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Origem e Diversificação dos Elapídeos
(Squamata, Serpentes) com Ênfase no Registro
Fóssil Do Cenozóico Europeu

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(Squamata, Serpentes), with Special Emphasis
on the European Cenozoic Fossil Record

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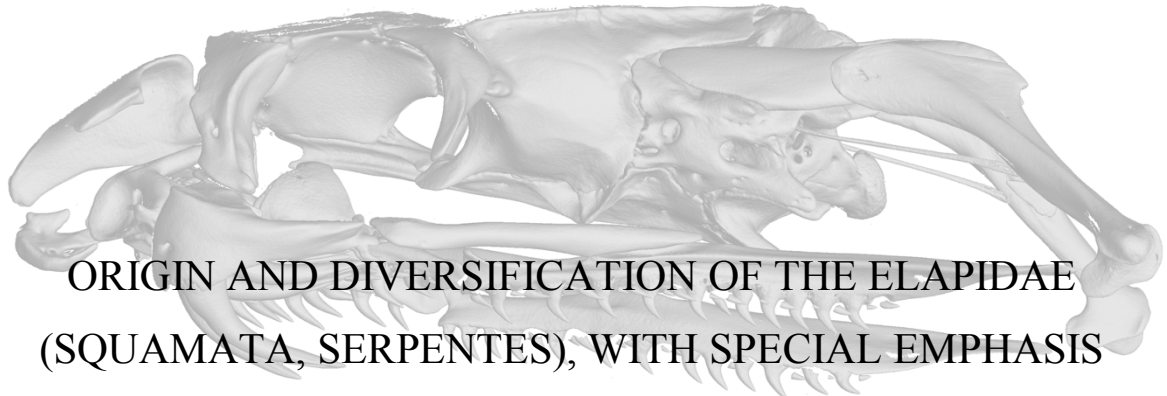
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ORIGEM E DIVERSIFICAÇÃO DOS ELAPÍDEOS
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ORIGIN AND DIVERSIFICATION OF THE ELAPIDAE
(SQUAMATA, SERPENTES), WITH SPECIAL EMPHASIS
ON THE EUROPEAN CENOZOIC FOSSIL RECORD

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Zoologia, na Área de Paleontologia.

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Resumo

Os elapídeos são um grupo diversificado de serpentes, incluindo 390 espécies inseridas em 57 gêneros (Uetz, 2022) com distribuição nas Américas, África (exceto Madagascar), Ásia e Austrália. Os elapídeos representam um grupo de serpentes derivadas amplamente estudado devido à sua importância médico-sanitária, em decorrência dos índices expressivos de acidentes ofídicos que ocorrem em países tropicais e subtropicais com seus membros (OMS, 2010). Contudo, sua história evolutiva permanece ainda pouco compreendida e, embora análises moleculares recentes indiquem que os elapídeos formam um grupo monofilético, suas relações mais inclusivas ainda são pouco resolvidas, sendo o único clado mais inclusivo com suporte robusto a irradiação Australo-Melanésia de elapídeos marinhos e terrestres, também conhecida como Hydrophiinae (*sensu* McDowell, 1970). Por outro lado, as relações menos inclusivas dentro dos elapídeos reúnem um conjunto muito mais expressivo de clados robustamente suportados, a maioria representando gêneros monofiléticos. Adicionalmente, a quantidade de análises filogenéticas no passado que continham espécies fósseis do grupo é pequena, geralmente com um número limitado de espécimes fósseis ou grupos biogeográficos incluídos. Embora evidências obtidas a partir de análises moleculares indiquem para uma origem asiática dos elapídeos, o registro fóssil mais antigo inequívoco do grupo é do Oligoceno Superior da África, sugerindo assim uma origem africana para o clado. O presente estudo traz uma revisão exaustiva do registro fóssil de elapídeos do Cenozóico Africano e Europeu, incluindo formas reconhecidas no passado como parte do gênero *Naja*: *N. austriaca*, *N. iberica*, *N. crassa*, *N. depereti* e *N. romani*. Em relação a *N. antiqua*, a presente análise não recuperou de maneira inequívoca sua inclusão no gênero *Naja*. Ainda, em relação às formas semifossoriais e de tamanho reduzido do Cenozóico Europeu, a evidência morfológica aqui apresentada não sustenta de maneira inequívoca uma origem asiática ou americana para a irradiação europeia, pelo contrário, justificando a inclusão dos fósseis *Micrurus gallicus* em um novo gênero de “cobra coral” europeia.

