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A review on diversity, bio-geography, and updated checklist of Cobras (*Naja*, Laurenti, 1768) (Squamata: Serpentes: Elapidae): Present and prehistoric

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Abstract

The *Naja* Laurenti, 1768, is a genus of venomous snakes widely considered as "true" cobras and belongs to the family Elapidae. The living species of this genus are mainly found in Africa and Asia. This review article provides an updated checklist of 35 recognized living species of the genus *Naja,* including 22 (63%) African species, 13 (37%) Asian species, and four currently recognized extinct cobra species from Miocene and Pliocene strata discovered in Africa and Europe. The *Naja* genus is divided into four subgenera: 1. The typical subgenus *Naja* is restricted to Asian species, 2. The subgenus *Uraeus,* Wagler, 1830, is revived for a group of non-spitting cobras found in the savannas and open lands of Africa and the Arabian Peninsula, 3. *Boulengerina*, Dollo, 1886, is used for non-spitting African cobra species, including forest, aquatic, and semi-fossorial forms. The 4th subgenus, *Afronaja*, is designated for all African spitting cobras. This review also summarizes the diversity, distribution, conservation status, and toxicity levels of some *Naja* species. The searches were limited to peer-reviewed journals written in English, excluding books and other non-English sources.

Keywords: Africa, Asia, Biogeography, Diversity, Naja, Toxicity

Introduction

The recently updated checklist of reptilian species released in August/September 2024 includes 4,474 taxa, with 12,386 species and 2,088 subspecies (Uetz et al., 2024). The distribution and diversity of reptilian fauna are extensive and depend on climate conditions and geographic location (Safi & Karl, 2024). As shown in Figure 2, African cobras account for approximately 63% of extant Naja species, while Asian cobras represent about 37%. Reptiles are a diverse class found in nearly all natural habitats around the world, except Antarctica (Hashmi and Safi, 2025). Most reptiles can survive and thrive in harsher environments than other cold-blooded animals because they use more energy for maintaining homeostasis (Ali et al., 2018; Safi et al., 2024). Snakes belong to the order Squamata and suborder Serpentes. The word serpent has an Anglo-Saxon origin, meaning “Snake” (Orimi et al., 2023). Over 3,900 species of snakes have been described worldwide (Uetz et al., 2024). Snakes have long been a subject of interest for researchers (Hashmi et al., 2024). They are medically significant since snakebites are a common global problem, with an estimated 5.5 million bites each year (Orimi et al., 2023). *Naja* is a genus of venomous elapid snakes commonly called cobras. It is one of the most widespread groups of venomous snakes in the Afrasian regions. Members of this genus are considered "true" cobras; however, some other snakes, such as the king cobra (*Ophiophagus*) and the Rinkhals (*Hemachatus*), are not true cobras because they do not belong to the genus *Naja* (Spawls and Branch, 1995; Zhao and Adler, 1993). Venomous snakes are undoubtedly among the biggest health risks to people in tropical and subtropical regions worldwide, with many snakebite incidents each year, especially in Asia, Africa, and South America (Hashmi et al., 2024). All species in the genus *Naja* can deliver a fatal bite to humans. The origin of the genus name “*Naja*” comes from the Sanskrit “Naga,” meaning "Snake." Members of *Naja* vary in size and are mostly slender-bodied. Many can reach total lengths of 1.84 m. The longest cobras can grow up to 3.1 m, with the forest cobra possibly being the longest species. All species can lift the front part of their bodies off the ground and flatten their necks to look larger to potential predators (Figure 3b). Fang structure varies; all species except the Indian Cobra (*Naja naja*) and Caspian Cobra (*Naja oxiana*) have some ability for spitting (Wüster & Thorpe, 1992) (Figure 3). Many cobra species, which are known as spitting cobras, have a special technique for venom delivery (similar to hypodermic needles), with short slits on the front teeth. Although often called "spitting", this action is more like squirting. The amount and accuracy of venom release vary

