Fossil calibration dates for molecular phylogenetic analysis of snakes 1: Serpentes, Alethinophidia, Boidae, Pythonidae

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ABSTRACT

Snakes possess a dense fossil record through the Late Cretaceous and Cenozoic and are an important clade for studies of molecular phylogenetics. The use of the snake fossil record has historically been a limited and inaccurate source of temporal data in molecular studies due to taxonomic and phylogenetic ambiguities. Here I provide 10 fossil calibration dates for phylogenetic analysis of higher-order interrelationships of snakes. Calibration points include apomorphy-based systematic justifications and precise dates for hard minimum divergence timings. Calibrated nodes are for the snake total clade, Alethinophidia, and boid and pythonid taxa. Hard minimum divergence timings range from earliest late Cretaceous to middle Miocene. These dates provide precise minima for constraining the early evolutionary history of Serpentes. Comparisons of phylogenetically justified calibrations with published studies that employed form-taxon assignments suggests greatly younger divergences for justified nodes and indicates that deep-time divergence estimates that have been correlated with tectonic histories may be considerably too old and reliant on presumptions of Early Cretaceous Gondwanan vicariance as a mechanism of speciation.

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INTRODUCTION

Serpentes has been a common study taxon for molecular phylogenetic analyses, both with respect to its position within Squamata and the interrelationships of constituent subclades (e.g., Heise et al., 1996; Slowinski and Lawson, 2002; Vidal and Hedges, 2002; Wilcox et al., 2002; Vidal and David, 2004; Vidal and Hedges, 2004, 2009; Lawson et al., 2004; Townsend et al., 2004; Bur-

brink, 2005; Gower et al., 2005; Lawson et al., 2005; Noonan and Chippindale, 2006a; Burbrink and Lawson, 2007; Sanders et al., 2010; Wiens et al., 2012; Pyron et al., 2013). The fossil record of snakes has been used to calibrate divergence timings in multiple phylogenies (e.g., Sanders et al., 2010; Pyron and Burbrink, 2012), including studies that have correlated fossil-based divergence timings with geologic and climatic events (Noonan and Chippindale, 2006a, 2006b). Despite this usage, the efficacy of snake fossils for calibration has historically been hampered by the nature of the fossil record and methodological approaches to systematics (see Sanders et al., 2010 for additional discussion).

The majority of the fossil record of snakes consists of isolated or associated precloacal vertebrae (e.g., Rage, 1984; Holman, 2000), and although snakes possess morphologically complex and distinct vertebral morphology relative to other squamates (e.g., Hoffstetter and Gasc, 1969), there is a finite number of discrete apomorphies available from which phylogenetic hypotheses can be inferred from vertebrae. Historically, studies of snake fossils have relied on general similarity, "gestalt" approaches, and spatiotemporal provenance for systematic assignments (see Rage, 1984; Holman, 2000, Bell et al., 2004; Head, 2005; Bell et al., 2010, for examples of application, discussion, and critique). The result of these methods is often the application of phylogenetically explicit clade names and identities to generalized form taxa that have no phylogenetic rationale (e.g., Szyndlar et al., 2008), which can produce widely inaccurate calibration points (e.g., Noonan and Chippindale, 2006a after Parham et al., 2012). Additionally, many extant snake taxa are not recognized in the fossil record (Figure 1), or have first occurrences that greatly postdate divergence timings estimated from the fossil record of sister taxa. Despite these limitations, the fossil record of snakes is dense and continuous from the Late Cretaceous on, and thus is an important datum for constraining the historical relationship between environmental change and biological evolution for a diverse and important vertebrate clade.

Here I provide a set of fossil calibration points for snake phylogeny, following the guidelines of Parham et al. (2012). Despite a long history of pronounced discordance between morphological and molecular phylogenetic hypotheses of Serpentes (e.g., Lee and Scanlon, 2002; Slowinski and Lawson, 2002; Wiens et al., 2010; Gauthier et al., 2012), fossils can be placed in molecular topolo-

gies where there is congruence in clade composition and discrete apomorphies can be identified for fossil specimens. As a result, the fossil record of snakes can be used to temporally calibrate molecular nodes (Figure 1). Molecular phylogenetic topologies are generally consistent for higher-order snake clades, but several crucial nodes, including the sister taxon to Serpentes, as well as the relationships of "aniliods", are controversial or poorly resolved between molecular studies (e.g, Wilcox et al., 2002; Vidal and Hedges, 2004; Gower et al., 2005; Reynolds et al., 2014). Except where noted, referred divergences are from the most recent and comprehensive molecular phylogenetic analyses (Pyron et al., 2013; Reynolds et al., 2013, 2014). This set of calibrations is the first of two, and focuses on the oldest Mesozoic and Paleogene calibration points, as well as calibrations for boid and pythonid taxa (sensu McDiarmid et al., 1999). Calibration dates for Caenophidia, the majority of snake diversity, will compose the second set.

Institutional Abbreviations

DGM, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; HJU-PAL EJ, Hebrew University of Jerusalem, Paleontological Collections, Jerusalem, Israel; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts, USA; MML-PV, Museo Municipal de Lamarque, Rio Negro, Argentina; MNHN, Muséum national d'Historie Naturelle, Paris, France; OMNH, Oklahoma Museum of Natural History, Oklahoma, USA; PTRM, Pioneer Trails Regional Museum, North Dakota, USA; QM F, Queensland Museum, Queensland, Australia; UF/IGM, University of Florida, Instituto Nacional de Investigaciones Geologico-Mineras, Bogota, Colombia; UNSM, University of Nebraska State Museum, Nebraska, USA.

PAN-SERPENTES

Node Calibrated. Divergence between the total clade of Serpentes and its nearest crown sister taxon: Iguania, Anguimorpha, or (Iguania+Anguimorpha).

Fossil Taxon. *"Coniophis* sp." (Gardner and Cifelli, 1999), best regarded as "Pan-Serpentes indeterminate."

Specimen. OMNH 33520, isolated precloacal vertebra.

Additional Materials. OMNH 33521, isolated precloacal vertebra.

