CHAPTER 3: ORIGIN AND EVOLUTION OF ELAPIDS AND NEW WORLD CORALSNAKES

Hussam Zaher, Felipe G Grazziotin, Ana Lúcia da Costa Prudente, Ana Bottallo de Aguiar Quadros, Vivian C Trevine, Nelson Jorge da Silva

To cite this version:

Hussam Zaher, Felipe G Grazziotin, Ana Lúcia da Costa Prudente, Ana Bottallo de Aguiar Quadros, Vivian C Trevine, et al.. CHAPTER 3: ORIGIN AND EVOLUTION OF ELAPIDS AND NEW WORLD CORALSNAKES. Advances in Coralsnake Biology: with an Emphasis on the South America, 2020, 978-0-97200154-6-2. mnhn-03786715

HAL Id: mnhn-03786715

https://mnhn.hal.science/mnhn-03786715

Submitted on 23 Sep 2022

CHAPTER 3: ORIGIN AND EVOLUTION OF ELAPIDS AND NEW WORLD CORALSNAKES

Hussam Zaher[1], Felipe G. Grazziotin[2], Ana Lúcia da Costa Prudente[3,4], Ana Bottallo de Aguiar Quadros[1], Vivian C. Trevine[2], and Nelson Jorge da Silva, Jr.[5]

[1]Museu de Zoologia, Universidade de São Paulo, São Paulo, São Paulo, Brazil.

[2]Laboratório Especial de Coleções Zoológicas, Instituto Butantan, São Paulo, São Paulo, Brazil.

[3]Laboratório de Herpetologia, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.

[4]Programa de Pós-Graduação em Biodiversidade e Evolução, Museu Paraense Emílio Goeldi e Universidade Federal do Pará, Belém, Pará, Brazil.

[5]Programa de Pós-Graduação em Ciências Ambientais e Saúde, Escola de Ciências Médicas, Farmacêuticas e Biomédicas, Pontifícia Universidade Católica de Goiás, Goiânia Goiás, Brazil.

1. INTRODUCTION

From an evolutionary perspective the radiation of elapids remains poorly understood, but when dealing with public health issues in tropical and subtropical countries, this family of snakes has been well documented in the indices of envenomation accidents (WHO, 2010). Until recently, elapids were believed to comprise one of the best delimited families in the Clade Colubroides (*sensu* Zaher et al., 2009), which is characterized by a venom inoculation system traditionally termed as "proteroglyph."

Morphological characters traditionally listed as synapomorphies for the Elapidae consist of fixed grooved teeth in the anterior portion of the maxilla (proteroglyph dentition), the lack of a loreal scale, a seromucous accessory gland situated in the anterior portion of the venom gland, the presence of a muscle known as the *adductor mandibulae externus superficialis* (AMES) that has differentiated into a glandular compressor, and hemipenes with a bifurcated spermatic sulcus (Underwood, 1967; Smith et al., 1977; McCarthy, 1985).

Nevertheless, in recent years molecular analyses have corroborated the hypothesis of polyphyly for the family presented by McDowell (1968), who suggested an independent origin for the genus *Homoroselaps*. Thus, morphological characteristics related to the proteroglyph venom inoculation system, which appear to support monophyly for the Elapidae, have evolved in parallel at least once in the atractaspidids (Cundall and Irish, 2008; Kelly et al., 2009).

More recent and inclusive analyses of the Colubroides largely have corroborated McDowell's views (Kelly et al., 2011; Pyron et al., 2013; Figueroa et al., 2016; Zheng and Wiens, 2016; Zaher et al., 2019). Nonetheless, Zaher et al. (2019) showed that interrelationships within elapids still recover a high number of unsolved or questionable phylogenetic affinities. Still, the elapid fossil record remains relatively scarce and underrepresents the known diversity, although it sheds some light on the origin and diversification of the group. Herein, we address these questions, and where possible emphasize matters related to the origin and evolution of the adaptive radiation of New World coralsnakes.

2. THE ELAPID FOSSIL RECORD

2.1. The Oligocene

The oldest fossil record of a probable elapid comes from the Late Oligocene of the Nsungwe Formation (~24.95 MA) in Tanzania (McCartney et al., 2014), where a colubroid fauna was represented exclusively by isolated or associated vertebrae, among which two posterior trunk vertebrae were attributed to two distinct elapid morphotypes. The association of these vertebrae with probable elapids was based on the presence of low and recurved hypapophyses and the absence of post-zygapophyseal foramina. The combination of these two conditions is considered characteristic of the axial skeleton of African elapids, which is absent in other colubroids on the continent (McCartney et al., 2014).

Scanlon et al. (2003) reported what they considered at that time to be the oldest record of an elapid, represented by a single vertebra, and dated to the Late Oligocene or Early Miocene (limit Chattian/Aquitanian, ~24 MA) from Riversleigh, in Australia. According to these authors, the morphology of the vertebra is nearly identical to those of the extant genus *Laticauda*. This finding still remains as the oldest fossil record of the Australo-Melanesian (Hydrophiinae) radiation of elapids.

2.2. Miocene-Pliocene

After the Oligocene, elapids already were present in the fossil record of the Early Miocene of Africa and the Middle Miocene of Australia. In Europe, vertebrae attributed to the extinct species *Naja romani* were discovered in sediments at Vieux Collonges, in France, and at Petersbuch 2, in Germany (Biozone MN 4, Burdigalian, ~16.7 MA). *Naja romani* originally was described in the genus *Paleonaja*, from a nearly complete skeleton from the Middle Miocene of La Grives-Saint-Alban, in France (Biozone MN 7–8, Lower Tortonian, ~11.2 MA) (Hoffstetter, 1939; Rage, 1984; Bachmayer and Szyndlar, 1985; Szyndlar, 1991; Szyndlar and Schleich, 1993). This appears to be one of the most common species of the European Miocene, with abundant records in the Late Miocene of Austria, Ukraine, Greece, and Hungary (Bachmayer and Szyndlar, 1985; Szyndlar, 1985, 1991; Szyndlar and Schleich, 1993).

Subsequently, *Naja crassa*, described by Hoffstetter (1939) from the same locality of La Grives-Saint-Alban, and *N. austriaca*, described by Bachmayer and Szyndlar (1985) from the Late Miocene of Kohfidisch in Austria (Biozone MN 11, Tortonian, ~8 MA), were synonymized with *N. romani* (Szyndlar and Rage, 1990; Szyndlar and Zerova, 1990). In addition, *Naja iberica*, described by Szyndlar (1985) from the Late Miocene of Algora, in Spain, (Biozone MN 13, Messinian, ~7.0 MA), appears to correspond to a distinct taxon from *N. romani* (Szyndlar and Rage, 1990). *Naja depereti* represents a third extinct species from this genus, described by Hoffstetter (1939) from isolated vertebrae from the Middle Pliocene of Fort du Serrat-d'en-Vacquer, near Perpignan, in France (Biozone MN 15, Zanclean, ~4.0 MA). Elapids, and especially cobras of the genus *Naja*, persisted in the European (both Western and Eastern) fossil record until the Late Pliocene (Rage and Sen, 1976; Bailon, 1989; Szyndlar and Zerova, 1990; Szyndlar, 2012).

In Africa, post-Oligocene elapids are known from three records attributed to *Naja*. *Naja antiqua* was described from cranial and post-cranial material from the Middle Miocene of Beni Mellal (equivalent to Biozone MN 7, Langhian, ~13.8 MA) in Morocco (Rage, 1976), while *Naja robusta*, consisting of a string of partially preserved and associated vertebrae, was described from the Late Pliocene of the Laetoli Beds Formation (Locality 10) in Tanzania (Meylan, 1987). A vertebra attributed to this genus was described from the Early Miocene of Arrisdrift in Namibia (equivalent to Biozone MN 4–5, continental European Orleanian ~20.44 to 15.97 MA) (Rage, 2003).

In Australia, elapids attributed by Scanlon et al. (2003) to the Hydrophiinae clade (*sensu* McDowell, 1970) were recorded in deposits at Riversleigh, from the Middle Miocene, Late Miocene, and possibly the Early Pliocene. This fauna depicts a past diversity with no clear close affinities to extant genera, as illustrated by *Incongruelaps iteratus* from the Middle Miocene of Riversleigh (Encore Site Local Fauna, ~10 MA).