between species, but all species use "spitting" as a defensive mechanism. The venom has little or no effect on unbroken skin, but if it enters the eyes, it can cause a severe burning sensation and temporary or permanent blindness if not washed out immediately and thoroughly. A recent study showed that all the spitting cobra lineages have evolved higher pain-inducing properties in their venom through increased phospholipase A2, which potentiate the algesic action of the cytotoxins present in most cobra venoms (Kazandjian, 2021). The Caspian Cobra (*N. oxiana*) of Central Asia is the most venomous *Naja* species (Figure 3a). According to a study by Kazemi-Lomedasht et al. (2019) the murine LD50 via intravenous injection (IV) value for *N. oxiana* (Iranian specimens) was estimated to be 0.14 mg/kg (0.067-0.21 mg/kg) more potent than the sympatric *N. naja karachiensis* and *N. naja indusi* found in Pakistan and far north and northwestern India (0.22 mg/kg), the Thai Cobra *N. kaouthia* (0.2 mg/kg), and *N. philippinensis* at 0.18 mg/kg (0.11-0.3 mg/kg) (Wong et al., 2019). Latifi (1984) described a subcutaneous value of 0.2 mg/kg (0.16-0.47 mg/kg) for *N. oxiana* (Khare et al., 1992). The Banded water cobra's LD50 was estimated to be 0.17 mg/kg via IV, according to Christensen (1968). *N. philippinensis* has an average murine LD50 of 0.18 mg/kg IV (Wong et al., 2019). Minton (1974) reported 0.14 mg/kg IV for the Philippine Cobra. The Samar cobra (*N. samarensis*), another cobra species endemic to the southern islands of the Philippines, is reported to have an LD50 of 0.2 mg/kg (Palasuberniam et al., 2021). The Thailand and eastern Cambodian species have similar venom potency to the Monocled Cobra (*N. kaouthia*), which also has an LD50 of 0.2 mg/kg. *N. oxiana*, in Pakistan and far northwestern India, also has a high venom potency of 0.22 mg/kg (Wong et al., 2019). Christensen (1968) also listed an IV LD50 of 0.17 mg/kg for *N. annulata.* Minton (1974) listed an LD50 of 0.3 mg/kg intravenously (IV), while Lee and Tseng listed a value of 0.67 mg/kg subcutaneously (SC) for the Chinese Cobra (*N. atra*). The forest/water cobra subgenus (*Boulengerina*) is another group of highly venomous cobras. The LD50 of the Cape Cobra (*N. nivea*) is 0.35 mg/kg (IV) and 0.4 mg/kg (SC) (Minton, 1974, 1996). The Senegalese Cobra (*N. senegalensis*) has a murine LD50 of 0.39 mg/kg (Tan et al., 2021) via IV (Wong et al., 2021). The Egyptian Cobra (*N. haje*) has an IV LD50 of 0.43 mg/kg (0.35–0.52 mg/kg) (Harrison et al., 2017). Approximately 30% of bites by cobra species are dry bites, which do not cause envenomation (Naik, 2017; Brown, 1973). The mortality rate for *N. atra* is between 15 and 20%, while it is 5–10% for *N. nigricollis* (Warrell and David, 2010). The mortality rate for *N. nivea* is 50% (Brown, 1973). Several factors influence the differences in

fatality cases among different species within the same genus. Among cobras, the cases of fatal outcomes of bites in both treated and untreated victims can be quite large. For example, mortality rates among untreated cases of envenomation by the cobras as a whole group range from 6.5–10% for *N kaouthia.* (Brown, 1973; Warrell, 1995) to about 80% for *N. oxiana.* These cases of bites are medically treated using normal treatment protocol for elapid-type envenomation; differences in prognosis depend on the cobra species involved. The most important factor in the difference in mortality rates among victims envenomed by a cobra is the severity of the bite. *N. oxiana* and *N. philippinensis* are the two cobras having the most toxic venom based on LD50 studies on mice, and death has been reported in as little as half an hour in cases of envenomation by both species (Watt et al., 1988). *N. oxiana* approaches 80%, the highest among all species within the genus *Naja*. Doses of anti-venom are not more effective for bites and envenomation by *N. oxiana* than they are for other Asian cobras, such as N. naja. Due to the dangerous toxicity of this species' venom, massive amounts of anti-venom are often required for patients (Latifi, 1984). There are currently 35 recognized extant *Naja* species, which consist of 22 (63%) African species and 13 (37%) Asian species (Kazemi et al., 2020) (Table 1). There are an additional four extinct species of Miocene-aged strata from northwestern Africa and Europe (Tables 1-2; Figure 2 & 4) (Rage, 1976; Szyndlar, 1985; Meylan, 1987; Wallach et al., 2009; Pokrant et al., 2017). Several recent systematic studies have revealed many species that were not mentioned in the previous listing or studies about *Naja* (Kazemi et al., 2021). *N. anchietae* (Bocage, 1879), Anchieta's cobra, is regarded as a subspecies of *N. haje* by Mertens (1937) and of *N. annulifera* by Broadley (1995). Broadley and Wüster (2004) regard it as a full species. *N. arabica* has long been considered a subspecies of *N. haje* but was recently raised to the status of species (Trape et al., 2009). Ashe's spitting cobra (*N. ashei*) is another newly discovered African species (Wüster and Broadley, 2007). *N. nigricincta* (Bogert, 1940) was long regarded as a subspecies of *N. nigricollis,* but it has recently been described as a new species (Wüster et al., 2007; Wallach et al., 2009). *N. senegalensis* (Trape et al., 2009) is another new species, which was previously considered a subspecies of *N. haje* of the West African savanna, while *N. Peroescobari* (Ceríaco et al., 2017) is another new species that was previously considered a subspecies of *N. melanoleuca of* São Tomé. *N. subfulva* (Laurent, 1955), *N. savannula* (Wüster et al., 2018), and *N. guineensis* (Wüster et al., 2018) are three new species previously considered populations of *N. melanoleuca* of West Africa. These species, which were previously assigned to the genera

