Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidea, Colubridae

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ABSTRACT

Caenophidia, the snake clade that includes the highest species richness, morphological diversity, and ecological breadth within Serpentes, has been extensively studied with respect to molecular phylogenetic systematics. The majority of the caenophidian fossil record, though dense, has been taxonomically defined on the basis of general anatomical similarity or shared geographic provenance with extant reference taxa. As a result, historical patterns of diversification within the clade are poorly constrained due to a paucity of reliable fossil calibration dates. Here we provide 10 fossil calibration dates for phylogenetic analysis of caenophidian relationships. Calibration points include apomorphy-based systematic justifications based on cranial and precloacal vertebral elements and precise dates for hard minimum divergence timings. Calibrated nodes are for Caenophidia, Acrochordus, Elapoidea, Colubridae, and constituent subclades. Hard minimum divergence timings range from late Cretaceous to Miocene. The spatial and temporal distribution of reliable first occurrence of colubroid taxa suggests late Paleogene intercontinental dispersals between Asia, North America, and Africa, followed by rapid diversification and subsequent dispersals into all non-Polar continents by the early Neogene.

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INTRODUCTION

The vast majority of extant snake diversity is contained in Caenophidia, a clade consisting of >2500 species (Vidal et al., 2009). Caenophidia was originally erected by Hoffstetter (1939) to include snakes more derived than “henophidian grade” taxa, considered at the time to include boids and aniloids. Morphological studies recognized a close relationship between relationship between Colubroidea, itself consisting of viperids, colubrids, elapids, homalopsids, and other “derived snakes”, and Acrochordus, the genus of file snakes, wart snakes, and elephant trunk snakes (e.g., Bellairs and Underwood, 1951), with explicit morphological phylogenetic analyses recovering a sister-taxon relationship between the two (e.g., Rieppel, 1988; Kluge, 1991; Cundall et al., 1993; Lee and Scanlon, 2000; Tchernov et al., 2000).

Numerous molecular phylogenetic studies of caenophidians have subsequently been conducted. Research foci associated with these analyses include molecular divergence timing estimates, biogeographic histories, diversification patterns, and the evolution of toxic venoms, making them the most intensely studied squamate clade with respect to molecular phylogenetics (e.g., Keogh, 1998; Burbrik et al., 2000; Gravlund et al., 2001; Burbrik, 2002; Vidal, 2002; Fry et al., 2003; Kelly et al., 2003; Keogh et al., 2003; Nagy et al., 2003; Pinou et al., 2004; Lawson et al., 2005; Lukoschek and Keogh, 2006; Burbrik and Lawson, 2007; Vidal et al., 2007; Fry et al., 2008; Sanders et al., 2008; Hedges et al., 2009; Kelly et al., 2009; Pyron and Burbrik, 2009a,b,c; Zaher et al., 2009; Burbrik and Pyron, 2010; Sanders et al., 2010; Vidal et al., 2010; Murphy et al., 2011; Pyron et al., 2013a,b). The majority of studies have recovered the same sister-taxon relationship between Acrochordus and taxa traditionally included in Colubroidea (but see Pyron et al., 2013a for an alternate hypothesis of sister-taxon relationships of Acrochordus).

The caenophidian fossil record has been more thoroughly documented than for any other squamate clade, with a few Late Cretaceous to early Paleogene records primarily, but not exclusively, from southern continental landmasses (e.g., Rage, 1975; Rage, 2008; Rage et al., 1992; Rage and Werner, 1999; Rage et al., 2008; Rage et al., 2013; Parmley and Holman, 2003; Head et al., 2005) and hundreds of records from the late Paleogene to Holocene of mainly North America and Europe (e.g., Rage, 1984[and references therein]; Szyndlar, 1984, 1985, 1987, 1991a, 1991b, 2012; Szyndlar and Schleich, 1993; Szyndlar and Rage, 1999; Holman, 2000 [and references therein]; Ivanov, 2000, 2002; Ivanov and Böhme, 2011), as well as records from South America, Africa, and Asia (e.g., Albino, 1996; Albino and Montalvo, 2006; Rage, 1973, 1976, 2003; Rage and Ginsburg, 1997; Rage and Danilov, 2008; Head, 2005, Head et al., 2006; Head et al., 2007; Head and Bell, 2008). The published record has been used to calibrate multiple caenophidian molecular phylogenies (e.g., Noonan and Chippindale, 2006; Burbrik and Lawson, 2007; Wüster et al., 2007, 2008; Alfaro et al., 2008; Sanders and Lee, 2008; Sanders et al., 2010; Kelly et al., 2009; Lukoschek et al. 2012; Pyron and Burbrik, 2012), with different fossils employed to produce highly disparate divergence estimates (Lukoschek et al., 2012).

There are multiple problems with calibrating molecular phylogenies using the published literature on fossil snakes (Head, 2015), especially for caenophidians: The absence of discrete apomorphies in vertebral morphology for most taxa limits testable, reproducible taxonomic hypotheses from isolated fossils. Additionally, considerable intracolumnar, individual, and ontogenetic variation exists in vertebral morphology, and very few studies have attempted to examine the influence of these factors in taxonomic assignments (Szyndlar, 2012 [but see Szyndlar, 1984 and LaDuke, 1991a for analyses of intracolumnar and individual variation]).

Because of these potential limitations, identity of snake fossils has traditionally relied on a generalized “vertebral form taxonomy” that uses overall, often proportional, shape to recognize taxa and implicitly does not follow a phylogenetic taxonomy, despite using the same taxon names (see Szyndlar et al., [2008] and Szyndlar, [2012] for discussion). Other approaches include general similarity/“gestalt” approaches (see Hecht and LaDuke, 1997 for discussion), unsupported authority statements, and the geographic provenance of extant taxa (e.g., Holman, 2000[and references therein]), which results in circularity in reconstructing temporal and spatial histories of extant clades (Bell et al., 2004; Bell et al., 2010). The caenophidian record does not lack utility, however. Diagnostic vertebral characters are observable (e.g., Hoffstetter and Gasc, 1969; Slowinski, 1994; Sheil and Grant, 2001, Head, 2005), and cranial remains are preserved for several key taxa.