In the New World, the first elapid fossil record is from the Middle Miocene, with a series of vertebrae from the Myers Farm Local Fauna, Webster County, Nebraska, United States (NALMA Barstovian; ~13.6 MA), and described by Holman (1977) as a member of the genus *Micrurus* based on the presence of pronounced hypapophyses on the posterior trunk vertebrae, as well as reduced neural spines. Rage and Holman (1984) later described *M. gallicus*, based on a vertebra from Grive M location, in France, dated as Middle Miocene (Biozone MN 7, Astaracian, ~13.8 MA). In the generic characterization of the material from Grive M, Rage and Holman (1984) used the same characteristics employed by Holman (1977) to designate the presence of *Micrurus* in the Middle Miocene of the United States.

Apart from the Middle Miocene at Grive M (Rage and Holman, 1984), *Micrurus gallicus* also was recorded from the Early Miocene at Béon 1 (Montréal-du-Gers), in France (Rage and Bailon, 2005) and Petersbuch 2, in Germany (Szyndlar and Schleich, 1993) (Biozone MN 4, Burdigalian, ~16.7 MA). Both occurrences suffer from the same diagnostic deficiencies. Previously, Auffenberg (1963) had recorded *Micrurus* sp. (*Micrurus* cf. *fulvius*) from the Pliocene of Haile VI (Locality A) in the United States. The absence of cranial elements associated with the vertebrae precludes any clear association of this material with *Micrurus*, casting doubt upon its presence in the Miocene of Europe.

3. A BRIEF HISTORY OF PHYLOGENETIC RELATIONSHIPS OF CORALSNAKES

McDowell (1967, 1969, 1986, 1987) suggested a close relationship between Asiatic and American coralsnakes. In his meticulous analysis of the anatomy of the corner of the mouth of snakes, he recognized some explicit characters that support the proximity of these two coralsnake radiations (McDowell, 1986), as well as more clearly defining the subdivision of Asiatic coralsnakes into four distinct subgroups. In turn, Cadle and Sarich (1981) conducted one of the first molecular phylogenies, using rabbit antibodies produced against serum albumin of colubrids, elapids, and viperids. Preliminarily, their study confirmed an unequivocal relationship between Asiatic elapids and New World coralsnakes, and they discussed the origin, dispersion, and separation of these lineages. Keogh (1998) and Slowinski and Keogh (2000) also recovered a clade formed by Asian and American coralsnakes in their molecular analyses, but in both studies their taxon sampling was limited.

Castoe et al. (2007) argued in favor of the monophyly of coralsnakes, but limited the group to *Sinomicrurus*, *Calliophis* (Asian radiation), and the American radiation, and only recognized a somewhat distant relationship of these taxa with *Hemibungarus* and *Bungarus*. Although Castoe et al. (2007) significantly advanced our understanding of the phylogenetic affinities between Old and New Worlds coralsnakes, their taxonomy remains poorly resolved. Additional studies with distinctly limited taxon sampling also supported the monophyly of coralsnakes (McCarthy, 1985; Slowinski 1995; Keogh, 1998; Slowinski and Keogh, 2000; Slowinski et al., 2001; Pyron et al., 2011, 2013; Lee et al., 2016).

Roze and Bernal-Carlo (1988) were the first to present a hypothesis regarding the phylogenetic relationships among the species of New World coralsnakes, based upon a matrix of 27 morphological and immunological characters. In this study, the genus *Micruroides* appears as the sister group of the clade formed by *Leptomicrurus* and *Micrurus*. As a result, the authors recognized four clades within *Micrurus*: (1) the *M. mipartitus* group (bicolored); (2) the Central and South American triadal *Micrurus*; (3) the monadal *Micrurus* with single bands; and (4) the triadal *Micrurus* of Mexico. Therefore, according to Roze and Bernal-Carlo (1988), the triadal species of *Micrurus* do not form a monophyletic group. This hypothesis deserves special attention. Aside from their limitations, the majority of subsequent studies adopted the results presented by Roze and Bernal-Carlo (1988; Fig. 1).

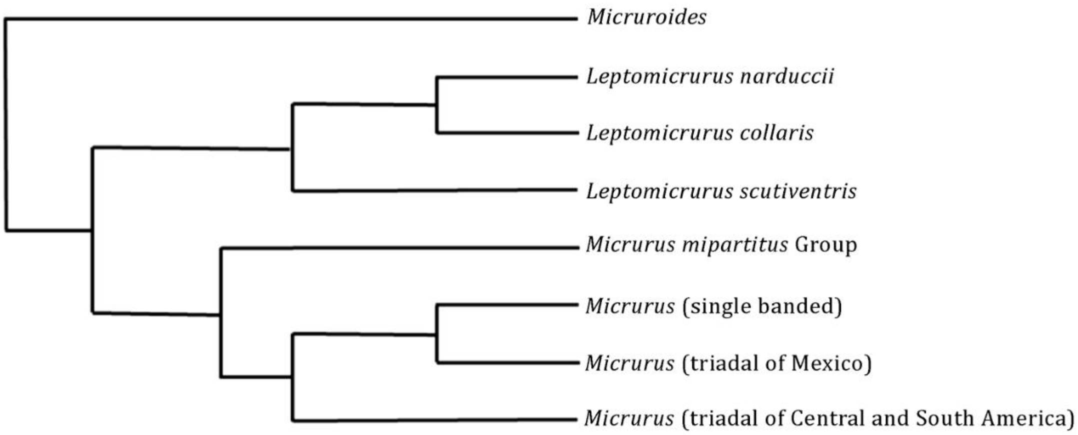


Fig. 1. The phylogenetic relationships for New World coralsnakes presented by Roze and Bernal-Carlo (1988).

Silva, Jr. and Sites, Jr. (2001) presented a molecular phylogenetic proposal for some species of South American coralsnakes with a triadal color pattern, and indicated the instability of some species (e.g., *Micrurus surinamensis* and *M. spixii*) and the poor support for groups known to be taxonomically complex. These authors also suggested that *M. lemniscatus* probably represents a polyphyletic group.

According to Renjifo et al. (2012), the South American monadal species of *Micrurus* (*M. albicinctus*, *M. corallinus*, and *M. psyches*) form a monophyletic clade with the North and Central American species (*M. diastema*, *M. fulvius*, and *M. tener*). The same authors also suggested that *M. mipartitus* and *M. dissoleucus* form a well-supported clade, contrary to the expectations of Roze and Bernal-Carlo (1988), Slowinski (1995), and Campbell and Lamar (2004).

4. A NEW PHYLOGENETIC HYPOTHESIS FOR THE ELAPIDS

The time-calibrated phylogeny presented here corresponds to an analysis of time of divergence between representatives of the family Elapidae (Fig. 2), conducted with penalized quasi-likelihood on a maximum likelihood tree, and based on a molecular matrix with 15 genes for 234 species of elapids, in a total of 1,316 terminal taxa when considering the outgroups (Appendix I). We followed Zaher et al. (2019) and combined two non-parametric measures of support—Felsenstein boostrap (BS) and Shimoidara-Hasegawa-Like test (SHL)—to assess the robustness of each clade in the molecular tree. We divided the combined SHL/BS support values into seven categories, and graphically illustrate them in Fig. 2, as follows: red = unambiguously supported; orange = robustly supported; blue = strongly supported; green = moderately supported; gray = ambiguously or poorly supported; and pale gray = unsupported (for additional information, see Zaher et al., 2019).

The topology of the tree recovers the family Elapidae with strong BS/SHL support values, whereas more inclusive relationships within elapids remain uncertain, with nearly all higher clades within the family showing ambiguously, poorly, and even unsupported combined BS/SHL values (see Zaher et al., 2019).

Similar results occurred in other works with meaningful elapid sampling (Pyron et al., 2011, 2013; Figueroa et al., 2016; Zheng and Wiens, 2016; Zaher et al., 2019), which indicate a deficiency in the available collection of information for the group. The only inclusive clade that is sustained in a robust manner (87% bootstrap support) is that of the Australo-Melanesian radiation of marine and terrestrial elapids, also known as the subfamily Hydrophiinae (Kelly et al., 2009; Sanders et al., 2013; Strickland et al., 2016). In contrast, less inclusive relationships among the elapids meet in a much more meaningful collection of clades that were sustained more robustly, in which the majority represent monophyletic genera.

4.1. Monophyly of elapid genera

Presently, fifty-seven genera are considered valid for the Elapidae (Appendix II). Of these, we sampled 49 (86%) in our phylogenetic analysis. The eight genera not sampled include: *Antaioserpens*, *Kolpophis*, *Loveridgelaps*, *Ogmodon*, *Parapistocalamus*, *Pseudohaje*, *Salomonelaps*, and *Thalassophis*. Of the 36 polytypic genera in the family, we included 35 (97%) in the analysis (only *Pseudohaje* was not sampled), of which 17 (47%) were recovered as monophyletic with strong or higher combined BS/SHL support values, and five (13%) were monophyletic, but with ambiguous or no BS/SHL support. Seven polytypic genera (19%) were not recovered as monophyletic (*Calliophis*, *Micrurus*, *Toxicocalamus*, *Suta*, *Parasuta*, *Hoplocephalus*, and *Simoselaps*). Six polytypic genera were represented by only one species, and their monophyly could not be tested, as follows: *Walterinnesia* (1/2), *Cacophis* (1/4), *Elapognathus* (1/2), *Cryptophis* (1/5), *Denisonia* (1/2), and *Leptomicrurus* (1/4).

