371837	V	2
P. buniana (Grismer et al. 2006)	Malaysia, Pulau Tioman	AM-B519	AY371752	AY371778	AY371818	AY371853	V	2
P. fucata (Vogel, David and Pauwels, 2004)	Thailand, Thammarat Prov.	AM A203	AY059537	AY059553	AY371796	AY059588	V	2
P. nebularis (Vogel et al. 2004)	Malaysia	AM-B238	AY371737	AY371774	AY371814	AY371839	V	2
P. popeiorum (Smith, 1937)	Laos, Phongsaly Prov.	FMNH-258950	AY059538	AY059554	AY059571	AY059590	V	2, 14
P. sabahi (Regenass and Kramer, 1981)	Borneo (East Malaysia)	AM B344	AY371736	AY371771	AY371815	AY371842	V	2
Parias								
P. flavomaculatus (Gray, 1842)	Philippines, Luzon	AM B3	AY059535	AY059551	AF171916	AY059584	O	5
P. hageni (Lidth de Jeude, 1886)	Thailand, Songhkla Prov.	AM B33	AY059536	AY059552	AY059567	AY059585	O	5
P. malcolmi (Loveridge, 1938)	Malaysia, Sabah	AM B349	AY371757	AY371786	AY371832	AY371861	O	5
P. schultzei (Griffin, 1909)	Philippines, Palawan	AM B210	AY352785	AY352725	AY352756	AY352819	O	5

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
P. sumatranus (Raffles, 1822)	Indonesia, Sumatra, Bengkulu Prov.	AM B367	AY371765	AY371791	AY371824	AY371864	O	5
Cryptelytrops (*C. fasciatus, C. honsonensis,* and *C. labialis* not in analysis)								
C. albolabris (Gray, 1842)	Hong Kong, Port Shelter Is., Yim Tin Tsi	MCZR-177966	AF057195	AF057242	AY223567	U41890	V	14
C. andersonii (Theobald, 1868)	India, Andaman Is.	AM A77	AY352801	AY352740	AF171922	AY352835	V	2
C. cantori (Blyth, 1846)	India, Nicobar Is.	AM A85	AY352802	AY352741	AF171889	AY352836	V	2
C. erythrurus (Cantor, 1839)	Myanmar, Rangoon	AM A209	AF517161	AF517174	AF171900	AF517217	V	14
C. insularis (Kramer, 1977)	Indonesia, Java	AM A109	AY352799	AY352738	AY352767	AY352833	V	2
C. kanburiensis (Smith, 1943)	Thailand	AM B522	AY289219	AY352737	AY289225	AY289231	V	2
C. macrops (Kramer, 1977)	Thailand, Bangkok	AM B27	AF517163	AF517176	AF517184	AF517219	V	2, 14
C. pupureomaculatus (Gray, 1832)	Thailand, Satun Prov.	AM A83	AF517162	AF517175	AF517188	AF517218	V	2
C. septentrionalis (Kramer, 1977)	Nepal, Mahattari Dist.	AM A100	AY059543	AY059559	AF171909	AY059592	V	14
C. venustus (Vogel, 1991)	Thailand, Thammarat Prov.	AM A241	AY293931	AY352723	AF171914	AY93930	V	2
Viridovipera								
V. gumprechti (David, Vogel, Pauwels and Vidal, 2002)	Thailand, Loei Prov.	AM A164	AF517168	AF517181	AY352766	AF157224	V	1
V. medoensis (Zhao, 1977)	Myanmar, Kachin	CAS 221528	AY352797	AY352735	AY352765	AY352831	V	1
V. stejnegeri (Schmidt, 1925)	Taiwan, Taipei	UMMZ-190532	AF057197	AF057244	AY223570	U41892	V	1, 14, 16
V. truongsonensis (Orlov, Ryabov, Thanh and H Cuc, 2004)		B659	EU443817	EU443818	EU443815	EU443816	V	1
V. vogeli (David, Vidal and Pauwels, 2001)	Thailand, Ratchasima Prov.	AM B97	AY059546	AY059562	AY059574	AY059596	V	1