Here we provide fossil calibrations for multiple caenophidian clades based on observable apomorphies. We restrict calibrations to taxa represented by either diagnostic cranial remains or
vertebrae that can be diagnosed by discrete characters or unique character combinations. Using this approach, we are only able to recognize 10 extant caenophidian taxa relative to the many dozens recognized by the aforementioned methods, but our calibrations are testable observations that allow analysis of systematic, ecological, and biogeographic hypotheses of extant caenophidians because their phylogenetic justifications are independent of the histories of those taxa. There are two published comprehensive molecular phylogenies of Caenophidia that can be used as scaffolds for node calibration (Pyron et al., 2013a, b). We use the topology of Pyron et al. (2013a) because it includes greater taxonomic and sequence sampling, but additionally consider the topology of Pyron (2013b) where appropriate.

Institutional Abbreviations
BSP, Bayerische Staatssammlung Für Paläontologie Und Historische Geologie, Munich; H-GSP, Harvard-Geological Survey of Pakistan; Islamabad, Pakistan; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts, U.S.A.; MGT, Université Montpellier; MNHN, Muséum National d’Histoire Naturelle, Paris, France; QM F, Queensland Museum, Queensland, Australia; UCBL, Université Claude Bernard, Lyon; UNSM, University of Nebraska State Museum, Nebraska, U.S.A. VAS, “R.S. Rana collection from Vastan” (Rage et al., 2008); Vb, the abbreviation “Vb” is not defined in Rage and Werner (1999); however, specimens labeled with “Vb” and field numbers were reported to be “…curated at the fossil collection of the Technical University of Berlin-Special Research Project 69…” (Rage and Werner, 1999: 87), and are now housed in the Museum für Naturkunde Berlin.

CALIBRATIONS

(1) Pan-Caenophidia

Node Calibrated. Divergence between the total clade of Caenophidia and its nearest crown sister taxon, Booiidea (sensu Head, 2015).


Specimen. Vb-681, incomplete precloacal vertebra.

Additional Materials. Six precloacal vertebrae.

Phylogenetic Justification. Krebsophis thobanus is unambiguously included within Russelophiidae on the basis of brief, ventrolaterally angled articular facets of the prezygapophyses and compressed prezygapophyseal buttresses that form a vertical ridge, as well as more ambiguously by an elevated posterior neural arch (Rage and Werner, 1999). Characters that unite Russelophiidae, including Krebsophis, with Caenophidia include a highly elongate centrum, relatively small, circular cotyle and condyle, and well-developed subcentral paralymphatic channels defining the lateral margins of a distinct haemel keel.

Minimum Age. 66 Ma, latest Maastrichtian.

Maximum Age. 72.1 Ma, latest Campanian to earliest Maastrichtian.

Age Justification. Krebsophis thobanus was recovered with a taxonomically diverse snake fauna from the Wadi Abu Hashim member of the Wadi Milk Formation of Sudan (Werner and Rage, 1999). The Wadi Milk Formation was considered Cenomanian based on palynological (Schrank,1990; Schrank and Awad, 1990) and fish data (see Werner and Rage, 1999). However, the snake fauna of Wadi Abu Hashim is much more biostratigraphically consistent with a Maastrichtian age assignment: Nigeophiids and large-bodied madtsoiids are only present in Maastrichtian sections of Madagascar and India (e.g., Prasad and Rage, 1995; Rage et al., 2004; LaDuke et al., 2010; Mohabey et al., 2011; Prichard et al., 2014), the oldest record of palaeophiids is from the Maastrichtian of Morocco (Rage and Wouters, 1979), the oldest aniliid anatomically consistent with “Coniophis” from Wadi Abu Hashim is Australophis from the late Campanian-Early Maastrichtian of Argentina (Goméz et al., 2008, see Head [2015] for discussion of the age of Australophis), and anatomically similar “Coniophis” is known from the Maastrichtian of India (Rage et al., 2004). Referral to two snake specimens from Wadi Abu Hashim to Early Cretaceous “lapparentophiid-grade snakes” by Rage and Werner (1999) was admittedly based solely on plesiomorphic characters, which are taxonomically uninformative. A Cenomanian age for madtsoiids, nigeophidiids, palaeophiids, and “Coniophis” form taxon aniioids would represent at least
20 million year range extension for all, of which there is no additional unambiguous evidence. Additionally, the Shendi Formation of Sudan, which shares a vertebrate fauna with the Wadi Milk Formation (J.M. pers. obs.) and previously considered a lateral extension of the Wadi Milk, has recently been dated as Campanian-Maastrichtian (Salih et al., 2015). Based on ages of comparable snake faunas from other Gondwanan landmasses and the age estimates for the Shendi Formation, we assign an age range for Krebsophis based on minima for the Campanian and Maastrichtian (Ogg et al., 2012).

**Discussion.** The systematic relationships of russellophiids are poorly constrained. Russellophis tenius was originally considered a primitive caenophidian by Rage (1975) on the basis of small prezygapophyseal accessory processes and synapophyseal morphology that is anatomically consistent with “henophidian” taxa. Subsequent records have been placed either within only Caenophidia (“?Russellophidiidae” Rage, 2008), or Colubroidea within Caenophidia (e.g., Rage et al., 2008). Explicit character support for inclusion of Russellophidiidae within the colubroid total clade has not been provided, but a testable hypothesis for the interrelationships of the clade is required to calibrate Caenophidia and potentially Colubroidea.Russellophiids share an elongate centrum with colubroids to the exclusion of Acrochordus, however, they lack vertebral synapomorphies of crown Caenophidia, including: well-developed prezygapophyseal accessory processes, well-differentiated para- and diapophyseal articular facets of the synapophyses, and pleurocentral hypapophyses present throughout the precloacal vertebral column. Due to these character distributions, placement of Russellophidiidae within Colubroidea cannot be supported, and the fossil record of the clade can only calibrate the caenophidian total clade.

(2) Pan-Colubroidea

**Node Calibrated.** Divergence between the total clade of Colubroidea and its nearest crown sister taxon, (Acrochordus+Xenodermatidae).

**Fossil Taxon.** Procerophis sahnii (Rage et al., 2008).

**Specimen.** VAS 1014, posterior trunk vertebra.

**Additional Materials.** Five precloacal vertebrae, two caudal vertebrae.

**Phylogenetic Justification.** Procerophis is assigned to Colubroidea on the basis of: elongate, narrow centrum and neural arch, paracotylar foramina, and an anteroposteriorly elongate neural spine that possesses a uniform width along its length.

