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

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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 coral snakes.

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/Aquitania, ~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).

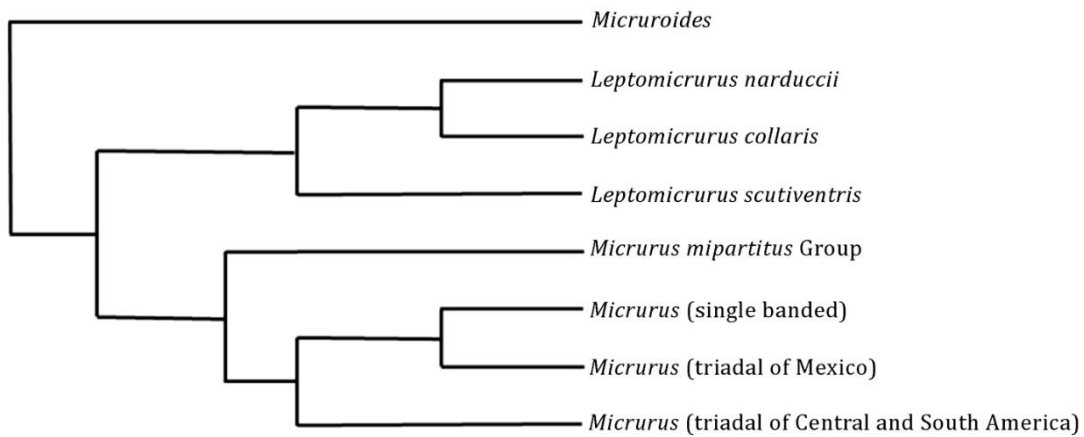


Fig. 1. The phylogenetic relationships for New World coralsnakes presented by Roze and Bernal-Carlo (1988).

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. dissolucus* 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 bootstrap (BS) and Shimodaira-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 (Pyrón 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%), *Brachyuropsis* (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 Hydrophiini (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.