Boulengerina and *Paranaja* into *Naja,* are also supported by molecular phylogenetic studies. These are closely related to the forest cobra (*N. melanoleuca*) (Wüster et al., 2007; Nagy et al., 2005). The controversial amateur herpetologist Raymond Hoser proposed *Spracklandus* for the African spitting cobras (Hoser, 2009). Wallach et al. (2009) suggested that this name was not published according to the Code and suggested instead the recognition of four sub-genera within *Naja: Naja* for the Asiatic cobras, *Boulengerina* for the forest and water cobras of Africa, *Uraeus* for the Egyptian and Cape cobra group, and *Afronaja* for the African spitting cobras. Asian cobras are believed to be further split into two groups, Southeastern Asian cobras (*N. siamensis, N. sumatrana, N. philippinensis, N. samarensis, N. sputatrix,* and *N. mandalayensis*) and Western Asian cobras (*N. oxiana, N. kaouthia, N. sagittifera,* and *N. atra*), with *N. naja* serving as a basic ancestral lineage to all species (Kazemi et al., 2020). Three out of the four currently recognized extinct cobra species, †*N. Antiqua* (Rage, 1976), †*N. Iberica* (Szyndlar, 1985), and †*N. Robusta* (Meylan, 1987) cannot be allocated to any sub-genus, as identifying syn-apomorphies is lacking (Rage, 1976; Szyndlar, 1985; Meylan, 1987), only one extinct species, †*N. romani* (Hofstetter, 1939) is placed in the subgenus *Naja,* Laurenti, 1768 (Wallach et al., 2009). Very few remains of elapid snakes are known from the Iberian Peninsula, including †*N. iberica,* a probable endemic extinct cobra species from the Late Miocene. Villa et al. (2024) provided a geographical overview of all known *Naja spp*. The Siwalik snake fauna data contains approximately 1,500 vertebrae collected from surface collection and screen washing of the bulk matrix in the Indian subcontinent. The data represent 12 taxa and morphotypes, including Elapidae and some other recognizable but unnamed morphotypes (Karl et al., 2024). Figure 1 illustrates the phylogenetic relationships among the recognized species of the genus *Naja.*