**Minimum Age.** 50.5 Ma, middle Ypresian.

**Maximum Age.** 72.1 Ma, earliest Maastrichtian.

**Age Justification.** Procerophis was recovered from a diverse snake fauna in the Cambay Formation, Gujarat, India. The Cambay Formation is minimally dated based on the occurrence of the planktonic foraminifera taxon Nummulites burdigalensis burdigalensis, which corresponds to Shallow Benthic Zone 10 (lower Cuisian, Serra-Kiel et al., 1998). SBZ 10 corresponds to planktonic foraminiferal zone P6b, which is middle Ypresian, approximately 53-50.5 Ma (Vandenberghe et al., 2012). Maximum age is for the early Maastrichtian based on the first occurrence of Caenophidia from the Wadi Milk Formation (Werner and Rage, 1999).

**Discussion.** Among extant colubroids, these characters are characteristic of colubrines. However, Procerophis possesses a plesiomorphic prezygapophyseal morphology (Rage et al., 2008), including prezygapophyseal articular facet long axis predominately anteriorly angled, and small accessory processes. Additionally, the haemal ridge is poorly differentiated from the ventral surface of the central body, unlike crown colubroids. Thaumastophis missiaeni, also from the Cambay Formation, similarly lacks a hypapophysis, and the majority of vertebral morphology is consistent with assignment to Colubroidea. However, the taxon possesses vertical, blade-like prezygapophyseal accessory processes, which are otherwise apomorphic for Acrochordus. As a result, the taxon is here considered Caenophidia indeterminate, following Rage et al. (2008).
Russellophis crassus, also from the Cambay Formation, is a potential alternate anchor taxon for the Pan-Colubroidea divergence. As previously noted, however, the systematic relationships of russellophiids relative to either the caenophidian crown or the colubroid total clade are poorly constrained. Colubroid characters including an elongate, narrow neural spine of a uniform transverse width that extends from the zygosphene to the posterior median notch of the neural arch, paracotylar foramina, comparatively well-developed prezygapophyseal accessory processes, and potentially well-differentiated dia-and parapophyseal articular facets, are present in Procerophis but absent in russellophiids (e.g., Rage, 1975; Rage and Werner, 1999; Rage, 2008), indicating that Procerophis is the most appropriate minimum divergence point for the colubroid total clade.

(3) Acrochordus javanicus

Node Calibrated. Divergence between Acrochordus javanicus and (A. arafurae+A. granulatus).


Specimen. H-GSP 41555, two precloacal vertebrae.

Additional Materials. Five precloacal vertebrae, two caudal vertebrae.

Phylogenetic Justification. Acrochordus dehmi is hypothesized to be the sister taxon to A. javanicus to the exclusion of A. arafurae or A. granulatus on the basis of parazygosphenal foramina located just ventrolaterally to the base of the zygosphene on the anterolateral surface of the neural arch (Head, 2005; Sanders et al., 2010). Acrochordus dehmi is placed within the genus Acrochordus on the basis of ventrally elongate and pendant synapophyses, hemispherical, vertically oriented and blade-like prezygaphophyseal accessory processes, and multiple paracotylar foramina (Hoffstetter, 1964; Head, 2005).

Minimum Age. 18.05 Ma.

Maximum Age. 23.03 ± 0.05 Ma, earliest Aquitanian, earliest Miocene (Hilgen et al., 2012).

Age Justification. The minimum age is based on dating of locality Y846 from the Kamlial Formation of the Siwalik Group on the Potwar Plateau of Pakistan, which is the oldest record of Acrochordus dehmi (Head, 2002, 2005). The maximum age follows Head et al. (2007) based on the first occurrence of the genus from the Aquitanian Kharinadi Formation, Gujarat, India.

Discussion. Bayesian molecular divergence estimates for Acrochordus javanicus from (A. arafurae+A. granulatus) based on the calibration points cited here model a divergence of 20.3 Ma with a range of 6.6-34.0 Ma (95% highest posterior density values) (Sanders et al., 2010). The fossil record of Acrochordus also constrains the divergence timing of Xenodermatidae following Pyron et al. (2013a); however, xenodermatids are more closely related to colubroids than Acrochordus in the topology of Pyron et al. (2013b).

(4) Viperinae

Node Calibrated. Divergence between total clades Crotalinae+Viperinae.

Fossil Taxon. “Vipera aspis complex” (Szyndlar and Rage, 1999).

Specimen. MNHN SG 13732, precloacal vertebra.

Additional Materials. MNHN SG 13733, posterior precloacal vertebra (Szyndlar and Rage, 1999).

Phylogenetic Justification. Assignment to Viperidae is based on a large, elongate, straight, and posteroventrally angled hypapophyses, laterally short prezygapophyseal accessory processes, large cotyle and condyle, low and flattened posterior neural arch, and elongate, anteroventrally angled parapophyseal process (sensu Head, 2005) (Szyndlar, 1991b; Szyndlar and Rage, 1999). Assignment to Viperinae relative to Crotalinae is based on the presence of low neural spines, which is restricted the “aspis complex: of extant European viperines (e.g., Szyndlar, 1984, 1991b, Szyndlar and Rage, 1999).

Minimum Age. 20.0 Ma, youngest age for MN2 (Agustí et al., 2001).

Maximum Age. 23.8 Ma (Agustí et al., 2001), oldest age for MN1 (see below).

Age Justification. The minimum age is for the youngest age for Neogene Mammal (MN) Biochron 2, based on the age of the
St-Gérand-le-Puy complex (Szyndlar and Rage, 1999, 2001). The youngest absolute age for MN2 is poorly constrained, but at minimum age of 20.0 Ma is estimated, based on correlation of the oldest MN3 fossil localities with Geomagnetic Polarity Timescale (GMPT) chron C6n (Agustí et al., 2001). Many St-Gérand-le-Puy localities are within MN 2a (e.g., Göhlich et al. 2005). If the St-Gérand-le-Puy viperid fossils are from these localities, then the minimum age would be slightly older at the top of GMPT chron 6AAn, dated to approximately 21.8 Ma (Sen, 1997 after Agustí et al., 2001). The maximum age is for the base of MN 1, the age of the oldest viperid fossil from Weisenau, Germany (Szyndlar and Böhme, 1993; Szyndlar and Rage, 1999, 2002).