Phylogenetic Justification. Both specimens possess unambiguous apomorphies of all known total clade Serpentes, including a well-developed zygo-
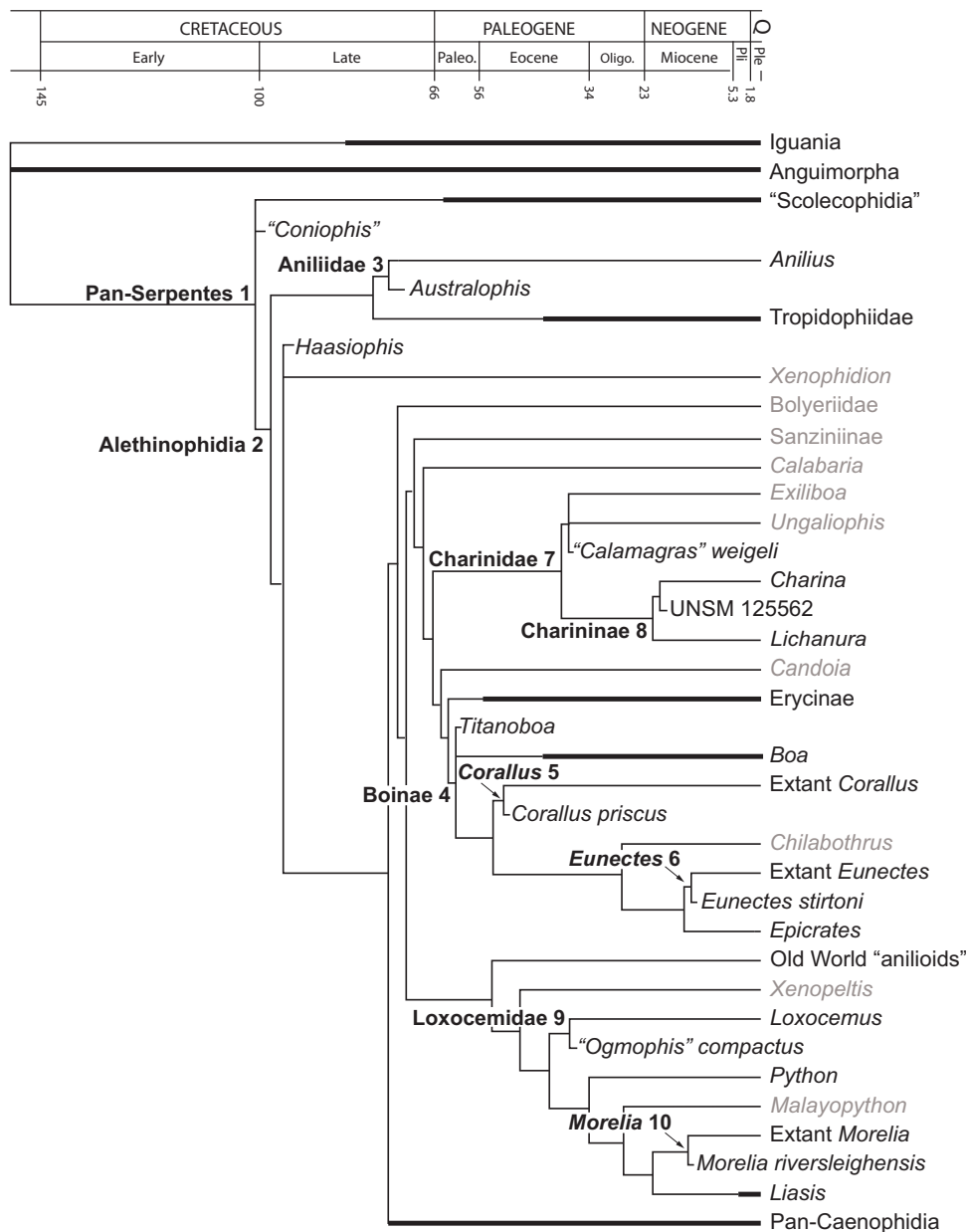
FIGURE 1. Time-calibrated phylogeny of Serpentes based on Pyron et al. (2013) and Reynolds et al. (2014). Numbers represent calibrated nodes in text. Fossil taxa are the calibration points for their respective nodes. Thickened bars represent well-sampled, taxonomically resolved stratigraphic distributions for the sister taxa to Pan-Serpentes and snake lineages whose first occurrences are determined by older sister taxa. Thin bars represent estimated stratigraphic distributions for taxa with poorly resolved fossil records, or no published fossil record (names in grey). "Scolecophidia" represents a paraphyletic grade with respect to Alethinophidia (see text).

sphene-zygantral articulation consisting of a transversely wide zygosphene with dorsolaterally angled articular facets and a medially convex anterior margin, and a deep zygantrum with distinct ventromedially angled articular facets. Additional characters include synapophyses with distinct para- and diapophyseal articular surfaces, and well-developed intergyapophyseal ridges. These

characters do not differentiate between crown and stem taxa, and there are no diagnostic characters present, or defined, for *Coniophis* (see below).
Minimum Age. 98.32 Ma (98.39 ± 0.07 Ma, Cifelli et al., 1997), early Cenomanian (Ogg et al., 2012).
Soft Maximum Age. ~113 Ma, Aptian-Albian boundary (Ogg et al., 2012).

Age Justification. Both specimens were collected in the uppermost Cedar Mountain Formation (Mussentuchit Member), Emery County, Utah. The Cedar Mountain Formation spans the Early Cretaceous and Early-Late Cretaceous transition (Cifelli et al., 1997). $^{40}Ar/^{39}Ar$ dating of Sanidine phenocrysts from smetitic ash horizons directly overlying snake-bearing fossil localities produced a weighted mean age of 98.39 ± 0.07 Ma, which is used as the hard minimum age for Serpentes. The soft maximum age is based on uncertainty in age estimates for late Albian snakes from Algeria (see discussion below).

Discussion. Gardner and Cifelli (1999) assigned the specimens to *Coniophis* on the basis of seven characters they considered diagnostic for the genus. The majority of the listed characters are either plesiomorphic for Serpentes (e.g., absence of prezygapophyseal accessory processes), or characteristic of fossorial ecomorphology (reduction of neural spine, absence of posteromedian notch, high-angled prezygapophyses). Only a single vertebral apomorphy has been proposed for *Coniophis*, a deep, ovate paracotylar fossae (Longrich et al., 2012), but this feature is present in a wide variety of taxa (e.g., Rage, 1984). Specimens assigned to *Coniophis* have been considered either "anilioids" (e.g., Hecht, 1959), or stem snakes (Longrich et al., 2012), but the Cedar Mountain record is not informative on the systematic relationships of "*Coniophis*". Similarly, the lack of phylogenetic resolution of the Cedar Mountain record limits calibration to a minimum age for Serpentes relative to the most closely related crown taxon and not calibrations within the clade.