Taxonomy

Class: Reptilia

Order: Squamata

Suborder: Serpentes

Family: Elapidae

Genus: *Naja*

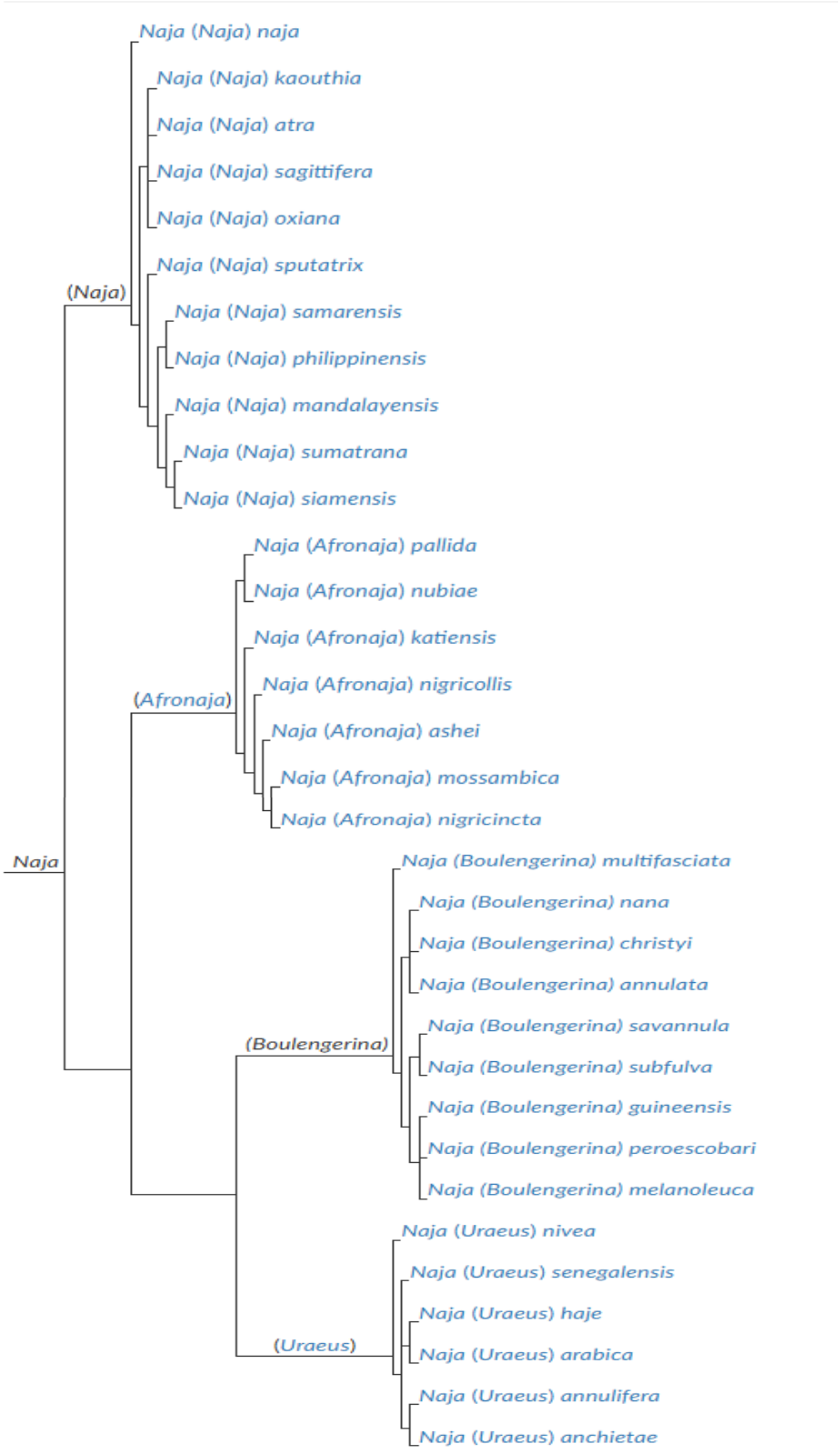

Figure 1. Phylogenetic Tree of Extant *Naja* Species Grouped by Subgenus.

Table 1. An Updated Checklist of *Naja spp.,* Their Zoogeographic Range, and IUCN Status.