Discussion. Viperids possess a distinct vertebral morphology that includes a straight, elongate, and posterovertrally oriented hypapophysis that is present throughout the prelcoacal vertebral column, strongly depressed neural arches, extremely elongate parapophyseal processes, relatively short prezygapophyses with short, blunt accessory processes, and large cotyle-condyle articulations. An anatomical distinction has been made between the "oriental vipers" (composed of species of the subgenus Montivipera and the Macrovipera) and the "Vipera aspis complex (composed of primarily V. aspis and V. ammodytes) based on small size, elongate centra and short neural spines in the latter complex (Szyndlar and Rage, 1999). Among extant taxa, these characters do distinguish the "aspis complex" species from other taxa, but there are no other vertebral characters that differentiate the majority of other viperine taxa from crotalines. As a result, the record described from the St-Gérand-le-Puy complex represents the oldest definitive viperine fossil record. The oldest records of vipers are from Weisenau (Szyndlar and Böhme, 1993) and the Harrison Formation of Nebraska (Holman, 1981), and predate the "V. aspis complex) by up to four million years. However, the identities of these records as either stem vipers, crown vipers, and/or crown crotalines cannot be unambiguously determined from vertebral characters. These record do not minimally calibrate the divergence of viperids, as they are predated by the first occurrence of the viperid sister taxon (see below). The oldest unambiguous crotaline fossil record consists of two maxillae from the late Miocene of Ukraine (Ivanov, 1999), and is much younger than the viperine record we cite to calibrate the viperine-crotaline divergence.

(5) Colubridae+Elapoidea

Node Calibrated. Divergence of crown colubroid lineages.


Specimen. MGT 3505 precloacal vertebra (holotype).

Additional Materials. MGT 3506, caudal vertebra, "plusieurs vertèbres dorsales et caudales" (Rage, 1974:295).

Phylogenetic Justification. Assignment to (Colubridae+Elapoidea) is based on the presence of: a well-developed, narrow haemel keel that is uniform in transverse width and extends from an expanded cotylar ventral lip anteriorly to terminate posteriorly just anterior to the condyle; epizygapophyseal spines, and; elongate prezygapophyseal accessory processes (Rage, 1974).

Minimum Age. 30.9 ± 0.1 Ma

Soft Maximum Age. Indeterminate.

Age Justification. The minimum age is based on the age of the type locality at Mas de Got A, which is correlated to Paleogene Mammal (MP) biochron 22. MP 22 ranges from 32.6 ± .1 Ma to 30.9 ± .1 Ma (Schmidt-Kittler, 1987; İslamoğlu et al., 2006; Szyndlar, 2012; Rage, 2006; Augé and Rage, 2014).

Discussion. Referral of Coluber cadurci to the total clade (Colubridae+Elapoidea) is unambiguously supported by the aforementioned character combination. The presence or absence of ventral hypapophyses throughout the precloacal vertebral column has traditionally been used to distinguish Colubrinae from Natricinae and/or Elapidae (Bell et al., 2003; Szyndlar, 2012), and was used in the original taxonomic assignment of C. cadurci (Rage, 1974); however, absence of continuous precloacal hypapophyses occurs in numer-
ous elapoid and dipsadine taxa in addition to Colubrinae (Dowling and Duellman, 1978 after Pyron et al., 2013), and the character cannot diagnose colubrines to the exclusion of other clades. Similarly Coluber cannot be diagnosed on the basis of vertebral morphology (Szyndlar, 2012), and referral to the genus has been subsequently recognized as non-phylogenetic (Rage, 1988:468). The morphology of the haemal keel in C. cadurci is consistent with colubrids and elapoids that similarly lack a hypapophyses, and is distinct from the morphology of the keel in russelophiids and more basal snakes in which the keel is often wide and more poorly defined (Head, 2015). As a result, Coluber cadurci provides a calibration for the total clade of (Colubridae+Elapoidea) but cannot constrain divergences within the clade.

Natrix mlynarskii is approximately coeval with C. cadurci, and was assigned to Natrix based on general resemblances with modern and fossil species of genus (Rage, 1988). The type specimen of N. mlynarskii is too incomplete for unambiguous referral to Natrix, but appears to possess a distinct, short hypapophysis similar to natricines, some dipsadines, and most elapoids. The records of Coluber cadurci and Natrix mlynarskii predate the oldest definitive records of elapoids from the late Oligocene by approximately 6 Ma (McCartney et al., 2014).

Older colubroid records that have been referred to Colubridae or constituent subclades extend into the early Paleogene of Asia and North America (Rage et al., 1992; Parmley and Holman, 2003). However, these records are too incomplete to distinguish from stem Colubroidea and are therefore uninformative with respect to divergence of the (Colubridae+Elapoidea) total clade. Similarly, additional records referred to Colubroidea from the Eocene of Africa and South Asia (Rage et al., 2003, 2008; Head et al., 2005; McCartney and Seiffert, 2015) demonstrate the occurrence of the total clade in the Old World, but cannot constrain the divergence timing of crown Colubroidea or the (Colubridae+Elapoidea) total clade.

(6) Naja

Node calibrated. Divergence between Naja and Haemachatus.

Fossil Taxon. Naja romani (Hoffstetter, 1939).

Specimen. UCBL 92856 partial skeleton including maxillae, prefrontal, postorbital, fragmentary parietal, parabasisphenoid, otocipital, supratemporals, quadrates, articular, splenial, and dentary (Hoffstetter, 1939).


Phylogenetic Justification. Assignment of to the genus Naja is based on an anteroposteriorly short and laterally recurved maxilla with two large anterior venom fangs and two solid posterior teeth (Hoffstetter, 1939; Bogert, 1943) and fenestra vestibuli completely or nearly completely bounded within the otocipital (Hoffstetter, 1939; Szyndlar and Rage, 1990).

Minimum Age. 17.0 Ma

Soft Maximum Age. Indeterminate.

Age Justification. The minimum age is based on the maximum age for MN4, the age of the Petersbuch 2 locality (Szyndlar and Schleich, 1993; Ivanov, 2000; Agustí et al., 2001).