The oldest fossil records of potential sister taxa to Pan-Serpentes provide disparate alternate calibrations from the oldest snake record. Current molecular phylogenies place Serpentes with Anguimorpha and Iguania (e.g., Townsend et al., 2004; Vidal and Hedges, 2005; Pyron et al., 2013) in the clade Toxicofera (Vidal and Hedges, 2005). Interrelationships of the three clades within Toxicofera include moderately supported monophyly of (Iguania+Anguimorpha) or (Anguimorpha+Serpentes) (Pyron et al., 2013). Numerous Mesozoic fossils have been referred to Anguimorpha; however, only *Dorsetisaurus* from the Lulworth Formation (Early Cretaceous, Berriasian) is consistently recognized as anguimorph (e.g., Hoffstetter, 1967; Evans, 1994; Evans et al., 2005; Conrad, 2008; Conrad et al., 2011). If either of the aforementioned phylogenetic hypotheses within Toxicofera is accurate, then the occurrence of *Dorsetisaurus* mini-

mally extends the age of the snake total clade to approximately 145 Ma at the base of the Berriasian. Assignment of late Jurassic specimens from North America to *Dorsetisaurus* is based on tooth crown morphology (Evans and Chure, 1998), whereas the Berriasian-aged type specimen of the genus is based on a taxonomically definitive skull (Hoffstetter, 1967). If further discovery provides more robust assignment of Tithonian-aged fossils to the taxon, then the calibrated age of Pan-Serpentes would be extended to ~152 Ma.

Conversely, if Iguania is the sister-taxon to Pan-Serpentes, then the first occurrence of the snake total clade may approximate the age of Cedar Mountain Formation record. The Early Cretaceous (Barremian, ~131 Ma) *Hoyalacerta* (Evans and Barbadillo, 1999) has been considered either a stem squamate or stem iguanian (Evans and Barbadillo, 1999; Conrad, 2008; Bolet and Evans, 2011), but the oldest unambiguous iguanians are recovered from the Late Cretaceous (Campanian, ~84 Ma) of Asia (e.g., Gao and Hou, 1995; Gao and Norell, 2000; Conrad and Norell, 2007; Alifanov, 2013), approximately 16 Ma younger than the oldest fossil record of Pan- Serpentes.

Lack of phylogenetic consensus within Toxicofera combined with great differences in first occurrence dates between Anguimorpha and Iguania result in potential temporal range extensions for Pan-Serpentes from 52 Ma to 0 Ma older than the Cedar Mountain Formation record. The "*Coniophis*" record described here is used to calibrate the snake total clade due to systematic ambiguity within Toxicofera and the absence of any definitive Early Cretaceous, but with the explicit recognition that a resolved sister taxon relationship between either Serpentes and Anguimorpha or Iguania and Anguimorpha requires a much older first occurrence for Pan-Serpentes.

If the "*Coniophis*" record falls within the crown Serpentes, then it predates the first occurrence of constituent clades by only ~ 4 Ma, based on the minimum age for the first occurrence of Alethinophidia (see below). Scolecophidia, the clade including Typhlopidae, Leptotyphlopidae and Anomalepididae, has been rendered paraphyletic in early and recent molecular analyses (Heise et al., 1996; Wiens et al., 2012). The oldest fossil records referred to scolecophidians are ?Anomalepididae from the Tornillo Formation (early Paleocene, Puercan ~ 65 Ma) of Texas (Standhardt, 1986; Schiebout et al., 1987), and Scolecophidia indet. from the late Paleocene of Morocco (Augé and Rage, 2006). Temporal differences between these

records and the calibrations for Pan-Serpentes and Alethinophidia (see below) indicate unrecovered histories of ~28- 45 Ma for Scolecophidia sensu lato (Figure 1).

The radiometric dates of the uppermost Cedar Mountain Formation provide the most accurate precise minimum age for the snake total clade, but older records have been reported. Hoffstetter (1959) described *Lapparentophis defrennei* from the Akhamil (Albian) of Algeria, but Akhamil has been reassessed as being either latest Albian or early Cenomanian (Cuny et al., 1990), approximately coeval with the Cedar Mountain record. Cuny et al. (1990) described Lapparentopheidae indet. and Serpentes indet. from El Kohol in Algeria, and reported the age of the specimens as late Albian. No evidence was provided for this age estimate, however. Other Cenomanian snake records include the marine pachyostotic taxa *Pachyrhachis*, *Haasiophis*, *Eupodophis*, *Mesophis*, *Pachyophis*, and *Simoliophis* from North Africa, Europe, and the Middle East (e.g., Nopcsa, 1923, 1925; Bolkay, 1925; Haas, 1979, 1980; Nessov et al., 1998; Tchernov et al., 2000; Rage and Escuillié, 2000, 2003), as well as the terrestrial taxon *Pouitella* and indeterminate or stem snakes from France (Rage, 1988; Vullo et al., 2011) and Brazil (Hsiou et al., 2009, 2014). All of these records have been estimated to be early to middle Cenomanian, in age, but are less temporally constrained than the Cedar Mountain record. A diverse snake fauna including madtsoiids, nigerophiids, palaeopheids, and Colubroidea from the Wadi Milk Formation of Sudan was originally estimated as Cenomanian in age (Rage and Werner, 1999), but is currently considered Maastrichtian (J. Müller, personal commun., 2013).

CROWN ALETHINOPHIDIA

Node Calibrated. Divergence between total clade (Aniliidae +Tropidophiinae) and total clade Macrostomata.

Fossil Taxon. *Haasiophis terrasanctus* Tchernov et al., 2000.

Specimen. HJU-PAL EJ 695, complete skeleton.

Phylogenetic Justification. *Haasiophis* is placed within Alethinophidia as either a stem or crown macrostomatan on the basis of numerous characters including (but not limited to): quadrate suspended from free-ending process of the supratemporal; anterior dentigerous process of palatine; "alethinophidian type" (Zaher and Rieppel, 1999) tooth attachment; and loss of pre-

maxilla-maxillary articulation (e.g., Tchernov et al., 2000; Gauthier et al., 2012).