The 17 monophyletic genera corroborated by our combined BS/SHL support values are: *Dendroaspis* (4/4 of the species sampled; 100% bootstrap), *Demansia* (3/14; 100%), *Aspidelaps* (2/2; 93%), *Laticauda* (6/8; 76%), *Furina* (2/5; 100%), *Aspidomorphus* (3/3; 100%), *Acanthophis* (8/8; 100%), *Pseudechis* (9/9; 97%), *Oxyuranus* (3/3; 99%), *Drysdalia* (3/3; 99%), *Austrelaps* (2/3; 100%), *Hemiaspis* (2/2; 99%), *Aipysurus* (7/9; 100%), *Elapsoidea* (3/10; 100%), *Naja* (28/32; 87%), *Vermicella* (6/6; 99%), and *Hydrophis* (37/48; 99%). The five polytypic genera recovered as monophyletic, but which are not corroborated by our combined support values are: *Bungarus* (11/15; < 70%), *Sinomicrurus* (4/6; < 70%), *Pseudonaja* (7/9; < 70%), *Brachyurophis* (6/8, < 70%), and *Emydocephalus* (2/3; < 70%). The seven genera that were not recovered as monophyletic were: *Micrurus* (30/81), *Calliophis* (8/11), *Toxicocalamus* (8/15), *Suta* (2/4), *Parasuta* (2/6), *Simoselaps* (5/5) and *Hoplocephalus* (2/3).

4.2. Topology of the phylogenetic tree

The species pertaining to *Calliophis* form a paraphyletic lineage that is the sister-group of all the other Elapidae (Fig. 2). The subsequent, less inclusive clade, which includes all elapid taxa except for *Calliophis*, shows poorly resolved higher-level affinities, with none of the deeper nodes retrieving significant values of combined statistical support. A basal dichotomy separates a clade including the genera *Sinomicrurus*, *Micruroides*, *Micrurus*, and *Leptomicrurus* from the rest of the Elapidae. We describe the relationships among representatives of this clade below, in a section on New World coralsnakes.

All other elapids are grouped into a clade that is not supported statistically (Fig. 2). Within this large clade, the supra-generic relationships with strong to robust combined support values are: (1) the subfamily Hydrophiinae; (2) tribe Hydrophiinii (all hydrophiines except *Laticauda*); (3) a clade formed by the genera *Walterinnesia, Aspidelaps, Hemachatus*, and *Naja*; and (4) the genera *Hemachatus* and *Naja*. Also recovered with high support were subclades that group species pertaining to subgenera of *Naja* (*sensu* Wallach et al., 2014): *Naja* (100%), *Afronaja* (99%), *Boulengerina* (98%), and *Uraeus* (100%). Among the subgenera of *Naja*, the clade formed by *Uraeus* and *Boulengerina* was recovered with strong bootstrap support (91%). Concerning the remaining suprageneric subclades recovered within the hydrophiine radiation, the following are recovered with strong or higher combined support values: (1) *Oxyuranus* and *Pseudonaja* (99%); (2) *Elapognathus*, *Rhinoplocephalus, Cryptophis*, and the paraphyletic genera, *Suta* and *Parasuta* (94%); (3) *Echiopsis*, *Drysdalia*, *Austrelaps*, *Hoplocephalus* (recovered as paraphyletic), *Paroplocephalus*, *Tropidechis*, *Notechis*, *Hemiaspis*, *Emydocephalus*, *Aipysurus*, *Parahydrophis*, *Ephalophis*, *Hydrelaps*, and *Hydrophis*

(93%); and (4) *Emydocephalus*, *Aipysurus*, *Parahydrophis*, *Ephalophis*, *Hydrelaps*, and *Hydrophis* (95%).

Contrary to our previous analysis (Zaher et al., 2016), our new analysis retrieves a monophyletic genus *Naja*, with *Hemachatus haemachatus* appearing as its sister group. Despite the low support levels recovered for the basal radiation of elapids, the African radiation, especially the one comprising *Walterinnesia*, *Aspidelaps*, *Hemachatus*, and *Naja*, is recovered here with robust combined supports. Moreover, the diverse fossil record of the genus *Naja* and the current position of the fossil species *Naja iberica*, *Naja austriaca*, and *Naja romani* within the subgenus *Boulengerina* (Quadros et al., 2019), seem to corroborate an early diversification of the genus from the African continent, with posterior diversification into the European Neogene.

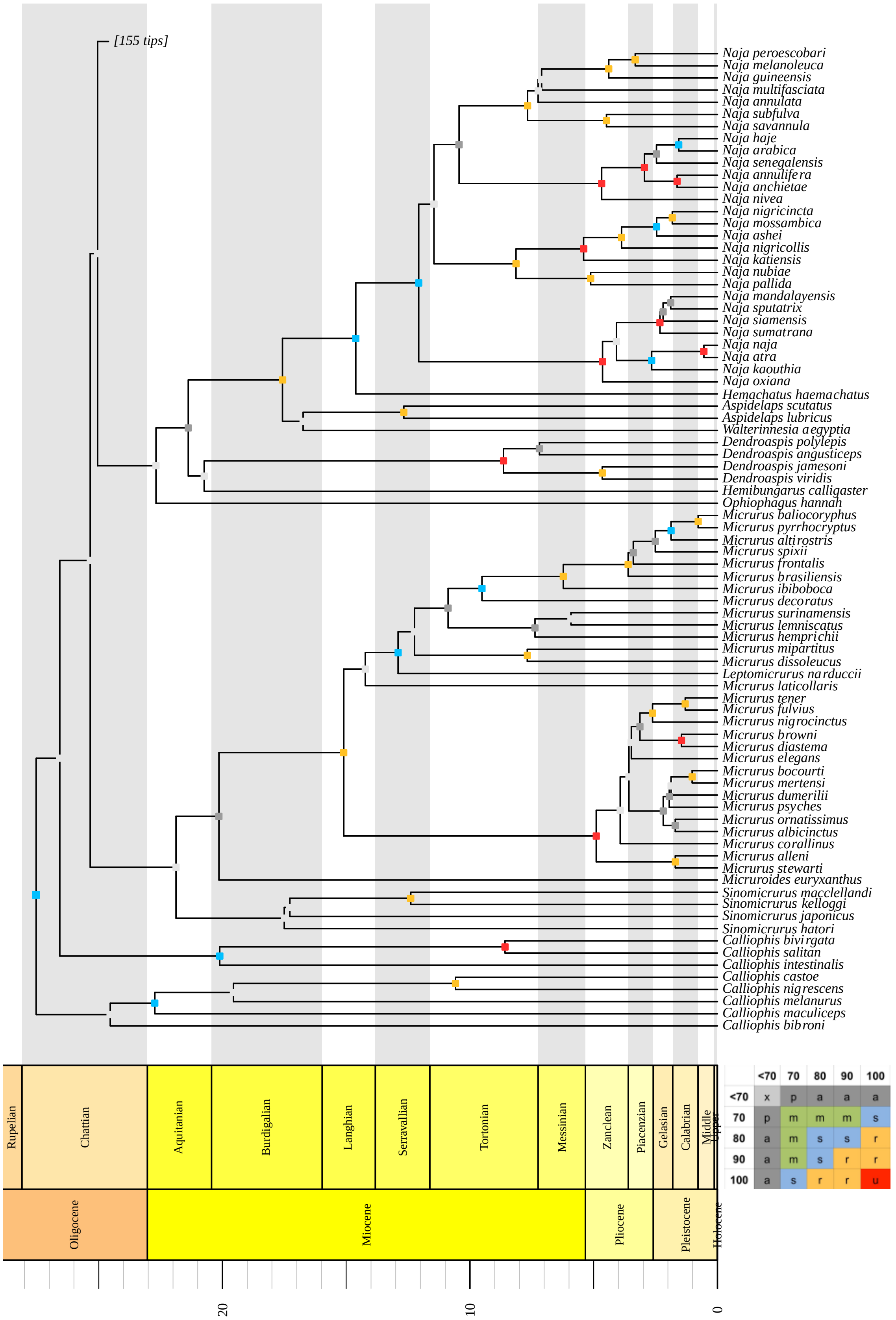


Fig. 2. A molecular phylogeny for 234 species of the family Elapidae, indicating the times of divergence calculated by penalized quasi-likelihood. The colored squares on each node represent bootstrap and SHL values, following the categories of combined clade support described in the text and summarized on the lower right corner of the figure.