Discussion. Hoffstetter (1939) erected the taxon Paleonaja romani based on UCBL 92856. He considered the taxon to be most closely related to Ophiophagus han nah among extant cobras, with similarities to extant Naja the result of parallel evolution: “Toutes ces observations et les caractères morphologiques de détail mentionnés plus haut conduisent à admettre que P. romani est plus proche de N. hannah que de toute autre espèce actuelle. Cependant, la dysharmonie de ses caractères ostéologiques rend improbab le une filiation directe de la forme Miocène au type actuel. Il semble plutôt que Palaeonaja romani représente un rameau parallèle à celui des Naja, et il convient de le
designer sous un nom générique nouveau." (Hoffstetter, 1939:65). Bogert (1943) recommended assigning *P. romani* to the genus *Naja*, on the basis of anatomical similarities with extant *N. haje*, but did not provide specific character evidence. Szyndlar and Rage (1990) *Paleonaja* with *Naja*, and assigned *N. romani* to the Asiatic clade of *Naja* on the basis of a short vidian canal with an anterior opening bounded by the parabasisphenoid and the fenestra vestibule bounded by the otocipital. Szyndlar and Zerova (1990) additionally proposed an Asian *Naja* affinity for *N. romani* on the basis of a narrow parabasisphenoid rostrum. Conversely, Wallach et al. (2014) assigned *N. romani* to the genus *Afronaja* as part of the African clade of cobras, without justification.

Based on cranial osteology, *Naja romani* can be used to unambiguously calibrate the divergence of *Naja* from *Haemachatus* (Pyron et al., 2013a). Calibrating divergences within *Naja*, however, is problematic. Of the characters used to unite *N. romani* with Asian *Naja* (*Naja* subgenus of Wallach et al., 2009), none are unambiguous synapomorphies of that clade: Enclosure of the fenestra vestibule within the otoocipital occurs in *Naja naja* but only polymorphically in other Asian species as well as African *N. haje* (Szyndlar and Rage, 1990); the anterior opening of the vidian canal within the parabasisphenoid additionally occurs in *Pseudohaje* and *Aspidelaps* (Szyndlar, 1992); short vidian canals occur in *Pseudohaje*, *Aspidelaps*, and *N. haje* (Szyndlar, 1992); and a comparably narrow parabasisphenoid occurs in *Aspidelaps*, and *N. haje* (Szyndlar, 1992). Additionally, *N. romani* possess the same maxillary tooth formula of two venom fangs and two solid posterior teeth as African *Naja*.

Other Neogene *Naja* species have been described on the basis of neurocranial anatomy. *Naja antiqua*, represented by a partial neurocranium and precloacal vertebrae from the middle Miocene (MN 7) of Morocco (Rage, 1976) and *Naja iberica*, represented by a partial neurocranium and skull roof from the latest Miocene (MN 13) of Spain (Szyndlar, 1985). Both taxa have been referred to the "African complex" of Szyndlar and Rage (1990) on the basis of neurocranial characters. However, these characters are either explicitly recognized as plesiomorphic for the genus (Szyndlar and Rage, 1990, Szyndlar, 1992), or are untested with respect to phylogenetic polarity. Because elapine osteology has not been either rigorously optimized on a molecular phylogenetic topology or been used to construct a phylogenetic hypothesis, there is no way to unambiguously place the fossil record within the phylogeny of living species, and we here use the record to only constrain the *Naja* total clade (Wallach et al., 2009). Fossils attributed to *Naja* primarily on the basis of precloacal vertebral morphology have been documented throughout the Neogene of Europe and Africa (Bachmeyer and Szyndlar, 1985, 1987; Szyndlar, 1985, 1991, 2009a,b; Meylan, 1987; Szyndlar and Zerova, 1987; Bailon, 1989; Szyndlar and Rage, 1990; Ivanov, 2000; Miklas-Tempfer, 2002; Rage, 2003; Daxner-Höck et al., 2004; Camora et al., 2010; Rage and Bailon, 2011; Blain et al., 2013); however, vertebral morphology is not diagnostic for the genus with respect to other elapid taxa (e.g., Smith, 1975; McCartney et al., 2014). The oldest record of the genus based on cranial elements is *Naja romani* from the early Miocene Petersbuch 2 locality of Germany (Szyndlar and Schleich, 1993). This record consists of a supraoccipital, frontal, dentary fragment, and partial compound bone. The supraoccipital is the only element explicitly discussed and is described as being morphology indifferent from supraocciptals of extant *Naja* species (Szyndlar and Schleich, 1993).

(7) Oxyuraninae

**Node Calibrated.** Divergence between *Laticauda*+Oxyuraninae.

**Fossil Taxon.** *Incongruelaps iteratus* Scanlon et al. (2003).

**Specimen.** QM F23085, right maxilla.

**Additional Materials.** Six precloacal vertebral.

**Phylogenetic Justification.** Assignment to Oxyuraninae is based on the presence of five posterior maxillary teeth and absence of a distinct palatine articular
facet on the palatine process of the maxilla (Scanlon et al., 2003).

**Minimum Age.** ~ 10 Ma (Myers et al., 2001; Scanlon et al., 2003).

**Maximum Age.** Indeterminate.

**Age Justification.** The minimum age is based on a combination of mammalian biostratigraphy and phylogenetic relationships of mammals from the Encore Local Fauna relative to the late Miocene Alcotta Local Fauna and the middle Miocene System C Local Fauna from Riversleigh (Myers et al., 2001).

**Discussion.** Scanlon et al. (2003) cited multiple qualitative characters of the maxilla that unite *Incongruelaps* with oxyurinines (sensu Sanders and Lee, 2008) and other elapids, and the aforementioned characters unite the taxon with Oxyurininae to the exclusion of *Laticauda*. The Australian fossil record of Elapids extends from the Quaternary through the Neogene (e.g., Smith, 1976; Scanlon, 2003). The oldest record was previously considered to be latest Paleogene based on a precloacal vertebra from the RSO site of Riversleigh (Scanlon et al., 2003); however, RSO has been radiometrically dated to 16.55 ± 0.29 Ma (Woodhead et al., 2016). A maximum age for the divergence of the total clade Hydrophiinae is potentially determined from the first occurrences of Elapidae (e.g., McCartney et al., 2014 vs. Kuch et al., 2006), but we refrain from such a calibration due to the coarse phylogenetic resolution of those records.

(8) **Bungarus**

**Node Calibrated.** Divergence between *Bungauras bungaroides*, *B. flaviceps*, and the *B. fasciatus* clade.

**Fossil Taxon.** *Bungarus* sp. Head (2005).

**Specimen.** H-GSP 53026, partial precloacal vertebra.

**Additional Materials.** Six precloacal vertebrae.

**Phylogenetic Justification.** Assignment to the clade consisting of *Bungarus* species more closely related to each other than to *B. bungaroides* or *B. flaviceps* is based on the presence of both expanded prezygapophyseal accessory processes and postzygapophyseal accessory processes (McDowell, 1970; Slowinski, 1994).