V. yunnanensis (Schmidt, 1925)		GP37	EU443811	EU443812	EF597522	EF597527	V	1
Ovophis in part (*O. tonkinensis* and *O. zayuensis* not in analysis)								
O. monticola (Günther, 1864)	China, Yunnan Prov., Nu Jiang Prefecture	CAS215050	DQ305416	DQ305439	DQ305462	DQ305480	O	1, 5, 7, 14
Gloydius (*G. himalayanus* and *G. monticola* not in analysis)								
G. blomhoffii (Boie, 1826)	Japan	AM B524	AY352780	AY352719	AY352751	AY352814	V	5
G. brevicaudus (Stejneger, 1907)	China	AM B525	AY352781	AY352720	AY352752	AY352815	V	5
G. halys (Pallas, 1776)	Kazakhstan	–	AF057191	AF057238	AY223564	AY223621	V	5, 14
G. intermedius (Strauch, 1868)	Japan (12S, 16S, cyt-*b*), Mongolia (ND4)	unknown (12S, 16S, cyt-*b*), NNU 95050 (ND4)	JN870184*	JN870194*	JN870201*	EF012788	V	5, 14
G. saxatilis (Emelianov, 1937)	–	Alec 60588-2	JN870185*	JN870195*	JN870202*	JN870210*	V	5
G. shedaoensis (Zhao, 1979)	China, Liaoning	ROM-20468	AF057194	AF057241	AY223566	AY223623	V	5, 17
G. strauchi (Bedriaga, 1912)	China, Jilin, Waqie Sichuan	ROM-20473	AF057192	AF057239	AY223563	AY223620	V	5
G. tsushimaensis (Isogawa, Moriya and Mitsui, 1994)	–	–	JN870186*	JN870196*	JN870203*	JN870211*	V	5

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
G. ussuriensis (Emelianov, 1929)	China, Jilin, Kouqian	ROM-20452	AF057193	AF057240	AY223565	AY223622	V	5, 14
Protobothrops								
P. cornutus (Smith, 1930)	Vietnam, Phong Nha-Ke NP	ZFMK-75067	AY294272	AY294262	AY294276	AY294267	O	5
P. elegans (Gray, 1849)	Japan, Ryukyu Is., Ishigaki	UMMZ-199970	AF057201	AF057248	AY223575	U41893	O	5
P. flavoviridis (Hallowell, 1861)	Japan, Ryukyu Is., Tokunoshima	UMMZ-199973	AF057200	AF057247	AY223574	U41894	O	1, 5, 18
P. jerdonii (Günther, 1875)	China, Nu Jiang, Yunnan	CAS215051	AY294278	AY294269	AY294274	AY294264	OV	1, 14
P. kaulbacki (Smith, 1940)	China	SYNU0400II30	DQ666056	DQ666055	DQ666060	DQ666057	O	5
P. mangshanensis (Zhao, 1990)	China, Hunan Prov.	AM B300	AY352787	AY352726	AY352758	AY352821	O	5
P. mucrosquamatus (Cantor, 1839)	Vietnam	ROM-2717	AY223653	AY223666	AY223577	AY223629	O	5, 14
P. sieversorum (Ziegler, Herrmann, David, Orlov and Pauwels, 2000)	Vietnam, Phong Nha-Quang Ping Province	ZFMK 75066	DQ305414	DQ305437	DQ305460	DQ305478	O	5
P. tokarensis (Nagai, 1928)	Japan, Ryukyu Is., Takarajima	FK-1997	AF057202	AF057249	AY223576	AY223628	O	1
P. xiangchengensis (Zhao, Jiang and Huang, 1979)	–	SCUM 035046	AY763189	AY763208	DQ666062	DQ666059	O	5
Ovophis okinavensis (Boulenger, 1892)	Japan, Okinawa	CLP-162	AF057199	AF057246	AY223573	U41895	O	1, 5
Trimeresurus gracilis (Oshima, 1920)	Taiwan	NTNUB 200515	DQ305415	DQ305438	DQ305460	DQ305478	V	2
Agkistrodon								
A. bilineatus (Günther, 1863)	Costa Rica, Guanacaste	WWL	AF156593	AF156572	AY223613	AY156585	V	19
A. contortrix (Linnaeus, 1766)	USA, Ohio, Athens Co.	Moody 338	AF057229	AF057276	AY223612	AF156576	V	5, 19