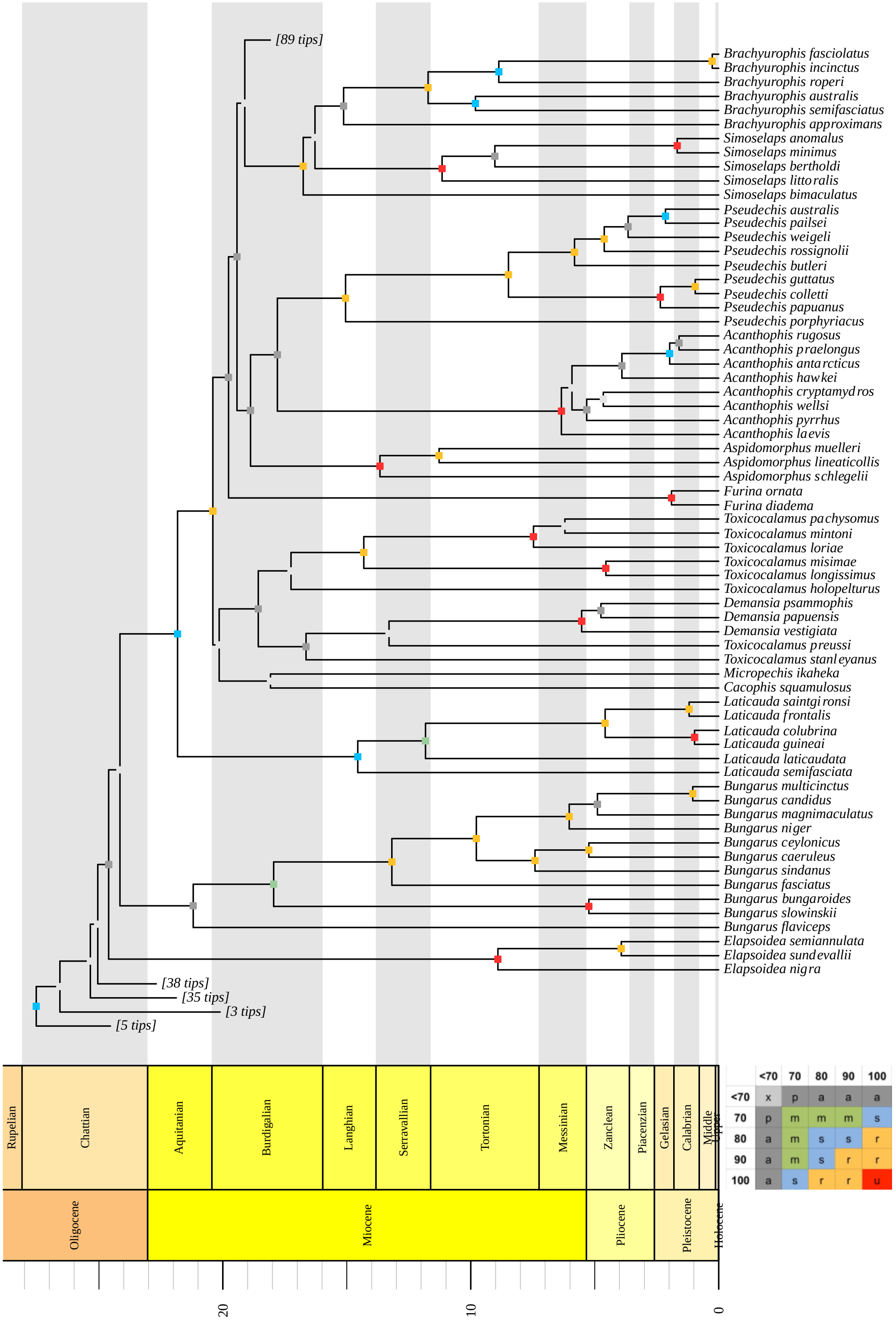
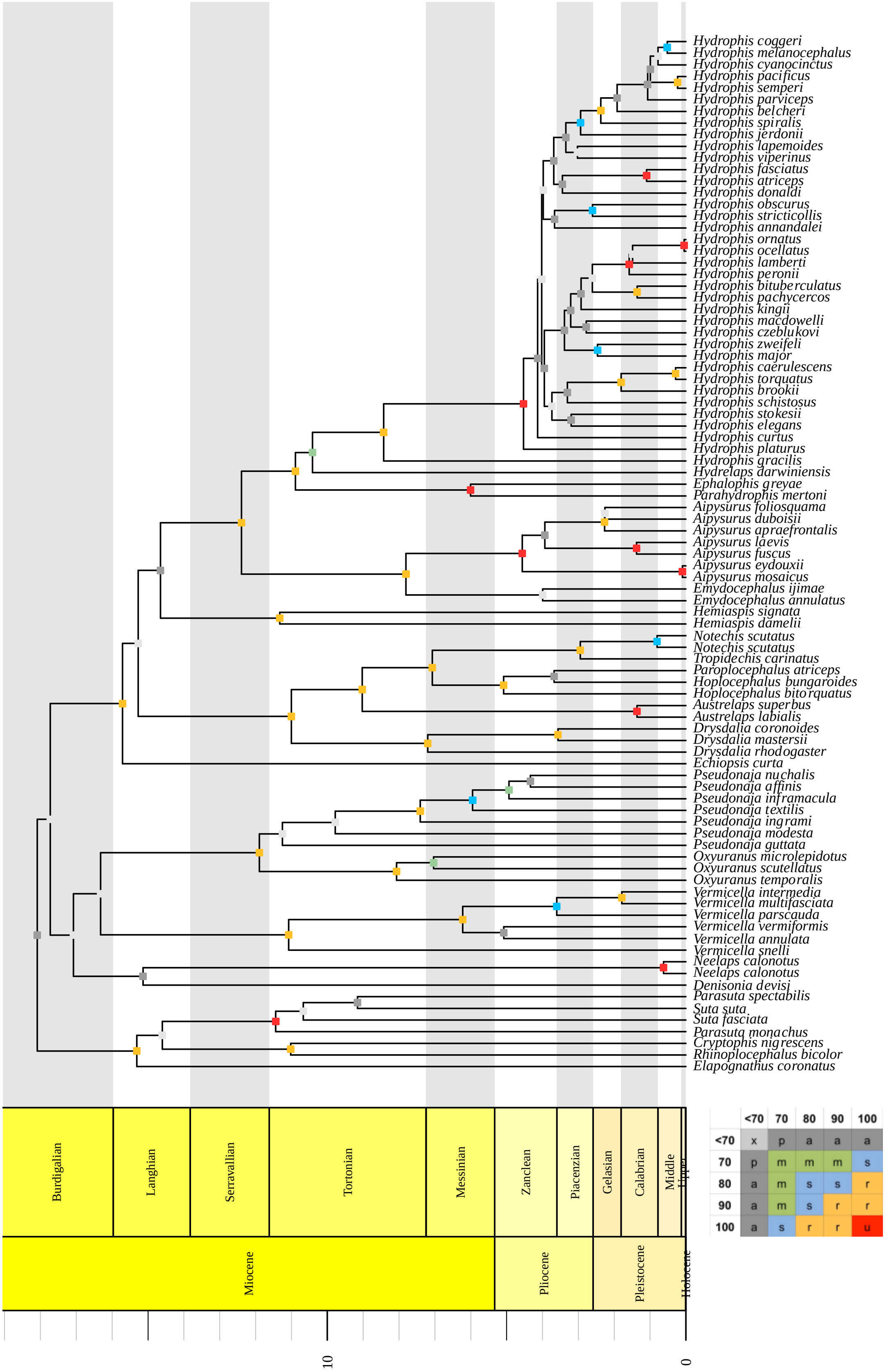


Fig. 2. Continued.



	<70	70	80	90	100
<70	x	p	a	a	a
70	p	m	m	m	s
80	a	m	s	s	r
90	a	m	s	r	r
100	a	s	r	r	u

Fig. 2. Continued.