Palavras-chave: fóssil, serpentes, sistemática, Cenozóico, Paleobiologia

Abstract

The family Elapidae is a largely diversified group of venomous snakes, including 390 species and 57 genera (Uetz, 2022) distributed in the Americas, Africa (except Madagascar), Asia and Australia. The elapids represent a widely studied group of caenophidian snakes due to their medical-sanitary importance, given the expressive rates of ophidian accidents caused in tropical and subtropical countries (WHO, 2010). However, their evolutionary history remains poorly understood, and while recent molecular analyses indicate that elapids form a monophyletic group, more specific relationships are still poorly resolved. Currently, the more inclusive relationships between elapids remain uncertain; the single most inclusive clade that is robustly sustained is the Australo-Melanesian irradiation of marine and terrestrial elapids, also known as Hydrophiinae radiation (*sensu* McDowell, 1970). On the other hand, the less inclusive relationships within elapids bring together a much more expressive set of robustly supported clades, most representing monophyletic genera. Apart from that, phylogenetic analyses that have included fossil taxa in the past were only a few, usually with a limited number of fossil specimens or geographic groups included. The molecular evidence indicates an Asian origin for the Elapidae, while the oldest known fossil record points to an African origin. Here, I present a thorough revision of the fossil record of elapids in the African and European Cenozoic, including past and currently recognized forms included in the genus *Naja*: *N. austriaca*, *N. iberica*, *N. crassa*, *N. depereti* and *N. romani*. *Naja antiqua* was not unambiguously recovered as a member of the genus *Naja*, but rather as a distinct African form. As for the European radiation of small Cenozoic semifossorial elapids, the morphological evidence at hand does not unambiguously support neither an American nor an Asiatic origin for the European radiation. Therefore, the present work also justifies the allocation of *Micrurus gallicus* in a new genus of European “coral snake”.

Key-words: fossil, snakes, systematic, Cenozoic, paleobiology

General Introduction

The family Elapidae Boie, 1827 is a well-diversified group of venomous caenophidian snakes comprising currently 390 species allocated in 57 genera with a distribution across the Americas, Africa (except Madagascar), Asia, and Australia (Rage, 1984a; Wallach *et al.*, 2014; Silva Jr. *et al.*, 2021; Uetz *et al.*, 2022). Elapids have been largely studied through a medical and sanitary point of view, given the high number of ophidian accidents that involves its members, most frequently in tropical and subtropical countries (WHO, 2010), but their evolutionary history is still only partially understood.

Traditionally, monophyly of elapids was sustained mainly by morphological features derived from their proteroglyphous venom delivery system—such as the presence of an accessory gland located on the anterior portion of the venom gland, a differentiated adductor mandibulae externus superficialis muscle acting as a compressor of the venom gland, and canaliculated teeth on the anterior portion of the maxilla (Fig. 1)—combined with meristic and hemipenial characters such as the absence of the loreal scale and presence of a forked spermatic sulcus on the hemipenis (Underwood, 1967; Smith *et al.*, 1977; McCarthy, 1985). However, a clear indication that the group represented a polyphyletic assemblage came from the first molecular studies, which corroborated previous morphological results from McDowell (1968) who's seminal work highlighted the independent origin of *Homoroselaps* from elapids, suggesting a closer affinity of the former with aparallactines instead (today's atractaspids). Thus, the 'proteroglyph' venom delivery system, which appeared to support the monophyly of the family (McCarthy, 1985), would have evolved independently twice within the elapoid radiation (McDowell, 1968, 1986, 1987; Cundall & Irish, 2008; Kelly *et al.*, 2009; Fig. 2). More recent and inclusive analyses of the Colubroides (*sensu* Zaher *et al.*, 2009) have largely corroborated McDowell's views (Kelly *et al.*, 2009; Pyron *et al.*, 2013; Figueroa *et al.*, 2016; Zheng & Wiens, 2016; Zaher *et al.*, 2019). However, Zaher *et al.* (2019) have shown that interrelationships within elapids still recover a high number of unsolved or questionable phylogenetic affinities.

Nowadays, elapids include the American and Asiatic coral snakes, the terrestrial Asiatic kraits, the African and Asiatic cobras and their allies, and the Australo-Melanesian terrestrial and marine radiation also recognized as the subfamily Hydrophiinae (McDowell, 1970; Sanders & Lee, 2008). According to recent large-scale molecular

analyses, the former three major groups are still in a state of taxonomic flux, while the Australo-Melanesian hydrophiine radiation proved to be a strongly supported clade (Pyron *et al.*, 2013; Zheng & Wiens, 2016; Figueroa *et al.*, 2016; Zaher *et al.*, 2019).

Slowinski *et al.* (2001) have shown that the Asiatic coral snakes previously allocated in the genera *Calliophis* and *Maticora* correspond to three major clades (Fig. 3): the tropical mainland genus *Calliophis* (including former *Maticora*), the northern subtropical genus *Sinomicrurus*, and the monotypic Philippine *Hemibungarus calligaster*. These authors also demonstrated convincingly that their newly erected genus *Sinomicrurus* was the sister group of the New World coral snakes *Micruroides* and *Micrurus*. Castoe *et al.* (2007) further corroborated Slowinsky *et al.*'s (2001) subdivision of the Asiatic coral snakes in an expanded molecular phylogeny that retrieved the hydrophiines as the sister group of two sister clades composed by the Asiatic and American coral snakes on the one hand, and the Afro-Asiatic cobras and their close allies on the other hand. Based on these results, they recognized the subfamilies Hydrophiinae and Elapinae, with the latter including the tribes Calliophiini for the genera *Sinomicrurus*, *Micruroides*, and *Micrurus* (including former *Leptomicrurus*) and Hemibungarini for *Hemibungarus*, *Elapsoidea*, *Dendroaspis*, *Ophiophagus*, *Bungarus*, *Aspidelaps*, *Walterinnesia*, and *Naja* (including former *Boulengerina* and *Paranaja*).