Minimum Age. 93.9 Ma.

Soft Maximum Age. 100.5 Ma.

Age Justification. Minimum and maximum ages are for the Cenomanian (Ogg et al., 2012). The only specimen of *Haasiophis* was recovered from the 'Ein Yabrud quarries in the Judean hills, Israel. 'Ein Yabrud is located in either the late Cenomanian Amminadav Formation or underlying early Cenomanian Bet Meir Formation (Chalifa and Tchernov, 1982; Chalifa, 1985; Braun and Hirsch, 1994). Fish biostratigraphy has been used to infer an early Cenomanian age for 'Ein Yabrud as part of the Bet Meir Formation (Chalifa and Tchernov, 1982), but subsequent placement of localities at the base of the Amminadav Formation (Chalifa, 1985; Braun and Hirsch, 1994) suggests a middle-late Cenomanian age, and 'Ein Yabrud is more recently considered early-middle Cenomanian (Tchernov et al., 2000; Rieppel et al., 2003). The age range presented here reflects both the overall uncertainty of the position of 'Ein Yabrud within the Cenomanian, and the absence of any definitive snake fossils globally prior to the earliest Late Cretaceous.

Discussion. Both *Haasiophis* and *Pachyrhachis problematicus* are from the same horizon in 'Ein Yabrud (Haas, 1979, 1980) but HJU-PAL EJ 695 is chosen as a calibration point because it is better preserved and more complete than any other single Mesozoic snake specimen.

The systematic relationships of *Haasiophis* have been controversial. The taxon has been considered a macrostomatan in most morphological phylogenetic analyses of snakes (e.g., Tchernov et al., 2000; Apesteguía and Zaher, 2006; Wilson et al., 2010 [as part of Pachyophiidae]; Longrich et al., 2012; Zaher and Scanferla, 2012). However, other analyses of snake phylogeny have placed *Haasiophis* along the snake stem based on alternate interpretations of skeletal morphology (Lee and Scanlon, 2002; Scanlon, 2006; Palci et al., 2013). Recent comprehensive analyses of Squamata based on morphology have placed *Haasiophis* within Alethinophidia as either sister-taxon to (Conrad, 2008) or nested within (Gauthier et al., 2012) Macrostomata. Molecular phylogenetic analyses do not explicitly identify Macrostomata (e.g., Pyron et al., 2013), but Macrostomata is employed here as the total clade of alethinophidians more closely related to each other than any are to (Aniliidae +Tropidophiinae) (e.g., Pyron et al., 2013, figure 21). Combined morphological and molecular

analysis of Squamata similarly places the taxon within a clade of "macrostomatans" (Wiens et al., 2010), and this topology is employed for calibration with the important caveat that tropidophiines, which possess macrostromatan suspensorial morphology but are sister taxon to Aniliidae in molecular phylogenetic analyses, have not been incorporated in combined analyses.

ANILIIDAE

Node Calibrated. Divergence between total clades Aniliidae and Tropidophiidae.
Fossil Taxon. *Australophis anilioides* Gómez et al., 2008.
Specimen. MML-PV181, precloacal vertebra.
Phylogenetic Justification. Assignment to Aniliidae Stejneger, 1907 sensu MacDiarmid et al. (1999) is based on the following apomorphic character combination: low neural arch does not rise much above zygapophyseal plane, neural spine reduced, elongate prezygapophyses that are elongate and high-angled, concave posterior margin of neural arch (Goméz et al., 2008).
Minimum Age. 72.1 Ma (Campanian-Maastrichtian boundary).
Soft Maximum Age. Indeterminate.
Age Justification. The Allen Formation is dated as late Campanian-Early Maastrichtian based on its stratigraphic position overlying the Anacleto Formation and underlying the Jagüel Formation (Gómez et al., 2008). The Anacleto Formation is dated to late Campanian based on magnetostratigraphic correlation to Chron C33R (83.5-79.5 Ma) (Dingus et al., 2000), whereas the Jagüel Formation is dated as mid-Maastrichtian to early Danian based on foraminiferal biostratigraphy (Leanza et al., 2004; Gómez et al., 2008). The horizon within the Allen Formation that produced *Australophis* specimens is measured at 48 meters below the K-Pg boundary and is considered no younger than early Maastrichtian (Gómez et al., 2008). The exact minimum age provided is for the Campanian-Maastrichtian boundary, which is likely to be slightly older than the actual age of the type specimen of *Australophis*.
Discussion. Molecular phylogenetic analyses consistently recover monophyly of *Anilius* with Tropidophiinae as the sister taxon to all other alethinophidians (e.g., Wilcox et al., 2002; Gower et al., 2005; Pyron et al., 2013), despite morphological support for tropidophiines being deeply nested macrostomatans and *Anilius* being nested within a monophyletic Anilioidea as sister taxon to South Asian *Cylindrophis*, *Anomochilus*, and Uro-

peltinae (e.g., Lee and Scanlon, 2002; Wilson et al., 2010; Gauthier et al., 2012). If future molecular studies corroborate morphological phylogenetic hypotheses then *Australophis* represents the oldest occurrence of crown group Anilioidea.

The fossil record of aniliids includes specimens from the Late Cretaceous through Cenozoic of South America and the Paleogene of North America (e.g., Hecht, 1959; Hoffstetter and Rage, 1977; Hecht and LaDuke, 1997; Rage, 1998; Head et al., 2006; Hsiou et al., 2010). Among named taxa, *Australophis* was considered morphologically most similar to extant *Anilius* and Paleogene *Hoffstetterella* from Brazil (Goméz et al., 2008), however, the taxon shares a thickened zygosphene with *Colombophis* from the Miocene of Colombia and Venezuela (Hoffstetter and Rage, 1977; Head et al., 2006; Hsiou et al., 2010). No explicit phylogenetic topology yet exists for *Australophis* relative to other aniliids.