A. piscivorous (Lacépède, 1789)	USA, South Carolina	CLP-30	AF057231	AF057278	AY223615	AF156578	V	5, 19
A. taylori (Burger and Robertson, 1951)	Mexico, Tamaulipas	CLP-140	AF057230	AF057230	AY223614	AF156580	V	19
Sistrurus								
S. catenatus (Rafinesque, 1818)	USA, Texas, Haskel Co.	Moody 502	AF057227	AF057274	AY223610	AY223648	V	1, 5, 19
S. miliarius (Linnaeus, 1766)	USA, Florida, Lee Co.	UTA-live	AF057228	AF057275	AY223611	U41889	V	1, 5, 19
Crotalus (*C. ericsmithi, C. lannomi, C. stejnegeri,* and *C. tancitarensis* not in analysis)								
C. adamanteus (Palisot de Beauvois, 1799)	USA, Florida, St. Johns Co.	CLP-4	AF057222	AF057269	AY223605	U41880	V	5, 19
C. aquilus (Klauber, 1952)	Mexico, San Luis Potosi	ROM-18117	AF259232	AF259125	AF259162	–	V	19
C. atrox (Baird and Girard, 1853)	USA, Texas, Jeff Davis Co.	CLP-64	AF0572225	AF057272	AY223608	AY223646	V	5, 19
C. basiliscus (Cope, 1864)	Mexico, Nayarit	ROM-18188 (12S, 16S, cyt-*b*), 822 (ND4)	AF259244	AF259136	AF259174	AY704894	V	19

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
C. catalinensis (Cliff, 1954)	Mexico, Baja California Sur, Isla Santa Catalina	ROM-18250 (12S, 16S, cyt-*b*), BYU-34641-42	AF259259	AF259151	AF259189	–	V	19
C. cerastes (Hallowell, 1854)	USA, California, Riverside Co.	ROM-FC-20099 (12S), ROM-19745 (16S, cyt-*b*)	AF259235	AF259128	AF259165	–	V	5, 19
C. culminatus (Klauber, 1952)	Mexico, Morelos	3291	–	–	AY704830	AY704880	V	19
C. durissus (Linnaeus, 1758)	Venezuela (12S, 16S, cyt-*b*), Brazil, Sao Paulo, Pindamonhangaba (ND4)	ROM-18138 (12S, 16S, cyt-*b*), IB 55601 (ND4)	AF259248	AF259140	AF259178	AF292608	V	5, 19
C. enyo (Cope, 1861)	Mexico, Baja California Sur	ROM-FC 441 (12S), ROM13648 (16S, cyt-*b*)	AF259245	AF259137	AF259175	–	V	19
C. horridus (Linnaeus, 1758)	USA, Arkansas (12S, 16S, cyt-*b*), USA, Texas, Lee Co. (ND4)	UTA-R14697 (12S, 16S, cyt-*b*), TNHC65471 (ND4)	AF259252	AF259144	AF259182	JN870207*	V	5, 19
C. intermedius (Troschel, 1865)	Mexico, Veracruz (12S, 16S, cyt-*b*), Mexico, Oaxaca, El Tejocote (ND4)	ROM-FC223 (12S), ROM-18164 (16S, cyt-*b*), JAC8881 (ND4)	AF259238	AF259131	AF259168	JN870208*	V	5, 19
C. lepidus (Kennicott, 1861)	Mexico, Chihuahua (12S, 16S, cyt-*b*), USA, Mew Mexico, Socorro Co. (ND4)	ROM-18128 (12S, 16S, cyt-*b*), UMMZ 199960 (ND4)	AF259230	AF259123	AF259160	U41881	V	5, 19
C. mitchelli (Cope, 1861)	USA, California, Imperial Co.	ROM-18178	AF259250	AF259142	AF259180	–	V	5, 19
C. molossus (Baird and Girard, 1853)	USA, Texas, El Paso Co.	CLP-66	AF057224	AF057271	AY223607	AY223645	V	5, 19
C. oreganus (Holbrook, 1840)	USA, California, Los Angeles Co. (12S, 16S, cyt-*b*), USA, Colorado, Moffat Co. (ND4)	ROM-19656 (12S, 16S, cyt-b), Kyle Ashton specimen, no number (ND4)	AF259253	AF259145	AF259183	AF194158	V	5, 19