S. No.	Species	Common name	Geographic range	IUCN Status
1.	*N. anchietae* (Bocage, 1879)	Anchieta's cobra (Angolan Cobra)	Angola, Botswana, Namibia, Zambia, and eastern Zimbabwe.	LC
2.	*N. annulata* (Buchholz and Peters, 1876)	Banded water cobra/the ringed water cobra	Cameroon, the Central African Republic, the Democratic Republic of the Congo (Zaire), the Republic of Congo, Equatorial Guinea, Gabon, Rwanda, and the province of Cabinda in Angola	LC
3.	*N. annulifera* (Peters, 1854)	Snouted cobra	Botswana, Malawi, Mozambique, South Africa, Swaziland, Zambia, Zimbabwe	LC
4.	*N. ashei* (Wüster and Broadley, 2007)	Ashe's spitting cobra (Giant spitting cobra)	Southern Ethiopia, Kenya, Somalia, eastern Uganda	LC
5.	*N. christyi* (Boulenger, 1896)	Congo water cobra	The Democratic Republic of the Congo (Zaire), the Republic of Congo, and the province of Cabinda in Angola	LC
6.	*N. guineensis* (Wüster et al., 2018)	Black forest cobra	Ghana, Guinea, Guinea-Bissau, the Ivory Coast, Liberia, Sierra Leone, Togo	Not evaluated yet
7.	*N. haje* (Linnaeus, 1758)	Egyptian cobra	Tanzania, Kenya, Somalia, Ethiopia, Uganda, South Sudan, Sudan, Cameroon, Nigeria, Niger, Burkina Faso, Mali, Senegal, Mauritania, Morocco, Algeria, Tunisia, Libya, and Egypt	LC
8.	*N. katiensis* (Angel, 1922)	Mali cobra (Katian spitting cobra)	Benin, Burkina Faso, Cameroon, Ghana, Guinea, the Ivory Coast, Mali, Gambia, Mauritania, Niger, Nigeria, Senegal, Togo	LC
9.	*N. melanoleuca* (Hallowell, 1857)	Central African forest cobra	Angola, Benin, Cameroon, the Central African Republic, the Republic of Congo, the Democratic Republic of the Congo (Zaire), Equatorial Guinea,	LC

			Gabon, Nigeria	
10.	*N. mossambica* (Peters, 1854)	Mozambique spitting cobra	Extreme southeastern Angola, Botswana, Malawi, Mozambique, Somalia, northeastern Namibia, South Africa, Swaziland, Tanzania (including Pemba Island), Zambia, Zimbabwe	LC
11.	*N. multifasciata* (Werner, 1902)	Many-banded cobra	Cameroon, Congo, the Democratic Republic of the Congo (Zaire), Gabon	LC
12.	*N. nana* (Collet & Trape, 2020)	Dwarf water cobra	Democratic Republic of Congo	Not evaluated yet
13.	*N. nigricincta* (Bogert, 1940)	Zebra spitting cobra	Angola, Namibia, South Africa	LC
14.	*N. nigricollis* (Reinhardt, 1843)	Black-necked spitting cobra	Angola, Benin, Burkina Faso, Burundi, Cameroon, the Central African Republic, Chad, the Democratic Republic of the Congo (Zaire) (except in the central region), Congo, Ethiopia, Gabon, Gambia, Ghana, Guinea-Bissau, Guinea, the Ivory Coast, Kenya, Liberia, Mali, Mauritania, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Sudan, Tanzania, Somalia, Togo, Uganda, Zambia	LC
15.	*N. nivea* (Linnaeus, 1758)	Cape cobra (Yellow cobra)	Botswana, Lesotho, Namibia, South Africa	LC
16.	*N. nubiae* (Wüster & Broadley, 2003)	Nubian spitting cobra	Chad, Egypt, Eritrea, Niger, Sudan	LC
17.	*N. obscura* (Saleh & Trape, 2023)	Obscure cobra	Egypt	Not evaluated yet
18.	*N. pallida* (Boulenger, 1896)	Red spitting cobra	Djibouti, Ethiopia, Kenya, Somalia, Tanzania	LC