Constraining the first occurrence of Tropidophiidae is especially problematic because the composition of the clade is controversial in addition to the aforementioned discrepancies between molecular and morphological phylogenetic hypotheses of the taxon within Alethinophidia. Fossil taxa have been assigned to Tropidophiidae based on size and general shape (e.g., *Dunnophis* Hecht, 1959; *Falseryx* Szyndlar and Rage, 2003). Attempts to devise morphological diagnoses for recognizing fossils have been based on an explicit use of a monophyletic Tropidophiidae consisting of extant ((*Tropidophis* + *Trachyboa*) + Ungaliophiinae), following McDowell (1987). Both Molecular and morphological phylogenies have proposed paraphyly of this clade (e.g., Wilcox et al., 2002; Scanlon, 2006), however, and only a single distinct vertebral apomorphy, the presence of anteroposteriorly elongate, squared off ventral hypapophyses in precloacal vertebrae, occurs in Tropidophiidae = (*Tropidophis* + *Trachyboa*). The oldest record of the clade based on this character is *Szyndlaria aureomontensis* from the middle Eocene of Lissieu, France (Augé and Rage, 2010). Lissieu is considered to correspond to the late Lutetian stage (Augé and Rage, 2010), which is no younger than 41.2 Ma (Vandenberghe et al., 2012). The late Lutetian is here used as the minimum first occurrence of crown Tropidophiidae (Figure 1).

BOINAE

Node Calibrated. Divergence between total clades Boinae and Erycinae.

Fossil Taxon. *Titanoboa cerrejonensis* Head et al., 2009.

Specimen. UF/IGM 1, precloacal vertebra.

Phylogenetic Justification. *Titanoboa* was united with Boinae on the basis of paracotylar fossae and foramina, straight, posteromedially angled interzygapophyseal ridges, and a vaulted posterior neural arch (Head et al., 2009).

Minimum Age. 58 Ma (Jaramillo et al., 2007).

Soft Maximum Age. ~64 Ma (Woodburne et al., 2014).

Age Justification. The minimum age is the youngest age estimate for palynological zone CU-02, which contains the horizon from which *Titanoboa* fossils were recovered in the Cerrejón Formation of Colombia (Jaramillo et al., 2007; Head et al., 2009). The soft maximum age is the maximum age estimate for the Tiupampan SALMA (Woodburne et al., 2014), the oldest SALMA that includes the oldest reported records of boid snakes (Albino and Brizuela, 2014).

Discussion. Head et al. (2009) did not provide an explicit phylogenetic hypothesis for relationships of *Titanoboa* within Boinae, but united the taxon with *Boa* on the basis of paracotylar foramina morphology. Albino and Brizuela (2014) additionally noted a convex anterior zygosphene margin as a shared character of *Titanoboa* and extant *Boa*. Preliminary analysis of cranial elements suggests *Titanoboa* may be on the boine stem (Head et al., 2013). Molecular hypotheses place *Boa* as the sister taxon to all other boines (e.g., Burbrink, 2005). As a result, the occurrence of *Titanoboa* provides a minimum age for the boine-erycine (Pyron et al., 2013) divergence regardless of its position with respect to either *Boa* or the boine crown.

With respect to differences between the boine total clade calibration and known temporal ranges of crown Boinae and total clade Erycinae, the minimum age estimate for *Titanoboa* is only ~ 8 Ma older than the oldest extant boine lineage (see *Corallus* below), and is ~ 16 Ma older than the oldest described record for *Boa* (Albino, 1993) from the late Eocene (Barrancan ~ 41.6-39.0 Ma Ré et al., 2010) of Argentina. The oldest diagnostic record of the erycine total clade is an apomorphic caudal vertebra from the early Eocene (Ypresian ~55 Ma) of France (Rage, 1977), and implies at least a three million year unrecovered history between Erycinae and the minimum age of *Titanoboa* (Figure 1). The erycine record is dense through the Cenozoic of Europe (e.g., Hoffstetter and Rage, 1972; Szyndlar and Schleich, 1994), and caudal vertebral morphology is diagnostic at generic levels for both fossil taxa and the traditional split between extant *Eryx* and *Gonglyophis* (Sood, 1941; Hoffstetter and Rage, 1972; Rage, 1972; Szyndlar, 1994). Molecular analyses have recovered a paraphyletic *Eryx* with respect to *Gongylophis* (e.g., Pyron et al., 2013), however, which limits the use of caudal vertebral morphology in calibrating divergences within crown Erycinae.

CORALLUS

Node Calibrated. Divergence between total clade *Corallus* and the total clade (*Chilabothrus*+(*Epicrates*+*Eunectes*)).

Fossil Taxon. *Corallus priscus* Rage, 2001.

Specimen. DGM 1332-R precloacal vertebra (holotype).

Additional Materials. 74 precloacal vertebrae.

Phylogenetic Justification. *Corallus priscus* was assigned to the genus *Corallus* by Rage (2001) on the basis of: horizontal zygapophyseal articular facets, vaulted neural arch, and a tall neural spine. Additionally, *C. priscus* shares small, irregularly occurring paracotylar foramina with extant species of the genus. The combination of neural spine height and anteroposterior width, bi-angled interzygapophyseal ridges, and zygosphene shape make specimens of *C. priscus* indistinguishable from extant *Corallus*.

Minimum Age. 50.2 Ma.

Soft Maximum Age. ~64 Ma (Woodburne et al., 2014).

Age Justification. *Corallus priscus* was recovered from fissure fills in travertine deposits at the locality of São José de Itaboraí in Rio de Janeiro, Brazil. The travertine layers are unconformably overlain by a basalt flow dated at 52.6 ± 2.4 Ma (Riccomini and Rodrigues-Francisco, 1992; Gomes Sant'Anna and Riccomini, 2001; Woodburne et al., 2014), which provides a hard minimum age for the taxon. The soft maximum age is the same as for *Titanoboa*.

Discussion. The fossil record of *Corallus* from Itaboraí represents the oldest record of an extant boid genus, and constrains the divergence of Neotropical Boinae to no younger than approximately 50 Ma. Molecular phylogenetic analyses place *Boa constrictor* as the sister taxon to *Corallus* + *Chilabothrus*+(*Eunectes*+ *Epicrates*) (Burbrink, 2005; Pyron et al., 2013; Reynolds et al., 2013, 2014). The first occurrence of *Boa* (Figure 1) and molecular topologies thus implies an approximately 19 Ma unrecovered history of the genus between the maximum age of the Barrancan SALMA and the

hard minimum age for *Corallus* (Head et al., 2012), assuming *Titanoboa* is a stem boine.