C. polystictus (Cope, 1865)	Mexico, Districto Federal	ROM-FC263 (12S, 16S), ROM-18139 (cyt-b)	AF259236	AF259129	AF259166	–	V	5, 19
C. pricei (Van Denburgh, 1895)	Mexico, Nuevo Leon	ROM-FC2144	AF259237	AF259130	AF259167	–	V	19
C. pusillus (Klauber, 1952)	Mexico, Michoacán	ROM-FC271	AF259229	AF259122	AF259159	–	V	19
C. ravus (Cope, 1865)	Mexico, Puebla, Zapotitlán	UTA-live	AF057226	AF057273	AY223609	AY223647	V	19
C. ruber (Cope, 1892)	USA, California, Riverside Co.	ROM-18197 (12S, 16S, cyt-*b*), RWV2001-08 (ND4)	AF259261	AF259153	AF259191	DQ679838	V	19
C. scutulatus (Kennicott, 1861)	USA, Arizona, Mojave Co. (12S, 16S, cyt-b), USA: New Mexico: Doña Ana Co. (ND4)	ROM-18210 (12S, 16S, cyt-b), UTEP-CRH 153 (ND4)	AF259254	AF259146	AF259184	AF194167	V	5, 19
C. simus (Latrielle, 1801)	Costa Rica, Guanacaste	WW-1312 (12S, 16S), WW-1097 (cyt *b*, ND4)	EU624240	EU624274	EU624302	AY704885	V	19
C. tigris (Kennicott, 1859)	USA, Arizona, Pima Co.	CLP-169	AF057223	AF057270	AY223606	AF156574	V	19
C. tortugensis (Van Denburgh and Slevin, 1921)	Mexico, Baja California Sur, Isla Tortuga	ROM-18192 (12S, 16S, ND4), ROM-18195	AF259257	AF259149	AF259187	DQ679839	V	19
C. totonacus (Gloyd and Kauffeld, 1940)	Mexico, Tamaulipas	SD	–	–	AY704837	AY704887	V	19
C. transversus (Taylor, 1944)	Mexico	KZ-shed skin	AF259239	–	AF259169	–	V	19

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
C. triseriatus (Wagler, 1830)	Mexico, Districto Federal, Xochomiko	ROM-18120	AF259234	AF259127	AF259164	–	V	5, 19
C. tzabcan (Klauber, 1952)	Belize, Corozal District	255 - Peter Singfield, live coll.	–	–	AY704806	AY704856	V	19
C. viridis (Rafinesque, 1818)	USA, Arizona, Coconino Co. (12S); USA, Colorado, Dona Ana Co. (cyt-*b*, ND4)	131S (12S), UTEP 17625 (cyt-*b*, ND4)	DQ020029	–	AF147866	AF194157	V	5, 19
C. willardi (Meek, 1905)	USA, Arizona, Cochise Co. (12S, 16S, cyt-*b*, ND4)	HWG-2575(12S, 16S, cyt-*b*), TNHC-W9306 (ND4)	AF259242	AF259134	AF259172	JN870209*	V	5, 19
Ophryacus								
O. melanurus (Müller, 1923)	Mexico	UTA-R34605	AF057210	AF057257	AY223587	AY223634	V	5, 19
O. undulatus (Jan, 1859)	Mexico	CLP-73	AF057209	AF057256	AY223586	AY223633	V	19
Lachesis								
L. acrochorda (Garcia, 1896)	Colombia	CLP-319	JN870187*	JN870197*	JN870204*	JN870212*	O	5, 19
L. melanocephala (Solórzano and Cerdas, 1986)	Costa Rica, Peninsula de Oro, Rincon	–	–	–	U96018	U96028	O	5, 19
L. muta (Linnaeus, 1766)	Peru	Cadle 135	AF057221	AF057268	AY223604	AY223644	O	5, 19
L. stenophrys (Cope, 1876)	Costa Rica, Limón	–	AF057220	AF057267	AY223603	U41885	O	5, 19
Bothriechis								
B. aurifer (Salvin, 1860)	Guatemala	UTA-R35031	DQ305425	DQ305448	DQ305466	DQ305483	V	5, 19
B. bicolor (Bocourt, 1868)	–	UTA-R34156	DQ305426	DQ305449	DQ305467	DQ305484	V	19