**Minimum Age.** 10.215 Ma (Barry et al., 2002).

**Maximum Age.** Indeterminate.

**Age Justification.** The minimum age is based on the maximum age estimate for locality Y-450, the oldest record of *Bungarus* from the Siwalik Group of the Potwar Plateau, Pakistan (Barry et al., 2002; Head, 2005). Precise magnetostratigraphic analysis combined with sedimentation rate estimates has resolved Siwalik Group fossil localities to a temporal resolution of 10^4 years (e.g., Flynn et al., 1990; Barry et al., 2002).

**Discussion.** Bungarus is one of the few snake taxa that can be diagnosed to subgeneric levels on the basis of vertebral synapomorphies (Hoffstetter, 1939; Slowinski, 1994). The hypertrophied, wing-like prezygapophyseal accessory processes are diagnostic for the genus, and the possession of the wing-like lateral postzygapophyseal processes diagnoses *Bungarus* species as more derived than *B. flaviceps* and *B. bungaroides* (McDowell, 1970; Slowinski, 1994). Presence of the posterior processes unites the Siwalik Group *Bungarus* with the unresolved polytomy of derived species from Slowinski (1994) or the clade subtended by *B. fasciatus* and *B. multicinctus* from Pyron et al. (2013b).

(9) **Heterodon + Farancia**

**Node Calibrated.** Divergence between the clade subtended by *Heterodon* and *Farancia*.

**Fossil Taxon.** *Paleheterodon tiheni* (see discussion).

**Specimen.** UNSM 46504, partial skull and associated vertebrae.

**Additional Materials.** None (see discussion).

**Phylogenetic Justification.** Assignment of UNSM 46504 to a clade including *Heterodon* to the exclusion of *Diadophis* and *Pseudoboa* is based on the character combination of: 1) a quadrate with a narrow and strongly recurved distal shaft and a wide, narrow suprastapedial crest; 2) a narrow ventrally curved compound bone; 3) A parietal with a broad, well-defined skull table; 4) a supraoccipital with a well-defined sagittal crest.

**Minimum Age.** ~ 12.08 Ma.
Maximum Age. Indeterminate.

Age Justification. The minimum age is based on the Swallow Ash of the lowermost Ash Hollow Formation, which succeeds the Valentine Formation (Tedford et al., 2005). The Myers Farm fauna is coeval with the Valentine Formation based on mammalian faunal composition and is considered latest Barstovian (e.g., Janis et al., 1998; Bair, 2011).

Discussion. *Paleoheterodon tiheni* was originally described on the basis of three precloacal vertebrae from the Barstovian Norden Bridge Quarry of Nebraska (Holman, 1964). Holman (1964:633) stated “The vertebrae of *Paleoheterodon* are undoubtedly closer to *Heterodon* than to any other North American genus” but did provide any character evidence in support and did not make any taxonomic comparisons in the description of the holotype. Holman (2000) noted that vertebral morphology of extant *Heterodon* differs from closely related dipsadine *Farancia* only in possessing a more depressed neural arch and a less anteroposteriorly undercut neural spine; however, there is no appreciable difference the amount of undercutting between the two taxa as illustrated by Holman (2000). Both *Heterodon* and *Farancia* do possess comparatively flattened and depressed neural arches. Whether this character is useful for recognizing Dipsadinae or constituent subclades will require additional taxonomic sampling. Holman (1977) described a partial skull and associated vertebrae from the late Barstovian Myers Farm locality of southern Nebraska as *Paleoheterodon tiheni*, uniting the taxon with *Heterodon* based on vertebral similarities but noting very different cranial morphologies. Holman (2000) noted that vertebral morphology of *Paleoheterodon* differed from *Heterodon* in having a less depressed neural arch, which, as previously noted, is the condition in *Farancia*.

Cranial elements referred to *Paleoheterodon tiheni* do show several similarities to extant *Heterodon*, contra Holman (1977, 2000). The distal quadrate is narrow and recurved. Conversely, the basicranium and skull roof are radically different between the two taxa. *Heterodon* possesses an apomorphically short posterior skull, whereas cranial elements of *Paleoheterodon* include a comparatively elongate parietal and supratemporal with well-developed muscle attachment crests. The parabasiphenoid of *Heterodon* is abbreviated posterior to the sella turcica, whereas the same region is elongate in *Paleoheterodon*.

Morphology of vertebrae and cranial elements referred to *Paleoheterodon* is consistent with both *Heterodon* and *Farancia* (e.g., Cundall and Rossman, 1984). There are four possibilities for the identity of the taxon: 1) it is sister-taxon to *Heterodon*; 2) it is sister taxon to *Farancia*; 3) it is sister taxon to *Heterodon*+*Farancia*; and 4) UNSM 46504 is a chimera of multiple taxa. The possibility that cranial elements referred to *Paleoheterodon tiheni* represent multiple taxa is supported by the taphonomy of the Myers Farm site. Contra Holman (1977) there is almost no articulation or association of microvertebrate remains from the locality. Among squamates, only two partial snake precloacal skeletons were preserved in articulation and direct association. *P. tiheni* cranial specimens show damage consistent with transport, and the possibility that association of elements is a postmortem assemblage of multiple individual animals. Additionally, isolated snake cranial elements of similar sizes to *P. tiheni* cranial specimens have been recovered from the locality (JJH pers. obs.), and the absence of articulation between any of the elements described by Holman (1977, 2000) limits the ability to unambiguously assign the remains to a single individual or taxon. Because of this, we restrict the elements assigned to UNSM 46504 to only calibrate the most exclusive clade including *Farancia* and *Heterodon* to the exclusion of (*Nothopsis*+*Pseudoboa*).

The oldest unambiguous record of *Heterodon* is *H. plionasicus* from the middle Pliocene Fox Canyon Fauna of Kansas is represented by a maxilla that is anatomical identical to *H. nasicus* (Peters, 1953; Holman, 2000).
(10) Pantherophis+Pituophis.

Node Calibrated. Divergence between the extant genera Pantherophis and Pituophis.

Fossil Taxon. Pantherophis.

Specimen. UNSM 125457, complete, articulated skull and anterior ~ 30 of precloacal vertebral column.

Additional Materials. None.

Phylogenetic Justification. Assignment to Pantherophis is based on a premaxilla with thin, dorsomedially angled maxillary processes, a blunt, rounded anterior margin, and laterally expanded ascending processes forming a keyhole shape in anterior view.