EUNECTES

Node Calibrated. Divergence between total clade *Epicrates* and *Eunectes*

Fossil Taxon. *Eunectes stirtoni* Hoffstetter and Rage, 1977.

Specimen. MNHN, VIV 7, right prootic.

Phylogenetic Justification. *Eunectes stirtoni* was erected and united with *Eunectes* within Boinae on the basis of diagnostic morphology including a shortened posterior margin behind the posterior trigeminal nerve foramen; an incomplete anterior trigeminal nerve foramen, a prominent, long "prootic process" (Tchernov et al., 2000) that forms the lateral edge of a narrow, well defined canal for the Vidian nerve (Hoffstetter and Rage, 1977).

Minimum Age. 12.375 Ma.

Soft Maximum Age. Indeterminate.

Age Justification. The type specimen of *E. stirtoni* was recovered from the Fish Bed of the Baraya member of the lower Villavieja Formation in the upper Magdalena River valley in central Colombia (Hoffstetter and Rage, 1977). ^{40}Ar/^{39}Ar dating of pumices from the underlying Monkey Beds and overlying San Francisco St. Beds of the Cerro Colorado Member of the Villavieja Formation constrains the ages of the Fish Bed to between 12.649 ± 0.258 and 12.111 ± 0.259 Ma (Flynn et al., 1997). The Fish Bed directly overlies the Monkey Beds, and the minimum age estimate for the Monkey Beds, 12.486 ± 0.111 Ma (Flynn et al., 1997), is used here as the minimum estimate for the *Eunectes*-*Epicrates* divergence.

Discussion. Morphology of the prootic and an associated basisphenoid referred to *Eunectes stirtoni* are very similar in general shape and discrete characters to extant *E. murinus* (Hoffstetter and Rage, 1977). Other fossils referred to *Eunectes* have been recovered from the middle-late Miocene of periequatoral South America, including La Venta in Colombia (Hoffstetter and Rage, 1977; Hecht and LaDuke, 1997), Venezuela (Head et al., 2006; Hsiou and Albino, 2010), and Brazil (Hsiou and Albino, 2009, 2010). These records consist of isolated or associated precloacal vertebrae, and referral to genus is based on overall similarity instead of discrete apomorphies. The Villavieja Formation record of *Eunectes* provides a minimum divergence timing for both (*Eunectes*+*Epicrates*) and (*Chilabothrus*+(*Epicrates*+*Eunectes*)) (Reynolds et al., 2013). If *E. stirtoni* is most closely related to *E. murinus*, then

the record described here minimally constrains divergence timings within the genus. Neogene fossil vertebrae have been compared with *Epicrates* (Hsiou and Albino, 2010), but this record cannot differentiate between that taxon and the newly recognized *Chilabothrus*, (Reynolds et al., 2013) and is not considered for calibration.

CHARINIDAE

Node Calibrated. Divergence between the total clades Ungaliophiinae (*Ungaliophis*+*Exiliboa*) sensu Pyron et al. (2014) and total clade Charininae (*Charina*+*Lichanura*) sensu Pyron et al. (2014).

Fossil Taxon. *Calamagras weigeli*.

Specimen. PTRM 19607, caudal vertebra.

Additional Materials. 19609, 19681, caudal vertebrae.

Phylogenetic Justification. Caudal vertebrae lacking paired haemapophyses, haemal keels present. This morphology is only present in *Ungaliophis* and *Exiliboa* among extant taxa (Smith, 2013).

Minimum Age. 35.2 Ma.

Soft Maximum Age. Indeterminate.

Age Justification. Minimum age is based on faunal correlation of Medicine Pole Hills fossil localities (Bowman County, North Dakota) with Flagstaff Rim localities (Natrona County, Wyoming), which are overlain by an ash layer (Ash B) that is ^{40}Ar/^{39}Ar dated at 35.41 ± 0.14 Ma (Obradovich et al., 1995). Smith (2011) recalculated the minimum estimate for the Medicine Pole Hills local fauna at 35.2 Ma.

Discussion. Numerous fossil taxa have been described as ungaliophiines, either explicitly as related to (*Ungaliophis*+*Exiliboa*) (e.g., Rage, 2008), or as part of a "Tropidophiidae" (Szyndlar et al., 2008) that is not supported by either morphological (Zaher, 1994) or molecular data (e.g., Wilcox et al., 2002). As noted by Smith (2013), the only fossil record that is united with (*Ungaliophis*+*Exiliboa*) on the basis of discrete apomorphies consists of isolated cloacal vertebrae assigned to *Calamagras*. Generic assignment of isolated vertebrae to *Calamagras* is problematic in that the generic and specific diagnoses for the taxon are do not include unique apomorphies or character combinations relative to other coeval, fossils, and are redundant with each other as described (Holman, 2000). Referral to *Calamagras* is tentatively followed here, but until the taxonomy and systematics of the genus can be unambiguously resolved, the record described in Smith

(2013) must be used as the minimum divergence timing for the total clade, and stratigraphically older records of the genus (e.g., Hecht, 1959; Rage, 1977; Danilov and Averianov, 1999) should not be cited. Usage of Charinidae follows Pyron et al. (2014).