B. lateralis (Peters, 1862)	Costa Rica, Acosta	MZUCR-11155	AF057211	AF057258	AY223588	U41873	V	19
B. marchi (Barbour and Loveridge, 1929)	Guatemala, Zacapa, Cerro del Mono	UTA-R52959	DQ305428	DQ305451	DQ305469	DQ305486	V	19
B. nigroviridis (Peters, 1859)	Costa Rica, San Gerondo de Dota	MZUCR-11151	AF057212	AF057259	AY223589	AY223635	V	5, 19
B. rowleyi (Bogert, 1968)	Mexico: Cerro Baúl	JAC 13295	DQ305427	DQ305450	DQ305468	DQ305485	V	19
B. schlegelii (Berthold, 1846)	Costa Rica, Cariblanco de Sarapiquí	MZUCR-11149	AF057213	AF057260	AY223590	AY223636	V	5, 19
B. supraciliaris (Taylor, 1954)	Costa Rica, San Vito	–	DQ305429	DQ305452	DQ305470	DQ305482	V	19
B. thalassinus (Campbell and Smith, 2000)	Guatemala, Zacapa	UTA-R52958	DQ305424	DQ305447	DQ305465	U41875	V	19
Atropoides								19
A. indomitus (Smith and Ferrari-Castro, 2008)	Honduras, Olancho	ENS-10630	–	–	DQ061194	DQ061219	V	19
A. mexicanus (Duméril, Bibron and Duméril, 1854)	Costa Rica	CLP-168	AF057207	AF057254	AY223584	U41871	V	19
A. nummifer (Rüppell, 1845)	Mexico, Puebla, San Andres Tziaulan	ENS-10515	DQ305422	DQ305445	DQ061195	DQ061220	V	19
A. occiduus (Hoge, 1966)	Guatemala, Escuintla	UTA-R29680	DQ305423	DQ305446	AY220315	AY220338	V	19

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
A. olmec (Perez-Higareda, Smith and Julia-Zertuche, 1985)	Mexico, Veracruz	JAC-16021	AY223656	AY223669	AY220321	AY220344	V	5, 19
A. picadoi (Dunn, 1939)	Costa Rica, Alajuella	CLP-45	AF057208	AF057255	AY223593	U41872	V	5, 19
Cerrophidion (*C. barbouri* not in analysis)								
C. godmani (Günther, 1863)	Costa Rica, San Jose	MZUCR-11153	AF057203	AF057250	AY223578	U41879	V	5, 19
C. petlalcalensis (Lopéz-Luna, Antonio, Vogt and Torre-Loranca, 1999)	Mexico, Veracruz, Orizaba	ENS-10528	DQ305420	DQ305443	DQ061202	DQ061227	V	19
C. tzotzilorum (Campbell, 1985)	Mexico, Chiapas, Las Rosas	ENS10529	JN870182*	JN870193*	DQ061203	DQ061228	V	19
Porthidium (*P. volcanicum* not in analysis)								
P. arcosae (Schätti and Kramer, 1993)	Ecuador	WWW-750	AY223655	AY223668	AY223582	AY223630	V	19
P. dunni (Hartweg and Oliver, 1938)	Mexico, Oaxaca	ENS-9705	AY223654	AY223667	AY223581	AY223630	V	19
P. hespere (Campbell, 1976)	Mexico, Michoacán	UOGV 726	–	–	EU017534	EU016099	V	19
P. lansbergii (Schlegel, 1841)	Venezuela, Falcón, San Antonio	WW-787	EU624242	EU624276	AY713375	AF393623	V	19
P. nasutum (Bocourt, 1868)	Costa Rica	MZUCR-11150	AF057204	AF057251	AY223579	U41887	V	19
P. ophryomegas (Bocourt, 1868)	Costa Rica, Guanacaste	UMMZ-210276	AF057205	AF057252	AY223580	U41888	V	19
P. porrasi (Lamar, 2003)	Costa Rica, Puntarenas	MSM	DQ305421	DQ305444	DQ061214	DQ061239	V	19
P. yucatanicum (Smith, 1941)	Mexico: Yucatán: Car. Yaxcabá-Tahdzibichen	JAC-24438	JN870189*	JN870198*	DQ061215	DQ061244	V	19