4.3. Phylogeny of the New World Coralsnakes

In our analysis, New World coralsnakes (*Micruroides*, *Leptomicrurus*, and *Micrurus*) form a clade that appears as the sister group of the Asian coralsnakes of the genus *Sinomicrurus*, although both hypotheses are retrieved with no significant combined supports. Conversely, the genus *Micrurus* (here including *Leptomicrurus*) is supported as a robust monophyletic group, which we retrieved with a basal dichotomy that separates the monadal species (except for *M. mipartitus*) from the triadal species. *Leptomicrurus* showed a strong association with the triadal clade of *Micrurus* (including *M. mipartitus*). Although *Leptomicrurus* nests unambiguously inside the radiation of the genus *Micrurus*, rendering the latter paraphyletic, we decided to follow the other chapters in this book to provide a consistent taxonomic framework throughout (see Chapters 4, 5, 6). Perhaps in the near future, with the advent of additional morphological and molecular evidence and better taxon sampling, additional taxonomic changes and splitting of the genus *Micrurus* can be regarded as necessary.

The clade formed by *Leptomicrurus narduccii*, *Micrurus mipartitus*, and the triadal species shows strong BS/SHL combined support values, whereas the monadal *Micrurus* is supported unambiguously. Although mostly resolved, the triadal clade still presents ambiguous and poorly supported internal relationships that deserve further investigation. Overall, two main subclades are recovered: one formed by *M. dissoleucus* and *M. mipartitus*, with robust combined supports (see Renjifo et al., 2012; Pyron et al., 2013, and Lee et al., 2016), and the other composed of *M. decoratus*, *M. ibiboboca*, *M. brasiliensis*, *M. frontalis*, *M. spixii*, *M. altirostris*, *M. pyrrhocryptus*, and *M. baliocoryphus*, with strong combined support values. The monadal clade retrieves four robustly to unambiguously supported subclades: (1) *M. stewarti* + *M. alleni*; (2) *M. mertensi* + *M. bocourti*; (3) *M. nigrocinctus* + *M. fulvius* + *M. tener*.

Although comparable to the phylogenies of Pyron et al. (2011, 2013), our results highlight a number of unsupported affinities within the New World coralsnakes, suggesting the pressing need for future studies that incorporate a more complex taxonomic arrangement of *Micrurus* at the generic level (see Chapters 4, 5, 6).

5. IMPLICATIONS OF THE FOSSIL RECORD FOR HYPOTHESES ON THE ORIGIN AND DIVERSIFICATION OF ELAPIDS

5.1. Origin of the Family Elapidae

Elapids first appear in the fossil record approximately 25 million years ago (MA), during the Late Oligocene, in African sediments of the Nsungwe Formation, in Tanzania (McCartney et al., 2014). One vertebra attributed to a hydrophiine, with probable affinities to *Laticauda*, also was encountered in Riversleigh, in sediments dated from the Latest Oligocene or Early Miocene of Australia (24 to 23 MA; Scanlon et al., 2003).

The presence of elapids in sediments of sub-Saharan Africa at the end of the Paleogene raises an important question about the hypothesis of an Asian origin for the group, which until recently had been the consensus view (Hoffstetter, 1939; Kelly et al., 2009). Following McCartney et al. (2014), the presence of elapids in the Nsungwe Formation indicates two possible scenarios: one of a rapid, initial dispersal of the family before the end of the Oligocene, from Asia to Africa, or alternatively, one of an elapid origin on the African continent instead of in Asia. Fossil elapids in the Nsungwe Formation approximate the most recent colubroidean molecular estimates given by Zaher et al. (2019), which suggest a Late Eocene origin for the group (Burbrink and Pyron, 2008; Pyron and Burbrink, 2012), but which still do not clarify the geographic location of this origin. The record of a hydrophiine in the Latest Oligocene or Earliest Miocene of Australia reinforces the hypothesis of a more ancient origin for the group, with subsequent dispersion and colonization of the Australian continent occurring during the Oligocene (Scanlon and Lee, 2004).

The estimated time of divergence for elapids in our phylogeny is concordant with other works (Table 1), and suggests an origin close to the Eocene–Oligocene boundary (~34 MA), and subsequent rapid diversification in the Oligocene associated with the overall climate shift that triggered a major terrestrial turnover known as the "Grande Coupure" (Zaher et al., 2019). Despite greater clarity surrounding the time of elapid divergence, neither the molecular phylogenies (including the present one) nor the available fossil record allow us to determine the biogeographic origin of the group. Beyond the discovery of elapids in the sub-Saharan African Oligocene and the unambiguous position of the family in the African "Elapoid" radiation that suggests an African origin, the basal paraphyletic disposition of a group of Asian coralsnakes in the recent molecular phylogenies tends to favor an Asiatic origin for the group.

Table 1. A comparison between the times of divergence calculated by various authors for some clades among the diversity of the Colubroides. () = confidence interval; — = Clade not presented in the analysis; * = terminals for the clade are found in the analysis, but the clade was not recovered; ~ = approximate confidence interval values retrieved from the chronogram presented; St = stem clade; and Cr = crown clade.

Clade		**This study**	**Burbrink and Pyron, 2008[1]**	**Wüster et al., 2008**	**Vidal et al., 2009**	**Kelly et al., 2009**	**Sanders et al., 2010**	**Pyron and Burbrink, 2012**	**Hsiang et al., 2015**	**Zaher et al., 2019**
Colubroides	St	57.38	58.7 (47.2–63.7)	70.2 (51.1–91.2)	90.7 (78–104)	63.0 (52.6–72.9)	~62 (52–77)	84.66 ~(75–94)	*	56
	Cr	54.63	38.2	—	82.2 (69–96)	—	~35 (28–45)	~75 (65–85)	*	53
Elapoidea	St	40.3	43.5	~52 (42-63)	46.3 (36-58)	45.8 (39.5-51.2)	~26 (21-31)	~50 (42-60)	~44 (34–51)	36
	Cr	38.58	*	~45 (35–55)	41.5 (32–53)	41.3 (35.7–46.3)	—	~45 (35–54)	~40 (38–48)	33
Elapidae	St	34.58	34	~40 (31–49)	41.5 (32–53)	37.4 (32.8-42.8)	~26 (21–31)	34.86 ~(25–45)	~40 (38–48)	30
	Cr	27.5	25.6	~30 (25–38)	—	31.2 (26.9–35.6)	—	—	~30.5 (18.5–41)	26

Nonetheless, and contrary to the position of some authors, the most recent elapid molecular phylogenies necessarily do not favor the Asiatic origin hypothesis, as illustrated in our own molecular analysis (Fig. 2), since the most inclusive elapid relationships, including the earliest-diverging elapid clades and relationships among the Asiatic and African clades still lack unambiguous support (Fig. 2). Moreover, beyond the recent discoveries about the ancient Asiatic colubroid fauna (Head et al., 2005; Rage et al., 2003; Kuch et al., 2006), still, no Paleogene elapid fossils are known from the Asian continent.

5.2. Origin and diversification of New World coralsnakes

Despite uncertainties concerning the biogeographic origin of the family, the present phylogeny agrees with most recent molecular results, which indicate an Asiatic origin for the radiation of New World coralsnakes (Hoffstetter, 1939). Here, we estimate the time of divergence between Asiatic and American coralsnakes at approximately 22 MA, with the colonization of the Americas by coralsnakes occurring in the Early Miocene, given that the diversification of the genus *Micrurus* was estimated at ~15 MA.

This first date coincides with the hypothesis of intercontinental dispersal via the Bering land bridge, which permitted faunal exchange between the eastern Palearctic and the Nearctic (Sanmartin et al., 2001; Guo et al., 2012). A second estimate greatly precedes the presumed date of the Pliocene connection between the Central and South American continents via the Isthmus of Panama, and is concordant with the scenario defended by Savage (1982), Estes and Báez (1985), and Vanzolini and Heyer (1985), who proposed that the dispersal of coralsnakes into the South American continent occurred during the Miocene.

Holman (1977), who recorded the first occurrence of an elapid in North America during the Middle Miocene, offered one line of evidence that favors this last scenario by allocating a series of vertebrae recovered from sediments of the Myers Farm Local Fauna Formation (Nebraska, United States) to the genus *Micrurus*. Although we agree with assigning these specimens to the family Elapidae, their inclusion in the genus *Micrurus* still seems premature, given that no known synapomorphy that characterizes this genus is present in the material he described.

Rage and Holman (1984) further expanded the generic definition of *Micrurus* by including the vertebrae of a small elapid encountered in the Middle Miocene of Europe, which they described as *M. gallicus*. Rage and Holman (1984) emphasized some subtle differences between the holotype of *M. gallicus* and the vertebral morphology of the genus *Micruroides*, but they did not compare the material with the small South Asian elapid radiation, or with a larger sample of species of the genus *Micrurus* itself (except for *M. fulvius* and *M. affinis*). More recently, Szyndlar and Schleich (1993), Augé and Rage (2000) and Rage and Bailon (2005) expressed reservations about including these vertebrae in the genus *Micrurus*, a conservative opinion with which we concur.