CHARININAE

Node Calibrated. Divergence between total clades *Charina* and *Lichanura*.
Fossil Taxon. Gen et sp. nov.
Specimen. UNSM 125562, caudal tailclub.
Phylogenetic Justification. UNSM 125562 is referred to the total clade of *Charina* (all fossil taxa more closely related to extant *Charina* than extant *Lichanura*) on the basis of the following caudal vertebral characters: 1) caudal tailclub composed of more than six vertebrae; 2) laterally expanded, lobate distal neural spine; 3) Anteriorly directed pterapophyses (="postzygapophyseal wing" of Szyndlar, 1994) present (Kluge, 1993; Szyndlar, 1994; Parham et al., 2012).
Minimum Age. 18.7 Ma (Tedford et al., 2004).
Soft Maximum Age. Indeterminate.
Age Justification. The minimum age is derived from radiometric dating of the Eagle Crag Ash, which overlies the top of the Harrison Formation, to 19.2 ± 0.5 Ma (MacFadden and Hunt, 1998; Tedford et al., 2004). Tedford et al. (2004, figure 6.2) indicate the top of the Harrison Formation may be as old as 20 Ma. Phylogenetic ambiguity in the fossil record of small boid snakes from North America (e.g., Holman, 2000 after Smith, 2013) greatly limits inference of a soft maximum as of this writing.
Discussion. The *Charina*+Ungaliophiinae divergence was previously calibrated at no younger than 16 Ma, based on a record of tailclubs from the Split Rock Formation of Wyoming (Parham et al., 2012). The Split Rock Formation is within the Hemingfordian NALMA, the top of which is dated at 16.0 Ma. Discovery of specimens referable to the total clade of (*Ungaliophis*+*Exiliboa*) from the Chadron Formation (Smith, 2013) extends that calibration point to 35.2 Ma. Ossified tailclubs referable to the *Charina* total clade from the Armstrong Ranch Quarry in the Harrison Formation of Sioux County Nebraska, extend the minimum age calibration of Charininae to 18.7 Ma, the youngest age estimate for the top of the Harrison Formation (Tedford et al., 2004). *Lichanura* has been reported from the middle Eocene Bridger Formation, based on synonymy of the fossil genus *Paraepicrates* to *Lichanura* (Hecht, 1959; Kluge, 1988). The basis for referral to *Lichanura* was based on two precloa-

cal characters (narrow-based neural spine and shallow neural arch posteromedian notch, Kluge, 1988), neither of which is diagnostic for the genus. In the absence of an unambiguous fossil record for *Lichanura*, the Miocene fossil record of apomorphic caudal tailclubs is recognized as the oldest record for *Charina* and constrains the minimum divergence between it and *Lichanura*. Usage of Charininae follows Pyron et al. (2014).

LOXOCEMIDAE

Node Calibrated. Divergence between total clades Loxocemidae and Pythonidae.
Fossil Taxon. "*Ogmophis*" *compactus*.
Specimen. PTRM 19378, left quadrate.
Phylogenetic Justification. PTRM 19378 is united with Loxocemidae on the basis of: 1) dorsal head expanded into broad plate; 2) dorsal head lies wholly in saggital plane; 3) well-defined lip present on lateral side of dorsal margin (Smith, 2013).
Minimum Age. 35.2 Ma.
Soft Maximum Age. Indeterminate.
Age Justification. Justification follows the rationale for Charinidae above.
Discussion. Morphological phylogenetic analyses of snakes have traditionally recovered either monophyly of (*Loxocemus* +*Xenopeltis*) as the sister-taxon to all other macrostomatans (e.g., Lee and Scanlon, 2002; Scanlon, 2006), or as a paraphyletic grade at the base of Macrostomata (Tchernov et al., 2000). Molecular phylogenetic analyses recover *Loxocemus* as the sister taxon of Pythonidae (e.g., Slowinski and Lawson, 2002; Pyron et al., 2013). Based on molecular topologies, PTRM 19378 constrains (Loxocemidae+Pythonidae) to no younger than late Paleogene. Smith (2013) associated isolated cranial elements including PTRM 19378 with vertebrae assigned to the vertebral form genus *Ogmophis* based primarily on relative abundances of elements collected by dry-screening and surface collection from a single locality, PTRM V89002 (Smith, 2013). As with *Calamagras* (see above), the diagnosis (Holman, 2000) used to assign specimens to *Ogmophis compactus* by Smith (2013) is problematic because it does not include any individual apomorphies or a unique character combination for either the genus or species, following descriptions of other taxa in Holman (2000). Thus, while the generic assignment of Smith (2013) is tentatively accepted for the purposes of identifying PTRM 19378 in snake phylogeny (Figure 1), the taxonomic and systematic ambiguity of "*Ogmophis*", requires restricting the

first occurrence of Loxocemidae to cranial remains described in Smith (2013), and not to stratigraphically older published records of the genus (Holman, 2000).

MORELIA

Node Calibrated. Divergence between *Morelia* and *Liasis*.

Fossil Taxon. *Morelia riversleighensis* Smith and Plane, 1985 vide Scanlon, 2001.

Specimen. QM F12926, right maxilla (holotype). "AR" is not listed as a formal collection abbreviation, but likely represents field numbers associated with specimens housed in the Queensland Museum.

Additional Materials. AR 13392, partial right mandible; AR 5658, premaxilla; AR 16880, left palatine. Other specimens are listed in Scanlon (2001).

Phylogenetic Justification. The hypodigm of *M. riversleighensis* is assigned to the genus on the basis of: 1) two teeth per side of the premaxilla; 2) anterior palatine teeth longer, thicker, and more vertical than posterior teeth; 3) deeply concave posterior margin of palatine choanal process; 4) concave anterior margin of premaxilla; 5) ventral openings of premaxilla channels posterior to tooth positions; and 6 maxillary lateral budges present (Scanlon, 2001, p. 6).

Minimum Age. 12.5 Ma.

Soft Maximum Age. Indeterminate.

Age Justification. *Morelia riversleighensis* was recovered from the Henk's Hollow Site in System C of the Riversleigh fossil sites (Scanlon, 2001). The minimum age estimate is based on faunal correlation between System C and the Bullock Creek Local Fauna (Travouillon et al., 2006; Travouillon et al., 2009, figure 1).

Discussion. *Morelia riversleighensis* was originally described as *Montypythonoides riversleighensis* (Smith and Plane, 1985), but was subsequently synonymized with *Morelia* by Kluge (1993). Scanlon (2001) provided a detailed description of Miocene pythonine fossils and synonymized *Morelia antiqua* from the middle Miocene Camfield Beds (Smith and Plane, 1985) with *M. riversleighensis.*

Other pythonine fossil records have been documented from the Neogene and Quaternary of Africa, Asia, Europe, and Australia (e.g., Portis, 1901; Hoffstetter, 1964; Rage, 1976; Thomas et al., 1982; Smith and Plane, 1985; Rage and Ginsburg, 1997; Ivanov, 2000; Scanlon, 2001; Scanlon and Mackness, 2002; Rage, 2003; Szyndlar and Rage, 2003; Head, 2005; Rage and Bailon, 2005; Head and Bell, 2008; Ivanov and Böhme, 2011).