Minimum Age. 11.93 Ma (Tucker et al., 2014).

Maximum Age. Indeterminate.

Age Justification. USNM 125457 was encased in a local ash deposit that is geochemically matched with the Ibex Hollow Tuff, radiometrically dated to 11.93 Ma (Tucker et al., 2014).

Discussion. USNM 125457 is a complete, slightly crushed and disarticulated skull of a colubrine snake. It possesses homodont maxillary dentition, a sharp, distinct lateral crest of the quadrate, and pterygoid dentition terminating well anterior to the quadrate ramus. Articulations of skull roofing elements, margins of the nasals, and morphology of the parabasisphenoid are identical to extant Pantherophis, and the lateral expansion of the premaxillary ascending process is uniquely shared between UNSM 125457 and extant Pantherophis species.

Holman (1982) described a well-preserved skeleton from the latest Miocene Santee Local Fauna as Elaphe vulpina, and provided a definition of the species on the basis maxillary and dentary tooth counts, ectopterygoid shape, and quadrate morphology; however, none of these characters is apomorphic with respect to other Pantherophis species (e.g. P. obsoleta). Elaphe buisi from the early Pliocene of Oklahoma was described on the basis of cranial remains (Holman, 1973), but the interrelationships of the taxon to Bogetophis relative to Pantherophis are undetermined (Holman, 2000), and the taxon is currently uninformative with respect to divergence timings.

UNSM 125457 calibrates the Pantherophis+Pituophis divergence, regardless of the identities of younger Pantherophis/Elaphe records. The oldest reports of Pituophis are based on four precloacal vertebrae from the late Miocene (Hemphillian) of Nebraska (Parmley and Holman, 1995:84). Assignment to Pituophis was based on ambiguous vertebral morphology (e.g., “neural spines high; neural arches vaulted”…) and a differential comparison with Pantherophis obsoleta. This identification additionally appears to include the distribution of extant Pituophis, which potentially introduces circularity in identifications and analysis of faunal histories (see Bell et al., 2010).

**DISCUSSION**

Other Possible Fossil Calibrations

The Neogene and Quaternary fossil record of colubrids includes several taxa described by cranial remains that have the potential to calibrate divergence timings of extant taxa, but are problematic with respect to systematics or anatomical interpretations. Malpolon myrarnings was described on the basis of a partial braincase from the late Pliocene of Spain and was assigned to the genus on the basis of: “considerable posterior expansion of the parietal, a very acute angle between the parietal crests throughout the bone, relatively very short basiarcheid portion of basiparabasial, ventral expansion of the middle of the basiphenoid, elongation of the vertebrae, a thin and sharp haemal keel, and straight posterior margins of the neural arch” (Szyndlar, 1988:693). However, Szyndlar (1988) noted other anatomical similarities with Elaphe s.l. and Coluber s.l.

Natrix longivertebrata has been described on the basis of vertebrae and cranial elements from the middle Miocene through Pliocene of western and central Europe (Szyndlar, 1984). Referral of N. longivertebrata to Natricinae is based on vertebral morphology (Szyndlar, 1984), and no unambiguous apomorphies nesting the taxon within extant natricine taxa have been provided.

Hierophis viridiflavus has been described as Coluber robertmertensi and Coluber viridiflavus from multiple late Pliocene and Pleistocene European localities (e.g., Mlynarski, 1964; Szyndlar, 1984; Ivanov, 1995; Szyndlar, 2012). A single character, a strongly posteriorly inclined anterior border...
of the vomerine process of the palatine, has been used to refer a specimen to *H. viridiflavus* (Szondlar, 1984); however, most of the described record for the species consists of vertebrae or other cranial elements. As a result, we do not formally include the taxon as a calibration point, but recognize its potential utility following reassessment and phylogenetic analysis.

Two fossil genera based partially on cranial remains have the potential for constraining inclusive colubroid clades. *Proplychis achoris* from the late Miocene of California includes a right maxilla possessing a unique combination of dental characters (Whistler and Wright, 1989), and *Dryinoides oxyrhachis* from the middle Miocene of Montana includes a partial skull roof and suspensorium (Auffenberg et al., 1958). Determination of the phylogenetic relationships of these taxa will very likely be important for understanding the evolution of modern North American colubrids.

The published fossil record of coral snakes consists of specimens from the Neogene and Quaternary of North America and Europe. All have been assigned to *Micrurus* (Holman, 1977; Rage and Holman, 1984; Holman, 2000; Ivanov, 2000; Szondlar, 2009; Ivanov and Böhme, 2011; Venczel, 2011). Holman (1977) and Rage and Holman (1984) distinguish *Micrurus gallicus* from the Astarcien of France and *Micurus* sp. indet. from the Barstovian of Nebraska from *Micruroides* on the basis of relatively taller neural spines in extant *Micrurus* and fossil specimens. Vertebral morphology cannot distinguish *Micrurus* from *Sinomicrurus* (Holman, 1977; Dowling and Duellman, 1978; Roze, 1996; Ikeda, 2007), and the records of *M. gallicus* and North American indeterminate species records cannot be unambiguously assigned to genus.

Vertebral anatomy of “Elapidae gen. et sp. indet.” (Ivanov, 2002) from the Merkur-North locality (early Miocene, MN3) of the Czech Republic is anatomically most similar to *Micruroides* and *Leptomicrurus* in possessing an extremely short neural spine (Holman, 1977; Roze, 1996); however, vertebral morphologies for *Maticora* and *Calliophis*, which are either considered the sister taxon to *Sinomicrurus*+(*Micrurus* + *Micruroides*) in the case of *Maticora*, or resolved as the sister taxon to all other elapids in the case of *Calliophis* (Pyron et al., 2013a, b), are undocumented. If morphologies for these taxa are indistinguishable from *Sinomicrurus*, *Micrurus*, and *Micruroides*, then the fossil records described here may only minimally constrain the divergence of crown Elapidae (Figure 1). Due to the lack of information on vertebral morphology in extant coral snakes, it is currently not possible to calibrate divergence timings with this undoubtedly important fossil record.