However, more densely sampled molecular phylogenies consistently retrieved Castoe *et al.*'s (2007) Calliophiini and Hemibungarini as polyphyletic (Pyron *et al.*, 2013; Zheng & Wiens, 2016; Figueroa *et al.*, 2016; Zaher *et al.*, 2019), but with no statistical support for any of the alternative topologies. Although these larger phylogenies strongly support a clade formed by *Hemibungarus*, *Naja* and its allies, as originally suggested by Castoe *et al.* (2007), they invariably retrieve the genera *Elapsoidea* and *Bungarus* with the Australo-Melanesian radiation.

Although molecular advances in elapid phylogeny are undeniable, relationships between the extant clades described above and the known fossil record of the family are still poorly understood. Traditionally, studies including fossil elapids focused primarily on the description of isolated taxa (Hoffstetter, 1939; Holman, 1977; Rage & Holman, 1984) or on the analysis of Cenozoic faunal assemblages from specific regions (Rage, 1976, 2013; Bachmayer & Szyndlar, 1985; Szyndlar, 1985; Bailon, 1989; Szyndlar & Zerova, 1990; Szyndlar, 1991; Szyndlar & Schleich, 1993; Augé & Rage, 1997; Ivanov, 2000, 2002a; Rage & Bailon, 2005; Ivanov & Böhme, 2011). On the other hand, phylogenetic analyses of extant taxa focused on the molecular evidence, disregarding any

morphological information from extant or extinct taxa (Sanders & Lee, 2008; Sanders *et al.*, 2013; Pyron *et al.*, 2013). A detailed study of the rich fossil record of elapids is still in need and has potential to help determine with more certainty the tempo and mode of evolution and radiation of the group during the Cenozoic. More specifically, the abundant presence of fossil representatives of the living genus *Naja* throughout the European Neogene (Szyndlar & Rage, 1990) and the alleged presence of the New World genus *Micrurus* in the continent during this same period (Rage & Holman, 1984) are two central issues that will be addressed in more detail here.

Conclusions

- While the molecular evidence at hand seems to indicate an Asian origin for the Elapidae, the oldest known fossil record of the group points to an African origin. Recent molecular phylogenies, including the one presented here, fail to recover a well supported dichotomous hierarchy for the early diverging elapid lineages, while robustly supporting the monophyly of the Australo-Melanesian radiation (Hydrophiinae).
- The fossil record of elapids in the African and European Cenozoic presents a previously unsuspected diversity of forms currently included in the genus *Naja*. The disappearance of the family Elapidae from Europe in the middle/late Pliocene is presumably linked to climatic changes towards a cooler environment. Elapids are presently extinct in Europe, but diversified in Africa (except Madagascar), Asia, Australia, and the Americas.
- The present study recognizes five valid species of *Naja* in the European Cenozoic: *Naja austriaca*, *N. iberica*, *N. crassa*, *N. depereti*, and *N. romani*. Revalidation of *N. austriaca* and *N. crassa*, previously considered to be synonyms of *N. romani*, is supported by a significant number of morphological differences.
- The present study also recognized five different morphotypes that could represent new taxa. However, the poorly preserved material available and the scarcity of cranial elements prevent any decisive assignment to a specific taxonomic rank.
- As for *Naja antiqua* from the Middle Miocene of Morocco, the phylogenetic analysis conducted in the present study did not recover it nested in the genus *Naja*; instead, *N. antiqua* was recovered as the sister group of the Eastern Brown snake, *Pseudonaja textilis*, from Australia. This result is probably biased by the absence of preserved morphological features that could further resolve its relationship with other African elapids. *Naja antiqua* shares with other representatives of the “Cobras clade” morphological features that favour its allocation in a new genus of extinct African elapid.
- According to the present study, the small semifossorial elapids assigned to *Micrurus gallicus* and *Micrurus* cf. *gallicus* retain a vertebral morphology that shares characteristics with both New World coral snakes (genera *Micrurus* and *Micruroides*) and the Asiatic fossorial *Sinomicrurus* and *Calliophis*. Therefore, the morphological evidence presented here neither unambiguously supports an American nor an Asiatic

origin for these semifossorial forms. The taxa currently recognized as *Micrurus gallicus* and *Micrurus* cf. *gallicus* further differ from representatives of the genera *Micrurus*, *Sinomicrurus*, and *Calliophis*, thus justifying their allocation in a new genus.

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