Bothrocophias (*B. colombianus* and *B. myersi* not in analysis)								
B. campbelli (Freire-Lascano, 1991)	Ecuador, Chimborazo, Pallatanga	INHMT, uncatalogued	–	–	AF292584	AF292622	V	19
B. hyoprora (Amaral, 1935)	Colombia, Letícia	–	AF057206	AF057253	AY223593	U41886	V	19
B. microphthalmus (Cope, 1876)	Peru, Pasco Dept.	LSUMZ H-9372	AY223657	AY223670	AY223594	AY223638	V	19
Rhinocerophis (*R. jonathani* not in analysis)								
R. alternatus (Duméril, Bibron and Duméril, 1854)	–	DLP-2879	AY223660	AY223673	AY223601	AY223642	V	19
R. ammodytoides (Leybold, 1873)	Argentina, Neuguen	MVZ-223514	AY223658	AY223671	AY223595	AY223639	V	19
R. cotiara (Gomes, 1913)	Brazil	WWW	AF057217	AF057264	AY223597	AY223640	V	19
R. fonsecai (Hoge and Belluomini, 1959)	Brazil, São Paulo, Campos do Jordão	IB 55543	–	–	AF292580	AF292618	V	19
R. itapetiningae (Boulenger, 1907)	Brazil, São Paulo, Itarapina	ITS427	EU867253	EU867265	EU867277	EU867289	V	19
Bothropoides (*B. lutzi, B. marmoratus* and *B. mattogrossensis* not in analysis)								
B. alcatraz (Marques, 2002)		CBGM baz001	–	–	AY865820	–	V	19
B. diporus (Cope, 1862)	Argentina, La Rioja, Depto. Castro Barros	PT3404	DQ305431	DQ305454	DQ305472	DQ305489	V	19

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
B. erythromelas (Amaral, 1923)	Brazil, Algóas, Piranhas	RG-829	AF057219	AF057266	AY223600	U41877	V	19
B. insularis (Amaral, 1921)	Brazil, São Paulo, Ilha Queimada Grande	WWW	AF057216	AF057263	AY223596	AY223641	V	19
B. jararaca (Wied, 1824)	Brazil, São Paulo, Itarapina	MM (19)6	EU867254	EU867266	EU867278	EU867290	V	19
B. neuwiedi (Wagler, 1824)	Brazil, São Paulo, Angatuba	IB 5555	–	–	AF292585	AF292623	V	19
B. pauloensis (Amaral, 1925)	–	CLP 3	EU867260	EU867272	EU867284	EU867296	V	19
B. pubescens (Cope, 1870)	Uruguay, Rocha, Potrerillo de Santa Teresa	N132 (12S, 16S), N331 (cyt-*b*, ND4)	JN870180*	JN870192*	JN870200*	JN870206*	V	19
Bothriopsis (*B. medusa and B. oligolepis* not in analysis)								
B. bilineata (Wied, 1825)	Colombia, Letícia	–	AF057214	AF057261	AY223591	U41875	V	19
B. chloromelas (Boulenger, 1912)	Peru, Pasco Dept.	LSUMZ 41037	DQ305430	DQ305453	DQ305471	DQ305488	V	19
B. pulchra (Shreve, 1934)	Ecuador, Zamora Chinchipe	FHGO live 2142	JN870179*	–	AF292593	AF292631	V	19
B. taeniata (Wagler, 1824)	Suriname	–	AF057215	AF057262	AY223592	AY223637	V	19
Bothrops (*B. andianus, B. barnetti, B. lojanus, B. muriciencis, B. pirajai, B. roedingeri, B. sanctaecrucis,* and *B. venezuelensis* not in analysis)								
B. asper (Garman, 1883)	Costa Rica	MZUCR-11152	AF057218	AF057265	AY223599	U41876	V	19
B. atrox (Linnaeus, 1758)	–	WWW-743	AY223659	AY223672	AY223598	AY223641	V	19
B. brazili (Amaral, 1923)	Venezuela, Amazonas	USNM RWM17831	EU867252	EU867264	EU867276	EU867288	V	19