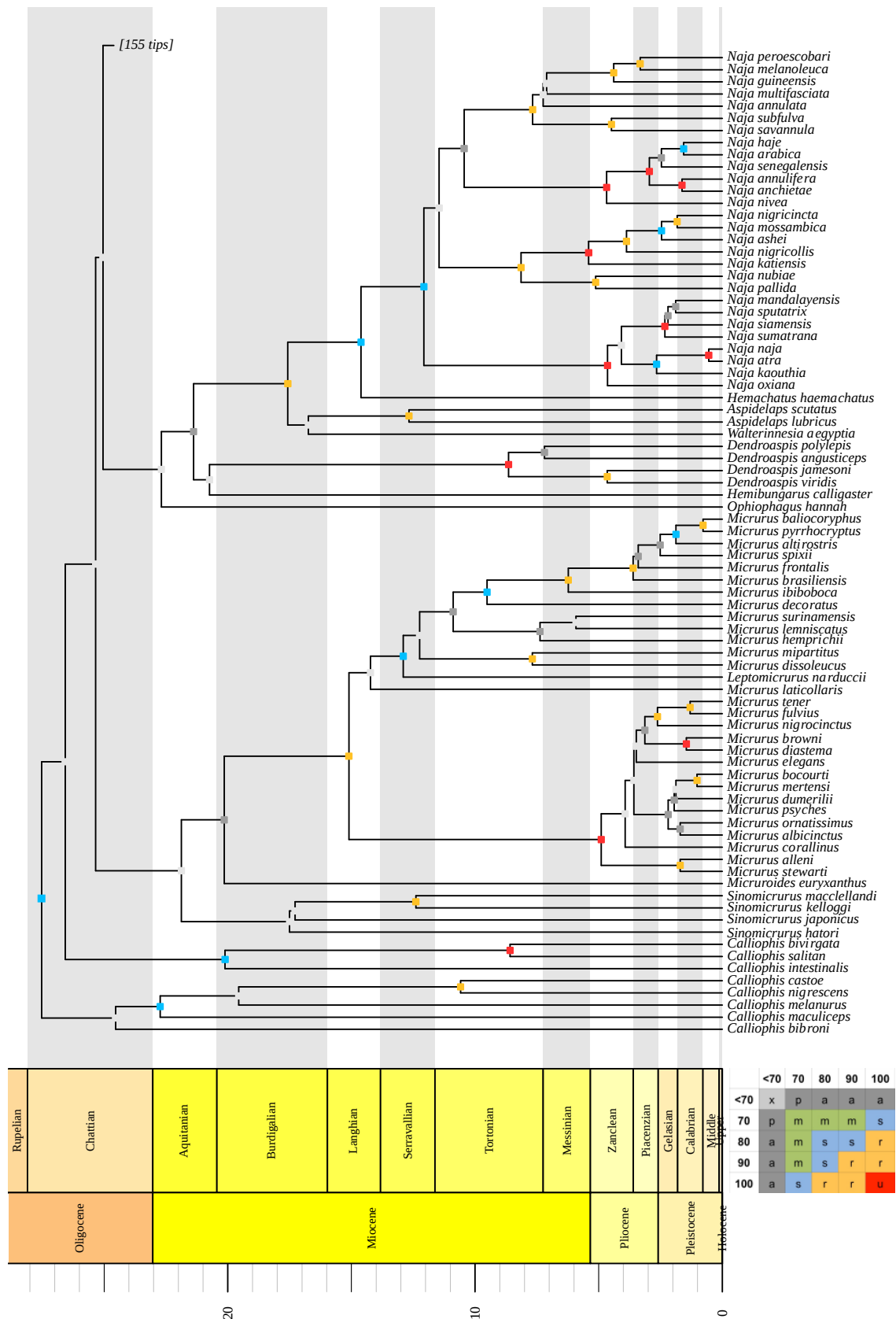


Fig. 2. A molecular phylogeny for 234 species of the family Elapidae, indicating the times of divergence calculated by penalized quasi-likelihood. The colored squares on each node represent bootstrap and SHL values, following the categories of combined clade support described in the text and summarized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