19.	*N. peroescobar* (Ceríaco et al., 2017)	São Tomé forest cobra	São Tomé and Príncipe (São Tomé)	EN
20.	*N. savannula* (Wüster et al., 2018)	West African banded cobra	Benin, Burkina Faso, Cameroon, Chad, Gambia, Ghana, Guinea, the Ivory Coast, Mali, Niger, Nigeria, Senegal, Togo	LC
21.	*N. senegalensis* (Trape et al., 2009)	Senegalese cobra	Benin, Burkina Faso, Ghana, Guinea, Mali, Niger, Nigeria, Senegal	LC
22.	*N. subfulva* (Laurent, 1955)	Brown forest cobra	Angola, Burundi, Cameroon, the Central African Republic, Chad, the Republic of Congo, the Democratic Republic of the Congo (Zaire), Ethiopia, Kenya, Malawi, Mozambique, Nigeria, Rwanda, Somalia, South Africa, South Sudan, Tanzania, Uganda, Zambia, Zimbabwe	LC
23.	*N. sumatrana* (Müller, 1887)	Equatorial spitting cobra	Brunei, Indonesia (Sumatra, Borneo, Bangka, Belitung), Malaysia, the Philippines (Palawan), southern Thailand, Singapore	LC
24.	*N. samarensis* (Peters, 1861)	Samar cobra	the Philippines (Mindanao, Bohol, Leyte, Samar, Camiguin)	LC
25.	*N. siamensis* (Laurenti, 1768)	Indo-Chinese	Cambodia, Laos, Thailand, Vietnam	VU
26.	*N. sputatrix* (F. Boie, 1827)	Javan spitting cobra	Indonesia (Java, the Lesser Sunda Islands, East Timor)	LC
27.	*N. philippinensis* (Taylor, 1922)	Philippine cobra	Philippines (Luzon, Mindoro)	NT
28.	*N. sagittifera* (Wall, 1913)	Andaman cobra	India (the Andaman Islands)	EN
29.	*N. oxiana* (Eichwald, 1831)	Caspian cobra	Afghanistan, northwestern India, Iran, Kyrgyzstan, Pakistan, Tajikistan, Turkmenistan, Uzbekistan	NT
30.	*N. naja* (Linnaeus, 1758)	Indian cobra (Spectacled cobra)	Bangladesh, Bhutan, India, Nepal, Pakistan, Sri Lanka	LC
31.	*N. mandalayensis* (Slowinski & Wüster, 2000)	Mandalay spitting cobra (Burmese spitting cobra)	Myanmar (Burma)	VU

32.	*N. kaouthia* (Lesson, 1831)	Monocled cobra	Bangladesh, Bhutan, Burma, Cambodia, southern China, eastern India, Laos, northwestern Malaysia, Nepal, Thailand, southeastern Tibet, Vietnam	LC
33.	*N. fuxi* (Shi et al., 2022)	Brown-banded cobra	China, Myanmar, Laos, Thailand, Vietnam	Not evaluated yet
34.	*N. Arabica* (Scortecci, 1932)	Arabian cobra	Oman, Saudi Arabia, Yemen	LC
35.	*N. atra* (Cantor, 1842)	Chinese cobra	Southern China, northern Laos, Taiwan, northern Vietnam	VU