B. caribbaeus (Garman, 1887)	Saint Lucia	released after sampling	–	–	AF292598	AF292636	V	19
B. isabelae (Sandner Montilla, 1979)	–	–	–	–	AF292603	AF292641	V	19
B. jararacussu (Lacerda, 1884)	–	DPL-104	AY223661	AY223674	AY223602	AY223643	V	19
B. lanceolatus (Bonnaterre, 1790)	Martinique	–	–	–	AF292599	AF292637	V	19
B. leucurus (Wagler, 1824)	–	CLP195	EU867255	EU867267	EU867279	EU867291	V	19
B. marajoensis (Hoge, 1966)	Brazil, Pará, Ilha de Marajó	–	–	–	AF292605	AF292643	V	19
B. moojeni (Hoge, 1966)	Brazil, São Paulo, Itarapina	ITS 418	EU867257	EU867269	EU867281	EU867293	V	19
B. osbornei (Freire-Lascano, 1991)	Ecuador, Pichincha, Pedro Vicente Maldonado	FHGO live 2166	–	–	AF292595	AF292633	V	19
B. pictus (Tschudi, 1845)	Peru, Ayacucho, Pullo	MM OP	–	–	AF292583	AF292621	V	19
B. punctatus (Garcia, 1896)	–	FHGO live 2452	–	–	AF292594	AF292632	V	19
Azemiopinae								
Azemiops feae (Boulenger, 1888)	China	CLP-157	AF057187	AF057234	AY223559	U41865	O	5, 14
Outgroups								
Acrochordus granulatus (Schneider, 1799)	–	NUM-AZ0375	NC007400	NC007400	NC007400	NC007401		
Leioheterodon madagascariensis (Duméril, Bibron and Duméril, 1854)	Madagascar	no data (12S), MRSN-FAZC 10621 (16S, cyt-*b*), RAN 42543 (ND4)	AF544768	AY188061	AY188022	U49318		
Malpolon monspessulanus (Hermann, 1804)	Morocco (12S), Greece (16S, cyt-*b*), Spain (ND4)	E2509.18 (12S), HLMD RA-2606 (16S, cyt-*b*), MVZ 186256 (ND4)	DQ451927	AY188068	AY188029	AY058989		

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
Malpolon monspessulanus (Hermann, 1804)	Morocco (12S), Greece (16S, cyt-*b*), Spain (ND4)	E2509.18 (12S), HLMD RA-2606 (16S, cyt-*b*), MVZ 186256 (ND4)	DQ451927	AY188068	AY188029	AY058989		
Mimophis mahfalensis (Grandidier, 1867)	Madagascar	MZUSP 12188 (12S, ND4), HLMD J68 (16S, cyt-*b*)	AF544771	AY188071	AY188032	AF544662		
Psammophis condanarus (Merrem, 1820)	Thailand (12S, 16S), Myanmar (cyt-*b*, ND4)	RH 5601 (12S, 16S), CAS 205003 (cyt-*b*, ND4)	Z46450	Z46479	AF471075	AY058987		
Lamprophis fuliginosus (Boie, 1827)	unknown (12S), Tanzania (16S, cyt-*b*), Burundi (ND4)	SH1210 (12S), CAS 168909 (16S, cyt-*b*), no data (ND4)	AY122681	AY188079	AF471060	AF544664		
Ophiophagus hannah (Cantor, 1836)	unknown (12S, 16S), Myanmar (cyt-*b*, ND4)	RH 6081 (12S, 16S), CAS 206601 (cyt-*b*, ND4)	U96803	Z46480	AF217842	AY058984		
Bungarus fasciatus (Schneider, 1801)	unknown (12S, 16S), Myanmar (cyt-*b*), Brunei (ND4)	RH 63881 (12S, 16S), CAS 207988 (cyt-*b*), UMMZ 201916 (ND4)	Z46466	Z46501	AF217830	U49297		
Naja kaouthia (Lesson, 1831)	Thailand, Chumphon Prov.	WW585	EU624235	EU624269	EU624298	EU624209		
Naja naja (Linnaeus, 1758)	Nepal	WW595	EU624236	EU624270	EU624299	AY713378		
Naja nigricollis (Reinhardt, 1843)	northern Cameroon, Kaélé, Lara	Latoxan live coll. N.ni.ssp. 9735002	EU624237	EU624271	EU624300	AY713377		