Despite all these advances in coralsnake evolution, present phylogenetic evidence fails to sustain the monophyly of Asiatic coralsnakes while providing ambiguous support for the monophyly of the American coralsnake radiation. Clearly, additional efforts on elucidating the molecular and morphological affinities of corasnakes are needed in order to more thoroughly address their evolutionary history.

LITERATURE CITED

AUFFENBERG, W.A. 1963. The fossil snakes of Florida. Tulane Studies in Zoology 10: 129–216.

AUGÉ, M., AND J.C. RAGE. 2000. Les squamates (Reptilia) du Miocène moyen de Sansan. *In* L. Ginsburg (Ed.), La faune Miocène de Sansan et son environement. Memoires du Muséum National d'Histoire Naturelle 183: 263–313.

BACHMAYER, F., AND Z. SZYNDLAR. 1985. Ophidians (Reptilia: Serpentes) from the Kohfidisch fissures of Burgenland, Austria. Annalen des Naturhistorischen Museum in Wien 87: 79–100.

BAILON, S. 1989. Les amphibiens et les reptiles du Pliocène supérieur de Balaruc II. Palaeovertebrata 19: 7–28.

BURBRINK, F.T., AND R.A. PYRON. 2008. The taming of the skew: estimating proper confidence intervals for divergence dates. Systematic Biology 57: 317–328.

CADLE, J.E., AND V.M. SARICH. 1981. An immunological assessment of the phylogenetic position of New World coral snakes. Journal of Zoology 195: 157–167.

CAMPBELL, J.A., AND W.W. LAMAR. 2004. The Venomous Reptiles of Western Hemisphere. Volume I. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, United States.

CASTOE, T.A., E.N. SMITH, R.M. BROWN, AND C.L. PARKINSON. 2007. Higher-level phylogeny of Asian and American coralsnakes, their placement within the Elapidae (Squamata), and the systematic affinities of the enigmatic Asian coralsnake *Hemibungarus calligaster*. Zoological Journal of the Linnean Society 151: 809–831.

CUNDALL, D., AND F. IRISH. 2008. The snake skull. Pp. 349–692 *In* Gans, C., A.S. Gaunt, and K. Adler (Eds.), Biology of the Reptilia. Vol. 20, Morphology H. Society for the Study of Amphibians and Reptiles, Ithaca, New York, United States.

ESTES, R., AND A. BÁEZ. 1985. Herpetofauna of North and South America during the late Cretaceous and Cenozoic: evidence for interchange? Pp. 139–197 *In* Stehli, F.G., and S.D. Webb (Eds.), The Great American Biotic Interchange. Plenum Press, New York, New York, United States.

FIGUEROA A., A.D. MCKELLY, L.L. GRISMER, C.D. BELL, AND S.P. LAILVAUX. 2016. A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. PLOS One 11: e0161070.

GUO, P., Q. LIU, Y. XU, K. JIANG, M. HOU, L. DING, R.A. PYRON, AND F.T. BURBRINK. 2012. Out of Asia: natricine snakes support the Cenozoic Beringian dispersal hypothesis. Molecular Phylogenetics and Evolution 63: 825–833.

HEAD, J.J., P.A. HOLROYD, J.H. HUTCHISON, AND R.L. CIOCHON. 2005. First report of snakes (Serpentes) from the Late Middle Eocene of the Ponduang Formation, Myanmar. Journal of Vertebrate Paleontology 25: 246–250.

HOFFSTETTER, R. 1939. Contribution à l'étude des Elapidae actuels et fossiles et de l'ostéologie des ophidiens. Archives du Muséum d'Histoire Naturelle de Lyon 15: 1–78.

HOLMAN, J.A. 1977. Upper Miocene snakes (Reptilia, Serpentes) from southeastern Nebraska. Journal of Herpetology 11: 323–335.

HOLMAN, J.A. 1984. *Texasophis galbreathi*, new species, the earliest New World colubrid snake. Journal of Vertebrate Paleontology 3: 263–306.

HSIANG, A.Y., D.J. FIELD, T.H. WEBSTER, A.D.B. BEHLKE, M.B. DAVIS, R.A. RACICOT, AND J.A. GAUTHIER. 2015. The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. BMC Evolutionary Biology 15: 87.

KELLY, C.M.R., N.P. BARKER, M.H. VILLET, AND D.G. BROADLEY. 2009. Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. Cladistics 25: 38–63.

KELLY, C.M.R., BRANCH, W.R., BROADLEY, D.G., BARKER, N.P., and VILLET, M.H. 2011. Molecular systematics of the African snake family Lamprophiidae Fitzinger, 1843 (Serpentes: Elapoidea), with particular focus on the genera *Lamprophis* Fitzinger 1843 and *Mehelya* Csiki 1903. Molecular Phylogenetics and Evolution 58: 415–426.

doi:10.1016/j.ympev.2010.11.010

KEOGH, J.S. 1998. Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. Biological Journal of the Linnean Society 63: 177–203.

KUCH, U., J., MÜLLER, C. MÖDDEN, AND D. MEBS. 2006. Snake fangs from the lower Miocene of Germany: evolutionary stability of perfect weapons. Naturwissenschaften 93: 84–87.

LANFEAR, R., B. CALCOTT, S.Y.W. HO, AND S. GUINDON. 2012. Partitionfinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1,695–1,701.

LEE, M.S.Y., K.L. SANDERS, B. KING, AND A. PALCI. 2016. Diversification rates and phenotypic evolution in venomous snakes (Elapidae). Royal Society Open Science 3: 150277.

MCCARTHY, C.J. 1985. Monophyly of the elapid snakes (Serpentes: Elapidae). An assessment of the evidence. Zoological Journal of the Linnean Society 83: 79–93.

MCCARTNEY, J.A., N.J. STEVENS, AND P.M. O'CONNOR. 2014. The earliest colubroid-dominated snake fauna from Africa: perspectives from the Late Oligocene Nsungwe Formation of southwestern Tanzania. PLoS One 9(3): e90415.

MCDOWELL, S.B. 1967. *Aspidomorphus*, a new genus of New Guinea snakes of the family Elapidae, with notes on related genera. Journal of Zoology 51: 497–543.

MCDOWELL, S.B. 1968. Affinities of the snakes usually called *Elaps lacteus* and *E. dorsalis*. Zoological Journal of the Linnean Society 47: 561–578.

MCDOWELL, S.B. 1969. *Toxicocalamus*, a New Guinea genus of snakes of the family Elapidae. Journal of Zoology 159: 443–511.

MCDOWELL, S.B. 1970. On the status and relationships of the Solomon Island elapid snakes. Zoological Journal of the Linnean Society 161: 145–190.

MCDOWELL, S.B. 1986. The architecture of the corner of the mouth of colubroid snakes. Journal of Herpetology 20: 353–407.

MCDOWELL, S.B. 1987. Systematics. Pp. 3–50 *In* Seigel, R.A., J.T. Collins, and S.S. Novak. Snakes: Ecology and Evolutionary Biology. McGraw-Hill Publishing Co., Inc., New York, New York, United States.

MEYLAN, P.A. 1987. Fossil snakes from Laetoli. Pp. 78–82 *In* M.D. Leakey and J.M. Harris (Eds.), Laetoli: A Pliocene Site in Northern Tanzania. Clarendon Press, Oxford, Great Britain.

PYRON, R.A., AND F.T. BURBRINK. 2012. Extinction, ecological opportunity, and the origins of global snake diversity. Evolution 66: 163–178.

PYRON, R.A., F.T. BURBRINK, G.R. COLLI, A.N.M. de OCA, L.J. VITT, C.A. KUCZYNSKI, AND J.J. WIENS. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. Molecular Phylogenetics and Evolution 58: 329–342.

PYRON, R.A., F.T. BURBRINK, AND J.J. WIENS. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13: 93.

QUADROS, A.B., K. MAHLOW, N.-E. JALIL, AND H. ZAHER. 2019. Phylogenetic affinities of the fossil elapids *Naja romani* and *Naja antiqua* (Serpentes, Elapidae). Journal of Morphology 280 (S1): S207.

RAGE, J.C. 1976. Les squamates du Miocène de Beni Mellal. Géologie Méditerranéenne 3: 57–69.

RAGE, J.C. 1984. Serpentes. Pp. 1–80 *In* Wellnhofer, P. (Ed.), Handbuch der Palaoherpetologie. Gustav Fischer, Stuttgart, Baden-Württmberg, Germany.