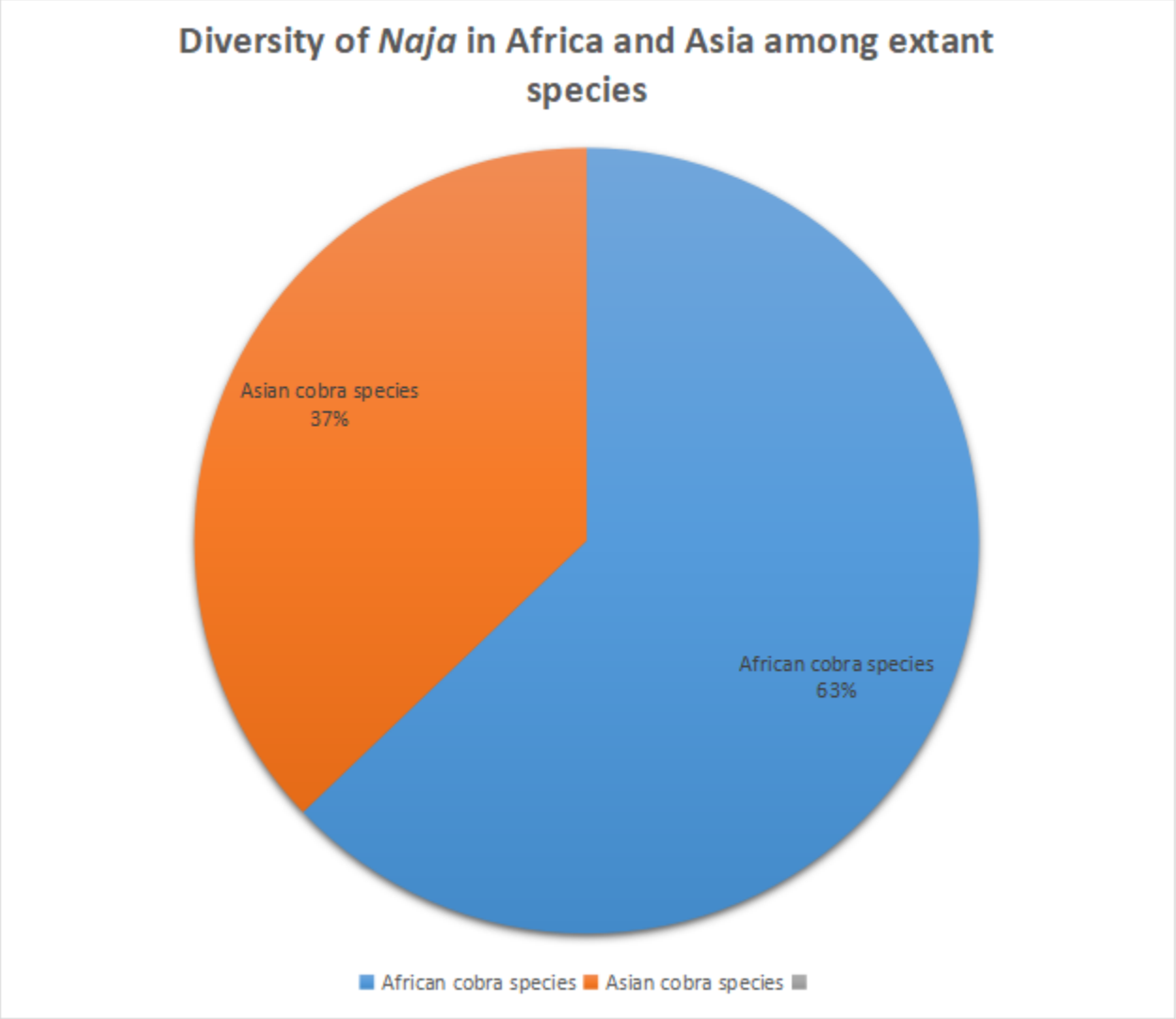

Figure 2. Diversity of the Extant *Naja spp*. in Africa and Asia.

Figure 3. (A) *N. oxiana* from KPK, Pakistan **(B)** *N. naja* from Karachi, Pakistan (Photos by Amtyaz Safi).

Table 2. Fossil Records of Naja spp., Their Locality, Age, and Bibliography.

S. No.	Taxon	Locality	Country	Age	Bibliography
1.	*N. antiqua*	Beni Mellal	Morocco	Early Middle Miocene	Rage, 1976; Rage, 1984; Bailon et al., 2017
2.	*N.* cf. *antiqua*	Guefaït-1	Morocco	Late Miocene (MN10)	Blain et al., 2013; Bailon et al., 2017
3.	*N. depereti*	Serrat d'en Vaquer, Roussillon	France	Early Pliocene (MN15)	Depëret, 1890-1897; Hoffstetter, 1939; Rage, 1984
4.	*N. iberica*	Algora	Spain	Late Miocene (MN13)	Szyndlar, 1985
5.	*N. naja*	Kurnool (Karnul) caves	India	Pleistocene	Lydekker, 1886; Hoffstetter, 1939
6.	*N.* cf. *naja*	Taurung-tung	Philippines	Late Pleistocene	Reis & Garong, 2001
7.	*N.* cf. *nigricollis*	Olduvai, Bed I	Tanzania	Early Pleistocene (Gelasian/Calabrian)	Rage, 1973; Rage, 1979
8.	*N. robusta*	Loc. 10W, Upper Laetolil Beds	Tanzania	Late Pliocene	Meylan, 1987; Rage & Bailon, 2011
9.	*N. romani*	Grund	Austria	Middle Miocene (MN5)	Miklas-Tempfer, 2003; Daxner-Höck et al., 2004
10.	*N. romani*	Kohfidisch	Austria	Late Miocene (MN11)	Bachmayer & Szyndlar, 1985; Bachmayer & Szyndlar, 1987; Szyndlar & Zerova, 1990; Szyndlar, 1991; Tempfer, 2005
11.	*N. romani*	La Grive-Saint-Alban	France	Middle Miocene (MN7+8)	Hoffstetter, 1938; Hoffstetter, 1939; Rage, 1984
12.	*N. romani*	Petersbuch 2	Germany	Early Miocene (MN4)	Szyndlar & Schleich, 1993; Ivanov, 2001
13.	*N. romani*	Rudabánya	Hungary	Late Miocene (MN9)	Bernor et al., 2004; Szyndlar, 2005
14.	*N. romani*	Solnechnodolsk	Russia	Late Miocene (MN13)	Syromyatnikova et al., 2021
15.	*N. romani*	Hrytsiv (Gritsev)	Ukraine	Late Miocene (MN9)	Szyndlar & Zerova, 1990; Szyndlar, 1991
16.	*N.* cf. *romani*	Vieux-Collonges	France	Early-Middle Miocene (MN4-5)	Hoffstetter, 1938; Hoffstetter, 1939; Ivanov, 2000; Ivanov, 2001
17.	*N.* cf. *romani*	Echzell	Germany	Early Miocene (MN4)	Vasilyan et al., 2022
18.	*N.* cf. *romani*	Ravin de la Pluie	Greece	Late Miocene (MN10)	Georgalis et al., 2018; Georgalis & Delfino, 2022
19.	*N.* cf. *romani*	Fălciu-Prut 1	Romania	Late Miocene (MN11-12)	Codrea et al., 2022