Naja nivea (Linnaeus, 1758)	South Africa (12S, 16S), unknown (cyt-*b*, ND4)	WW1295 (12S, 16S), no data (cyt-*b*, ND4)	EU624238	EU624272	AF217827	AY058983		
Cerberus rynchops (Schneider, 1799)	Polillo (12S, 16S), Myanmar (cyt-*b*), Sabah (ND4)	USNM 497590 (12S, 16S), CAS 206574 (cyt-*b*), FMNH 251594 (ND4)	AF499289	AF499303	AF471092	U49327		
Natrix natrix (Linnaeus, 1758)	France	no data	AF158461	AF158530	AY866537	AY873736		
Contia tenuis (Baird and Girard, 1852)	unknown (12S, 16S), California (cyt-*b*, ND4)	no data (12S, 16S), CAS 202582 (cyt-*b*), CAS207044 (ND4)	AY577021	AY577030	AF471095	AF402656		
Diadophis punctatus (Linnaeus, 1766)	unknown (12S, 16S), Florida (cyt-*b*), California (ND4)	no data (12S, 16S), CAS 184351 (cyt-*b*), SDSNH 68893 (ND4)	AY577051	AY577023	AF471094	DQ364667		
Heterodon simus (Linnaeus, 1766)	unknown (12S, 16S), Florida (cyt-*b,* ND4)	no data (12S, 16S), CAS195598 (cyt-*b,* ND4),	AY577020	AY577029	AF217840	DQ902310		
Borikenophis portoricensis (Reinhardt and Lütken, 1862)	Puerto Rico (12S, 16S, cyt-*b*), British Virgin Islands (ND4)	SBH 160062 (12S, 16S), CAS 200813 (cyt-*b*), FK 2440 (ND4)	AF158448	AF158517	AF471085	U49308		
Farancia abacura (Holbrook, 1836)	Georgia (12S), unknown (16S, cyt-*b*), Florida (ND4)	RH 53660 (12S), no data (16S, cyt-*b*), UMMZ 205023 (ND4)	Z46467	AY577025	U69832	U49307		
Coronella girondica (Daudin, 1803)	unknown (12S), Morocco (16S, cyt-*b*, ND4)	no data (12S), E512.20 (16S), MVZ 178073 (cyt-*b*, ND4)	AY122835	AY643353	AF471088	AY487066		
Elaphe sauromates (Pallas, 1811)	unknown (12S, 16S), European Turkey (cyt-*b*, ND4)	SH972 (12S), no data (16S), LSUMZ 40626 (cyt-*b*, ND4)	AY122795	AF215267	AY486931	AY487067		
Dinodon semicarinatum (Cope, 1860)	unknown	no data	AB008539	AB008539	AB008539	AB008539		

Species	Locality	Voucher/sample	DNA				Rep. mode	Source
			12S	16S	cyt *b*	ND4		
Macroprotodon brevis (Günther, 1862)	Spain	E608.6 (12S, 16S, MVZ186073 (cyt-*b*, ND4)	AY643280	AY643321	AF471087	AY487064		
Eirenis modestus (Martin, 1838)	unknown (12S, 16S), Turkey (cyt-*b*, ND4)	no data (12S, 16S), HLMD J159 (cyt-*b*, ND4)	AY039143	AY376780	AY486933	AY487072		
Hemorrhois algirus (Jan, 1863)	unknown (12S), Tunisia (16S), Morocco (cyt-*b*, ND4)	MHNG 2415.6 (12S), E1110.1 (16S), HLMD RA1187 (cyt-*b*, ND4)	AY039149	AY643349	AY486911	AY487037		
Hemorrhois hippocrepis (Linnaeus, 1758)	unknown (12S), Morocco (16S), Spain (cyt-*b*, ND4)	MHNG 2415.94 (12S), E2509.2 (16S), MNN 11988 (cyt-*b*, ND4)	AY039158	AY643350	AY486916	AY487045		
Hemorrhois nummifer (Reuss, 1834)	unknown (12S), Armenia (16S, cyt-*b*, ND4)	SH548 (12S), ZISP 27709 (16S, cyt-*b*, ND4)	AY039163	AY376771	AY376742	AY487049		

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