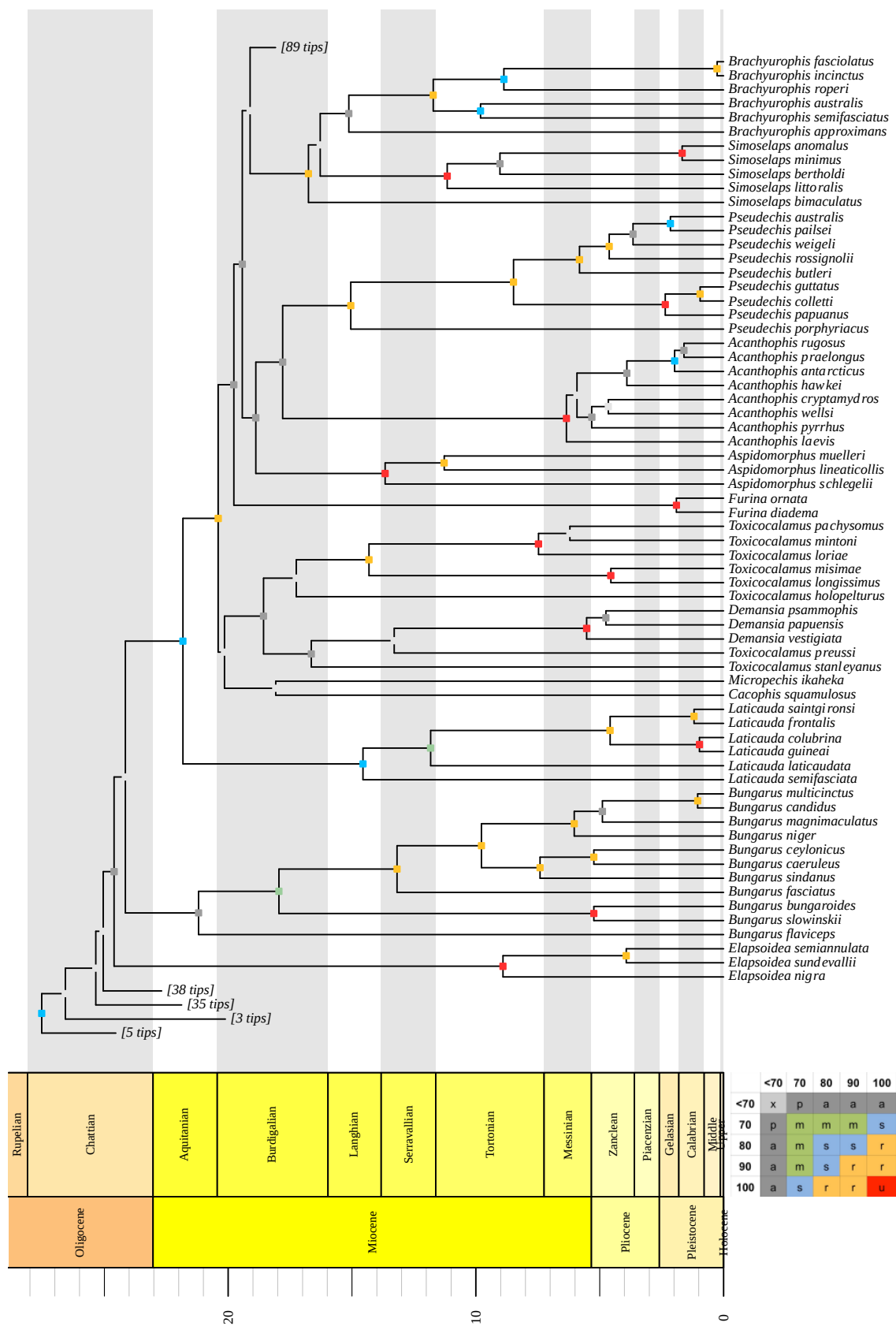


Fig. 2. Continued.