RAGE, J.C. 2003. Squamate reptiles from the early Miocene of Arrisdrift (Namibia). Pp. 43–50 *In* Senut, B., and M. Pickford (Eds.), Geology and Palaeobiology of the Central and Southern Namib. Volume 2: Palaeontology of the Orange River Valley, Namibia. Memoir of the Geology Survey of Namibia (Ministry of Mines and Energy, Windhoeck), 19.

RAGE, J.C., AND S. BAILON. 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). Geodiversitas 27: 413–441.

RAGE, J.C., AND S. SEN. 1976. Les amphibiens et les reptiles du Pliocène supérieur de Çalta (Turquie). Pp. 127–134 *In* Géologie Méditerranéenne. Tome 3, Numéro 2, 1976.

RAGE, J.C., AND J.A. HOLMAN. 1984. Des serpents (Reptilia, Squamata) de type nord-américain dans le Miocène française. Évolution parallèle ou dispersion? Geobios 17: 89–104.

RAGE, J.C., AND Z. SZYNDLAR. 1986. *Natrix longivertebrata* from Europe Neogene, a snake with one of the longest known stratigraphic ranges. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1986: 56–64.

RAGE, J.C., S. BAJPAI, J.G.M. THEWISSEN, AND B.N. TIWARI. 2003. Early Eocene snakes from Kutch, western India, with a review of the Palaeophiidae. Geodiversitas 25: 695–716.

RAGE, J.C., A. FOLIE, R.S. RANA, H. SINGH, K.D. ROSE, AND T. SMITH. 2008. A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India. Acta Palaentologica Polonica 53: 391–403.

RENJIFO, C., E.N. SMITH, W.C. HODGSON, J.M. RENJIFO, A. SANCHEZ, R. ACOSTA, J.H. MALDONADO, AND A. RIVEROS. 2012. Neuromuscular activity of the Colombian coral snakes *Micrurus dissoleucus* and *Micrurus mipartitus*: an evolutionary perspective. Toxicon 59: 132–142.

ROZE, J.A., AND A. BERNAL-CARLO. 1988. Las serpientes venenosas del género *Leptomicrurus* (Serpentes, Elapidae) de Suramérica com descripción de uma nueva subespécie. Bollettino del Museo Regionale di Scienze Naturali di Torino 5: 573–608.

SANDERS, K.L., A. HAMIDY, J.J. HEAD, AND D.J. GOWER. 2010. Phylogeny and divergence times of filesnakes (Achrochordus): inferences from morphology, fossils and three molecular loci. Molecular Phylogenetics and Evolution 56(3): 857–867.

SANDERS, K.L., M.S.Y. LEE, MUMPUNI, T. BERTOZZI, AND A.R. RASMUSEN. 2013. Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). Molecular Phylogenetics and Evolution 66: 575–591.

SANDERSON, M.J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. Molecular Biology and Evolution 19: 101–109.

SANMARTIN I., H. ENGHOF, AND F. RONQUIST. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biological Journal of the Linnean Society 73: 345–390.

SAVAGE, J.M. 1982. The enigma of the Central American herpetofauna: dispersals or vicariance? Annals of the Missouri Botanical Garden 69: 464–547.

SCANLON, J.D., AND M.S.Y. LEE. 2004. Phylogeny of Australasian venomous snakes (Colubroidea, Elapidae, and Hydrophiinae) based on phenotypic and molecular evidence. Zoologica Scripta 33: 335–366.

SCANLON, J.D., M.S.Y. LEE, AND M. ARCHER. 2003. Mid-Tertiary elapid snakes (Squamata, Colubroidea) from Riversleigh, northern Australia: early steps in a continent-wide adaptive radiation. Geobios 36: 573–601.

SILVA, JR., N.J., AND J.W. SITES, JR. 2001. Phylogeny of South American triad coral snakes (Elapidae: *Micrurus*) based on molecular characters. Herpetologica 57: 1–22.

SLOWINSKI, J.B. 1995. A Phylogenetic analysis of the New World coral snakes (Elapidae: *Leptomicrurus*, *Micruroides* and *Micrurus*) based on allozymic and morphological characters. Journal of Herpetology 29: 325–338.

SLOWINSKI, J.B., AND J.S. KEOGH. 2000. Phylogenetic relationships of elapid snakes based on cytochrome b mtDNA sequences. Molecular Phylogenetics and Evolution 15: 157–164.

SLOWINSKI, J.B., J. BOUNDY, AND R. LAWSON. 2001. The phylogenetic relationships of Asian coral snakes (Elapidae: *Calliophis* and *Maticora*) based on morphological and molecular characters. Herpetologica 57: 233–243.

SMITH, H.M., R.B. SMITH, AND H.L. SAWIN. 1977. A summary of snake classification (Reptilia, Serpentes). Journal of Herpetology 11(2): 115–121.

SMITH, S.A., AND B.C. O'MEARA. 2012. TreePL: divergence time estimation using penalized likelihood for large phylogenies. Bioinformatics 28: 2,689–2,690.

STAMATAKIS, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post analysis of large phylogenies. Bioinformatics 30: 1, 312–1, 313.

STRICKLAND, J.L., S. CARTER, F. KRAUS, AND C.L. PARKINSON. 2016. Snake evolution in Melanesia: origin of the Hydrophiinae (Serpentes, Elapidae), and the evolutionary history of the enigmatic New Guinean elapid Toxicocalamus. Zoological Journal of the Linnean Society 178: 663–678.

SZYNDLAR, Z. 1985. Ophidian fauna (Reptilia, Serpentes) from the uppermost Miocene of Algora (Spain). Estudios Geologicos 41: 447–465.

SZYNDLAR, Z. 1991. A review of Neogene and Quaternary snakes of central and eastern Europe. Part II. Natricinae, Elapidae, Viperidae. Estudios Geologicos 47: 237–266.

SZYNDLAR, Z. 2012. Early Oligocene to Pliocene Colubridae of Europe: a review. Bulletin de la Société Géologique de France 183(6): 661–681.

SZYNDLAR, Z., AND J.C. RAGE. 1990. West Palearctic cobras of the genus *Naja* (Serpentes: Elapidae): interrelationships among extinct and extant species. Amphibia-Reptilia 11: 385–400.

SZYNDLAR, Z., AND H.H. SCHLEICH. 1993. Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern

Germany. Stuttgarter Beiträge zur Naturkunde (Series B) 192: 1–47.

SZYNDLAR, Z., AND G.A. ZEROVA. 1990. Neogene cobras of the genus *Naja* (Serpentes, Elapidae) of east Europe. Annalen des Naturhistorischen Museums in Wien 91A: 53–61.

UETZ, P., P. FREED, AND J. HOŠEK (Eds). 2019. The Reptile Database <www.reptile-database.org>, accessed November 2018.

UNDERWOOD, G. 1967. A Contribution to the Classification of Snakes. Publication no. 653, British Museum (Natural History), London, England, United Kingdom.

VANZOLINI, P.E., AND W.R. HEYER. 1985. The American herpetofauna and the interchange. Pp. 475–487 *In* Stehli, F. G., and S. D. Webb (Eds.), The Great American Biotic Interchange. Plenum Press, New York, New York, United States.

VIDAL, N., J.C. RAGE, A. COULOUX, AND S.B. HEDGES. 2009. Snakes (Serpentes). Pp. 390–397 *In* Hedges, S.B., and S. Kumar (Eds.), The Timetree of Life. Oxford University Press, United Kingdom, Published in New York, United States.

WALLACH, V., K.L. WILLIAMS, AND J. BOUNDY. 2014. Snakes of the World: A Catalogue of Living and Extinct Species. CRC Press, Boca Raton, Florida, United States.

WORLD HEALTH ORGANIZATION (WHO). 2010. Guidelines for the Management of Snake-Bites. Regional Office for South-East Asia, New Delhi, India.

WÜSTER, W., L. PEPPIN, C.E. POOK, AND D.E. WALKER. 2008. A nesting of vipers: phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). Molecular Phylogenetics and Evolution 49: 445–459.

ZAHER, H., F.G. GRAZZIOTIN, J.E. CADLE, R.W. MURPHY, J.C. MOURA-LEITE, AND S.L. BONATTO. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American xenodontines: a revised classification and descriptions of new taxa. Papéis Avulsos de Zoologia 49: 115–153.

ZAHER, H., F.G. GRAZZIOTIN, A.L.C PRUDENTE, AND N. J. SILVA, JR. 2016. Origem e Evolução dos Elapídeos e das cobras-corais do Novo Mundo. Pp. 24–45 *In* Silva Jr., N.J. (Org.), As cobras-corais do Brasil: biologia, taxonomia, venenos e envenenamentos. Ed. Da PUC Goiás, Goiânia, Brazil.