**Comparisons with Previous Fossil Calibrations for Caenophidians**

Fossil calibrations have been applied to molecular phylogenetic analyses of most caenophidian clades, with little consensus on particular fossils. Noonan and Chippindale (2006) used the fossil record of nigerophiids snakes to calibrate a Paleogene divergence for *Acrochordus*. This calibration is highly problematic because the fossil record of nigerophiids extends into the Cretaceous and because there is no evidence to support monophyly of *Acrochordus* and Nigeroiiidae (see Sanders et al., 2010 for additional discussion). Sanders et al. (2010) calibrated divergence timings for *Acrochordus* species as well as singleton representatives of Colubridae and Elapidae and two vipers based on the *Acrochordus* fossil record described here and the early Miocene viperid and elapid records of Kuch et al. (2006). Lukoschek et al. (2012) iteratively used different calibrations ranging from 34-80 Ma to calibrate the divergence of *Acrochordus* based on correct ages of nigerophiids and early records of colubroids.

Wüster et al. (2008) employed similar records to those described here to minimally calibrate the divergence of Eurasian viperines, but used a reported record of late Miocene *Sistrurus* (Parmley and Holman, 2007) that we do not recognize due to absence of character support for assignment beyond Viperidae. Wüster et al. (2007, 2008), and Kelly et al. (2009) followed the interpretation of *Naja romani* as a member of the Asian *Naja* clade (Szondlar and Rage, 1990) to calibrate the divergence of Asian and African species. Conversely this analysis restricts calibrations of *N. romani* to only the *Naja* total clade (see also Lukoschek et al., 2012).

Fossil calibrations for Hydrophiinae have primarily employed an early Miocene record referred to *Laticauda* by Scanlon et al. (2003) (Wüster et al., 2007). Both the age and identity of the record have been revised (see Sanders and Lee, 2008 for discussion), and our recommended use of *Incongruelaps* as the minimum calibration for *Laticauda* and Oxyuraninae is temporally consistent with the divergence estimated by Sanders and Lee (2008) using other dates.

Calibrations for Colubroidea and Colubridae are highly divergent (e.g., Wüster et al., 2007;
FIGURE 1. Phylogeny of Caenophidia from Pyron et al. (2013a) temporally calibrated on minimum ages reported here. Taxon names in grey have not been described in the fossil record. Taxon names in black have been described from fossils. See Holman (2000) and Szyndlar (2012) for records. Taxa labeled with two identifiers represent the most inclusive clades subtended by those identifiers following Pyron et al. (2013a).
Alfaro et al. 2008; Lukoschek et al., 2012), and rely on reports of colubroids as early as Cenomanian (Rage and Werner, 1999, but see Head et al., 2005; Head, 2015; this study) to the first occurrence of Coluber cadurci (Lukoschek et al., 2012). Pyron and Burbrink (2012) employ the same calibration as advocated here for Colubroidea, the Paleogene taxon Procerophis. They calibrate the stem-group age of Colubridae using the Oligocene taxon Texasophis. The identity of Texasophis as a member of the Colubridae+Elaopoidea crown has not been determined by unambiguous apomorphies, however, and we recommend the slightly younger Coluber cadurci as the calibration of that clade.

Biogeographic Histories Inferred from the Fossil Record

A direct reading of the of Caenophidia fossil record indicates a latest Late Cretaceous origin likely in Gondwanan landmasses based on African and South American russellogophids (Rage and Werner, 1999; Rage, 2008) with the oldest colubroids occurring in continental sediments of the Cambray Formation of northern India by the early Eocene (Rage et al., 2008). Whether or not the Cambray colubrid record represents a Gondwanan fauna subsequently docked with Asia or an Asian fauna dispersing into India is indeterminate due to the Laurasian composition of the local mammal faunas (Rana et al., 2008; Rose et al., 2008) and early Paleogene records of European russellophids (Rage, 1976). Unambiguous pan-colubroid disperses across Europe and Asia and into North America and Africa by the late Eocene (Rage et al., 1992; Parmley and Holman, 2003; Head et al., 2005; McCartney and Seiffert, 2015). Colubroids anatomically consistent with the crown clade of Colubridae+Elaopoidea appear in North America and Europe during the early to middle Oligocene (Holman, 1999; Szyndlar, 2012), and appear in Sub-Saharan Africa by the late Oligocene (McCortney et al., 2014).

Dispersal of caenophidians into South America from North America and Australia from Asia occurred during the Neogene. Colubroid fossils are present in South America from the middle Miocene on (Hoffstetter and Rage, 1977; Albino, 1996; Albino and Montalvo, 2006; Head et al., 2006; Albino and Brizuela, 2014), consistent with an early to middle Miocene immigration conduit between Central and South America, as evidenced by other snake taxa (Head et al., 2012). The first occurrence of colubroids in Australia is late early Miocene and consists of elapoid remains (Scanlon et al., 2003 after Woodhead et al., 2016).

Among colubroid subclades, the temporal and geographic origins of Elapoidea and Viperidae are most poorly understood. The high diversity of Elapoidea, as well as endemicity of many subclades, in Africa is suggestive of an African origin for the clade, and the oldest fossils referred to Elapidae are from the late Oligocene of Africa (McCartney et al., 2014). However, an African origin requires either an early Paleogene immigration into Africa with subsequent isolation or a Gondwanan origin of the clade, which would require an Early Cretaceous divergence from Colubridae. This section scenario is highly unlikely given everything that is known about the fossil record of caenophidians, the fossil records of “henophidian” sister taxa, and rates of molecular evolution.

The origin and earliest evolution of Viperidae is unknown in the fossil record. Viperids first appear in the early Miocene of Europe and then the late early Miocene of North America, Asia, and Africa (Szyndlar and Rage, 1999). Immigration into South America occurred by the middle Miocene (Albino and Montalvo, 2006). Despite the distinctive morphology of both cranial and axial osteology in vipers, there is no fossil evidence of the clade in the Paleogene. The sister-taxon relationships with Colubridae+Elaopoidea requires at least a mid-Paleogene divergence of the viperid lineage, and the absence of identifiable vipers from approximately-aged sediments in Europe, North America, and North Africa suggests that the evolution of the viperid crown clade and its diagnostic skeletal morphology may have been a comparatively recent event relative to colubrids and elapoids.

For caenophidians, as well as other squamates, the last occurrence of archaic taxa and the first occurrence of specimens referable to extant taxa is during the Miocene for the majority of documented clades. Whether the timing of modernization in squamate faunas results from climatic changes from the Paleogene world, biotic changes in ecosystem trophic structures (Rabb and Marx, 1973; Parmley and Holman, 1995), or the evolution of highly toxic venoms (e.g, Savitzky, 1980), remains to be determined, but will require combining fossil, sedimentological, and molecular data in a comprehensive study.

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