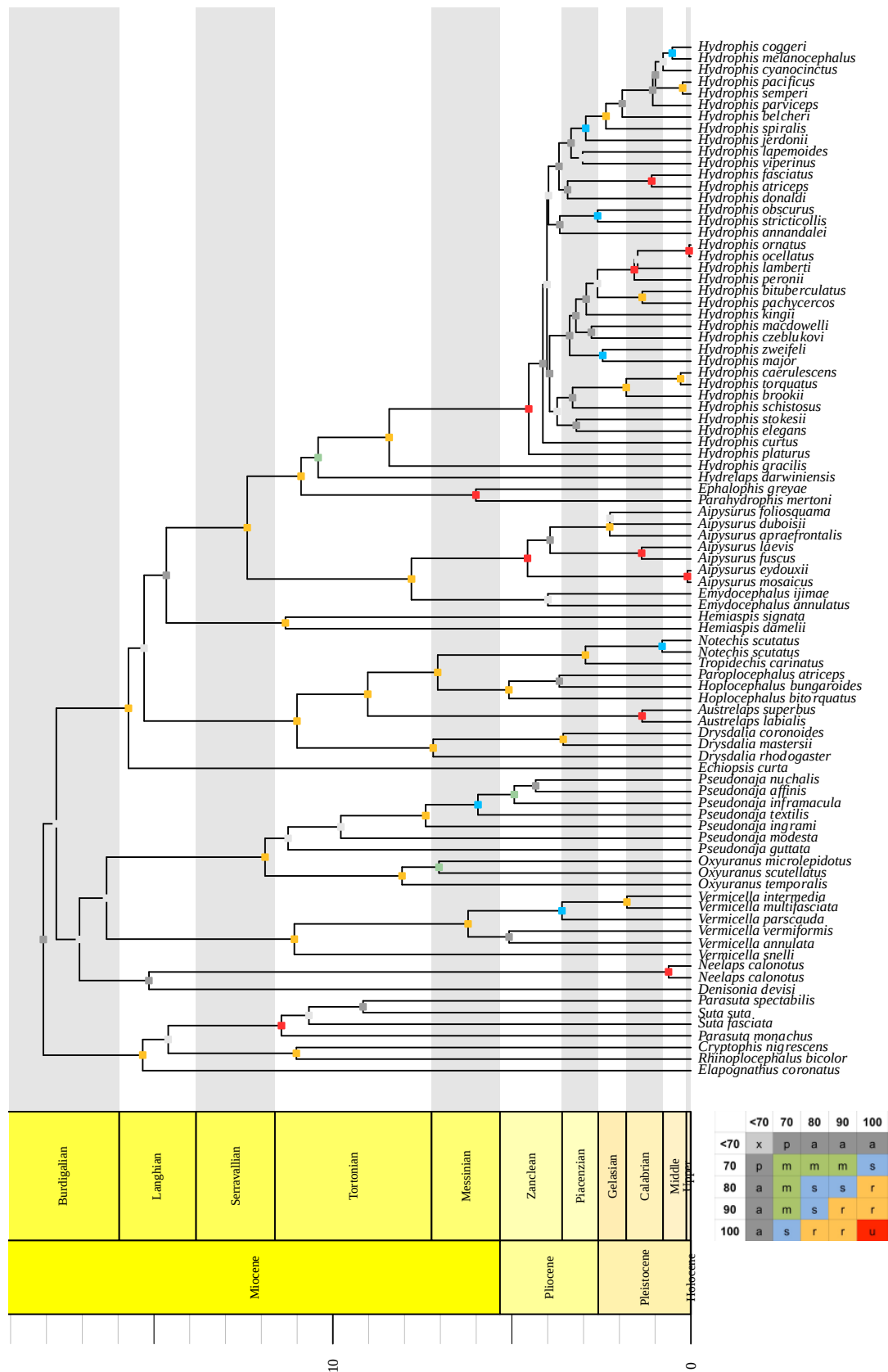


Fig. 2. Continued.

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 coral snakes 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 coralsnakes are needed in order to more thoroughly address their evolutionary history.

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

<i>Naja savannula</i>			MH337598.1	MH337408.1	
<i>Naja subfulva</i>			MH337603.1	MH337409.1	
<i>Neelaps calonotus</i>					EU546884.1
<i>Notechis scutatus</i>					EU546905.1
<i>Pseudechis pailsei</i>			KX981633.1	KX981677.1	KX981761.1
<i>Pseudechis rosignolii</i>			KX981621.1	KX981652.1	KX981750.1
<i>Pseudechis weigeli</i>			KX981632.1	KX981659.1	KX981773.1
<i>Sinomicrurus hatori</i>		KP772310.1			
<i>Toxicocalamus holopelturus</i>	KT968666.1	KU128773.1	KT778515.1	KU128798.1	KU128746.1
<i>Toxicocalamus longissimus</i>	KT968675.1	KU128781.1	KT778523.1	KU128805.1	KU128752.1
<i>Toxicocalamus mintoni</i>	KT968692.1		KT778543.1	KU128822.1	KU128769.1
<i>Toxicocalamus misimae</i>	KT968682.1	KU128784.1	KT778533.1	KU128812.1	KU128759.1
<i>Toxicocalamus pachysomus</i>	KT968679.1		KT778530.1	KU128809.1	KU128756.1
<i>Toxicocalamus stanleyanus</i>	KT968671.1	KU128777.1	KT778520.1	KU128801.1	KU128749.1
<i>Vermicella parscauda</i>	MH198531.1				
<i>Vermicella vermiformis</i>	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), <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*, *Brachyuropis*, *Aipysurus*, *Laticauda*, *Pseudechis*, *Pseudonaja*, *Calliophis*, *Elapsoidea*, *Toxicocalamus*, *Bungarus*, *Demansia*, *Naja*, *Hydrophis*, *Leptomicrurus*, and *Micrurus*.

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