ZAHER, H., R.W., MURPHY, J. C. ARREDONDO, R. GRABOSKI, P.R. MACHADO-FILHO, K. MAHLOW, G.G. MONTIGELLI, A.B. QUADROS, N.L. ORLOV, M. WILKINSON, Y.-P. ZHANG, AND F.G. GRAZZIOTIN. 2019. Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). PLOS One 14(5): e0217959.

ZHENG, Y., AND J.J. WIENS. 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. Molecular Phylogenetics and Evolution 94: 537–547.

APPENDIX I. PHYLOGENETIC ANALYSIS EMPLOYED

With the objective of establishing phylogenetic relationships among the Caenophidia (the group to which so-called "advanced" snakes are assigned), Zaher et al. (2019) produced a molecular matrix of 15 genes with 1,278 terminals. The sequences in this matrix were generated by the authors or obtained from GenBank, a public database at the National Institutes of Health (NIH). A molecular matrix produced by these authors was used for a phylogenetic analysis restricted to the family Elapidae. From this matrix, all sequences were extracted for 196 species of elapids, representing 85% of all elapid genera and 55% of the species. An additional 19 species from this matrix were included as an outgroup, making a total of 215 terminals. Of the 15 genes sampled in this matrix, six were mitochondrial (12S, 16S, cytb, cox1, nd2, and nd4) and nine were nuclear (amel, bdnf, cmos, hoxa13, jun, nt3, r35, rag1, and rag2). The number of terminals per gene varied from 13 for cox1 to 186 for nd4, with a mean of 76 terminals per gene (a mean of 113 terminals per mitochondrial gene and 56 per nuclear gene).

To find the best evolutionary model and the best scheme to partition the data, we used the program PartitionFinder v.1.0 (Lanfear et al., 2012). Coding genes previously were partitioned in each codon position and ribosomal RNAs (12S e 16S) were treated as independent partitions, totaling 41 partitions. The program RAxML v.8.0 (Stamatakis, 2014) was utilized to estimate a maximum likelihood tree and bootstrap values for the clades. By means of the command "–f a" 1,000 rapid bootstrap replicates were conducted. For every five replicates, a generated tree was used as the initial tree for a complete search of maximum likelihood based on the original matrix. To estimate approximate dates of cladogenic events suggested by the maximum likelihood tree, we used the program treePL (Sanderson, 2002; Smith and O'Meara, 2012), which employs the method of penalized quasi-likelihood to estimate time of divergence by assuming an auto correlated molecular clock (Sanderson, 2002). The cross-validation algorithm (RSRCV, random subsample and replicate cross-validation) was used to determine the smoothing parameter for penalized quasi-likelihood, being configured in the range of 0.001 to 100. The calibration points chosen for the analysis of divergence time was based on nine points defined by Zaher et al. (2019) for dating the tree of the Caenophidia. The present analysis, however, was limited to only five points, to adapt the dating to the smallest time window for the matrix produced for the Elapidae.

The calibration points used were as follows (see Zaher et al, 2019 for more details):

(1) *Procerophis sahnii* (Rage et al., 2008)—Set as the Most Recent Common Ancestor (MRCA) of *Acrochordus granulatus* and *Xenodermus javanicus* (Colubroides *stem clade*), using 94 and 54 MA as the earliest and latest dates, respectively.

(2) *Texasophis galbreathi* (Holman, 1984)—Set as the MRCA of *Coluber constrictor* and *Heterodon platirhinos* (Colubridae *stem clade*). The earliest data for this point was placed at 54 MA and the latest at 33.3 MA.

(3) Viperidae *gen. and sp. indet.* (Kuch et al., 2006)—Set as the MRCA of *Homalopsis buccata* and *Azemiops feae* (Viperidae *stem clade*). The earliest date used for the clade was 54 MA and the most recent was 19.5 MA.

(4) Elapidae *gen. and sp. indet.* (Kuch et al., 2006)—Set the MRCA of *Naja naja* and *Rhamphiophis oxyrhynchus* (Elapidae *stem clade*). The earliest date for this clade was configured at 54 MA and the most recent at 19.5 MA.

(5) *Natrix longivertebrata* (Rage and Szyndlar, 1986)—Set as the MRCA of *Storeria dekayi* and *Rhabdophis subminiatus* (Natricidae *crown clade*), and its earliest and latest dates were set at 54 and 13.8 MA, respectively.

List of added taxa and sequences to the dataset provided by Zaher et al. (2016).

Taxon	**12S**	**16S**	**cmos**	**cox1**	**cytb**	**nd4**	**nt3**	**RAG1**
Acanthophis cryptamydros		KT026509.1			KT026560.1			
Acanthophis hawkei		KT026515.1			KT026542.1			
Acanthophis laevis		KT026517.1			KT026544.1			
Aipysurus foliosquama		KU240026.1						
Bungarus magnimaculatus				KY769768.1				
Calliophis bibroni					KU754313.1			
Calliophis intestinalis						KX130759.1		
Calliophis salitan						KX130755.1		
Hydrophis annandalei		KU240027.1			KU240025.1	KU240028.1		
Hydrophis bituberculatus						KU240029.1		
Hydrophis torquatus						KU240030.1		
Micrurus alleni		KX660164.1			KX660439.1	KX660567.1		
Micrurus bocourti						KP998038.1		
Micrurus browni					KU754313.1	KU754414.1		
Micrurus dumerilii						KP998029.1		
Micrurus elegans					KU754339.1	KU754449.1		
Micrurus laticollaris					KU754347.1	KU754446.1		
Micrurus mertensi						KP998037.1		
Micrurus nigrocinctus				MH140285.1	KU754344.1	KU754421.1		
Micrurus ornatissimus						KP998028.1		
Micrurus stewarti				MH140292.1		KX090916.1		
Micrurus tener	KR814629.1	KR814656.1	KR814672.1		KR814692.1	KU754396.1		KR814745.1
Naja guineensis					MH337582.1	MH337376.1		
Naja peroescobari					MH337634.1	MH337440.1		

Naja savannula				MH337598.1	MH337408.1		
Naja subfulva				MH337603.1	MH337409.1		
Neelaps calonotus							EU546884.1
Notechis scutatus							EU546905.1
Pseudechis pailsei				KX981633.1	KX981677.1	KX981761.1	
Pseudechis rossignolii				KX981621.1	KX981652.1	KX981750.1	
Pseudechis weigeli				KX981632.1	KX981659.1	KX981773.1	
Sinomicrurus hatori			KP772310.1				
Toxicocalamus holopelturus	KT968666.1	KU128773.1		KT778515.1	KU128798.1		KU128746.1
Toxicocalamus longissimus	KT968675.1	KU128781.1		KT778523.1	KU128805.1		KU128752.1
Toxicocalamus mintoni	KT968692.1			KT778543.1	KU128822.1		KU128769.1
Toxicocalamus misimae	KT968682.1	KU128784.1		KT778533.1	KU128812.1		KU128759.1
Toxicocalamus pachysomus	KT968679.1			KT778530.1	KU128809.1		KU128756.1
Toxicocalamus stanleyanus	KT968671.1	KU128777.1		KT778520.1	KU128801.1		KU128749.1
Vermicella parscauda	MH198531.1						
Vermicella vermiformis	MH198535.1						

APPENDIX II. LIST OF GENERA ACTUALLY VALIDATED FOR THE ELAPIDAE

Modified from Uetz et al. (2019), The Reptile Database, http://www.reptile-database.org, accessed August, 2019; and Wallach et al. (2014), Snakes of the World: A Catalogue of Living and Extinct Species.

Monotypic genera (21): *Antaioserpens*, Kolpophis*, Loveridgelaps*, Ogmodon*, Parapistocalamus*, Salomonelaps*, Thalassophis*, Echiopsis, Ephalophis, Hemachatus, Hemibungarus, Hydrelaps, Micropechis, Micruroides, Neelaps, Notechis, Ophiophagus, Parahydrophis, Paroplocephalus, Rhinoplocephalus,* and *Tropidechis.*

Polytypic genera (36): *Pseudohaje*, Aspidelaps, Denisonia, Elapognathus, Hemiaspis, Walterinnesia, Aspidomorphus, Austrelaps, Drysdalia, Emydocephalus, Hoplocephalus, Oxyuranus, Cacophis, Dendroaspis, Suta, Cryptophis, Furina, Simoselaps, Sinomicrurus, Parasuta, Vermicella, Acanthophis, Brachyurophis, Aipysurus, Laticauda, Pseudechis, Pseudonaja, Calliophis, Elapsoidea, Toxicocalamus, Bungarus, Demansia, Naja, Hydrophis, Leptomicrurus,* and *Micrurus*.

* Genera not sampled in the phylogenetic analysis of this chapter.