Most records have been assigned to extant genera based on overall similarity of vertebral morphology. *Python europaeus* was erected using a precloacal vertebra as holotype (Szyndlar and Rage, 2003) on the justification of shared provenance with a partial palatine that had previously been assigned to the genus on the basis of an enclosed maxillary nerve foramen (Ivanov, 2000). An enclosed maxillary nerve foramen is plesiomorphic for pythonines, however (Kluge, 1993), and the character cannot differentiate between *Python* and other taxa. As a result, there is no other published record that can be unambiguously assigned to a crown genus or species on the basis of discrete apomorphy, despite very likely belonging to extant taxa.

Molecular phylogenetic analyses have resulted in paraphyly of multiple pythonine taxa, including *Python* and *Morelia* (Rawlings et al., 2008; Reynolds et al., 2014). As a result, the morphological topology incorporating *M. riversleighensis* (Scanlon, 2001) cannot be directly compared to molecular hypotheses. The Riversleigh and Camfield records do provide a minimum occurrence for divergence of *Liasis* relative to the grade of taxa currently and previously included in *Morelia* (Kluge, 1993; Reynolds et al., 2014). The *Liasis-Morelia* divergence calibrated here additionally constrains minimum divergence timings of *Antaresia*, *Simalia*, *Aspidites*, and *Bothrochilus* (Reynolds et al., 2014).

DISCUSSION

Comparisons to Calibrated Nodes from Other Studies

Taxa used to estimate hard minimum ages for nodes listed here are generally consistent with those employed by recent molecular phylogenetic analyses to temporally calibrate the deepest divergences in snakes: Sanders et al. (2010) included the same "*Coniophis*" record as part of their uniform prior calibration of the snake crown; Pyron and Burbrink (2012) calibrated the snake total clade using the Most Recent Common Ancestor (MRCA) within Toxicofera (see discussion of Pan-Serpentes in this analysis); and Pyron and Burbrink (2012) used pachyophiids, including *Haasiophis*, to calibrate the MRCA of Alethinophidia.

There have been limited attempts to use fossil to calibrate divergence timings within Boidae due to a lack of phylogenetic resolution and perceived taxonomic ambiguity in vertebral anatomy (see Sanders et al., 2010 for discussion). This study provides the most explicitly justified calibration points for Boidae Pythonidae, and other non-

caenophidian macrostomatans by restricting calibration points to fossils that are diagnosable to extant genera (e.g., *Corallus*, *Eunectes*, *Charina*, *Morelia*), or are referable to higher clades on the basis of discrete, testable characters (e.g., *Titanoboa*, "*Calamagras*" *weigeli*, "*Ogmophis*" *compactus*). Importantly, none of the calibration points justified here unambiguously extend the boid or pythonid fossil records into the Cretaceous (Figure 1). Previous reports of Cretaceous "boids" have been based on fragmentary remains (e.g., Albino, 2000) and were used to establish Cretaceous-aged uniform priors for Boidae (Sanders et al., 2010). These records are no longer considered to represent Mesozoic records of basal macrostomatans (e.g., Albino and Brizuela, 2014), and although the total clade of Booidea (sensu Gauthier et al., 2012) can be calibrated to no younger than Maastrichtian based on the oldest record of Caenophidia (Figure 1), there are no definitive Mesozoic records of crown clades with Booidea.

Implications of Revised Calibrations for Biogeographic Hypotheses

Revised younger calibration points for Booidea will likely provide different divergence timings relative to previous studies that correlate molecular divergences with Cretaceous tectonic histories to infer a Gondwanan vicariant biogeographic mode for boid taxa (Noonan and Chippindale, 2006a, 2006b). Sanders et al. (2010) and Parham et al. (2012) previously identified multiple issues with calibration points in these studies, but specific differences with previous calibrations within Booidea require additional commentary. The minimum divergence timing between *Charina* and *Exiliboa* was calibrated to be greater than 55 Ma by Noonan and Chippindale (2006b) based on the occurrence of the Paleogene taxon *Dunnophis*. There is no anatomical evidence linking *Dunnophis* to either taxon. Instead, the calibration using apomorphic characters in this analysis minimally constrains the divergence to no younger than 35.2 Ma based on the occurrence of "*Calamagras*" *weigeli*. Neither this study nor Noonan and Chippindale (2006b) provides soft maxima for most calibrated nodes, but an approximately 20 Ma contraction in minima presented here would almost certainly result in younger divergence estimates if incorporated. Similarly, the hard minimum for Booidea based on the stratigraphic distribution of Caenophidia presented here would be latest Cretaceous in age, whereas Noonan and Chippindale (2006b)

provided a minimum of > 75 Ma based on the occurrence of *Dinilysia*. *Dinilysia* is either a stem snake (Zaher and Scanferla, 2012) or a stem alethinophidian (Wilson et al., 2010), and therefore does not provide an accurate minimum age for the booid total clade (Sanders et al., 2010). A Maastrichtian minimum age for booids based on Caenophidia could be up to 10 Ma younger than the minimum estimated from *Dinilysia*, further suggesting younger divergence dates if justified calibrations are employed.

The first occurrences of boids and pythonids greatly postdate the tectonic events that have been proposed to explain their modern distributions. Gondwanan fragmentation was initiated by the late Jurassic (Jokat et al., 2003), with separation and isolation of Africa by the end of the Early Cretaceous and Madagascar by the mid Late Cretaceous. While it may be tempting to invoke poor fossil record quality to explain this discrepancy, diverse fossil snake records of putative stem snakes and indeterminate taxa have been documented throughout Late Cretaceous deposits of South America (e.g., Apesteguía and Zaher, 2006; Albino and Brizuela, 2014; Hsiou et al., 2014), India (Rage and Prasad, 1992; Prasad and Rage, 1995; Rage et al., 2004; Wilson et al. 2010; Mohabey et al., 2011), and Madagascar (LaDuke et al, 2010; Pritchard et al., 2014). Recent discovery of extralimital distributions of boids based on the occurrence of the boine *Rukwanyoka* from the late Oligocene of Tanzania (McCartney et al., 2014) additionally confounds a Gondwanan vicariant signal with respect geographic distribution. This record may indicate that extant boid distributions result from Neogene or younger regional extinction instead of Cretaceous Gondwanan vicariance. Based on discrepancies between the fossil record and biogeographic events inferred from previous molecular divergence timings, a new set of divergence timing estimates, incorporating the explicitly justified records described here, will be required to assess the contribution of continental-scale vicariance to the distributions of extant booid snakes.

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