20.	*Naja* sp.	Gratkorn	Austria	Middle Miocene (MN7+8)	Böhme & Vasilyan, 2014
21.	*Naja* sp.	Isle d'Abeau	France	Middle Miocene (MN7+8)	Szyndlar & Rage, 1990
22.	*Naja* sp.	Sète	France	Early Pliocene (MN15)	Szyndlar & Rage, 1990; Bailon, 1991
23.	*Naja* sp.	Vieux-Collonges	France	Early-Middle Miocene (MN4-5)	Ivanov, 2000; Ivanov, 2001
24.	*Naja* sp.	Rothenstein 1/13	Germany	Middle Miocene (MN5)	Szyndlar, 2009
25.	*Naja* sp.	Sandelzhausen	Germany	Middle Miocene (MN5)	Szyndlar, 2009
26.	*Naja* sp.	Maramena 1	Greece	latest Miocene/earliest Pliocene (MN13/14)	Szyndlar, 1991; Szyndlar, 1995; Georgalis et al., 2019; Georgalis & Delfino, 2022
27.	*Naja* sp.	Tourkobounia 1	Greece	Late Pliocene (MN16)	Szyndlar & Zerova, 1990; Szyndlar, 1991; Georgalis & Delfino, 2022
28.	*Naja* sp.	Layer XIX, Qafzeh Cave	Israel	Late Pleistocene	Biton & Bailon 2022; Biton & Bailon 2023
29.	*Naja* sp.	Irhoud Ocre	Morocco	Early Pleistocene (Gelasian)	Bailon et al., 2017
30.	*Naja* sp.	Altıntaş	Turkey	Late Miocene (MN9)	Syromyatnikova et al., 2022
31.	*Naja* sp.	Çalta	Turkey	Early Pliocene (MN15)	Rage & Şen, 1976
32.	*Naja* sp.	Loc. 21, Al-Sarrar	Saudi Arabia	Late Early Miocene	Rage 1982
33.	*Naja* sp.	ACM/C3-A7	Spain	Middle Miocene (MN7+8)	Carmona et al., 2010; Villa et al, 2024
34.	*Naja* sp.	ACM/C4-A1	Spain	Middle Miocene (MN7+8)	Carmona et al., 2010; Villa et al, 2024
35.	*Naja* sp.	ACM/C5-C3	Spain	Middle Miocene (MN7+8)	Carmona et al., 2010; Villa et al, 2024
36.	*Naja* sp.	Córcoles	Spain	Early Miocene (MN4)	Alférez Delgado & Brea López, 1981; Szyndlar & Alférez, 2005
37.	*Naja* sp.	Hostalets de Pierola	Spain	Middle-Late Miocene (MN6-9)	Villa et al., 2024
38.	*Naja* sp.	Hostalets de Pierola Inferior	Spain	Middle-Late Miocene (MN6-9)	Villa et al., 2024
39.	*Naja* sp.	Layna	Spain	Early Pliocene (MN15)	Jaen & Sanchíz, 1985; Szyndlar, 1988; Szyndlar & Rage, 1990
40.	*Naja* sp.	Librilla	Spain	Late Miocene (MN13)	Alberdi et al., 1981; Szyndlar, 1985; Szyndlar & Rage, 1990
41.	*Naja* sp.	Moreda	Spain	Pliocene (MN15-16)	Bailon, 1991; Bailon, 1992
42.	*Naja* sp.	Venta del Moro	Spain	Late Miocene	Alberdi et al., 1981;

				(MN13)	Marquina et al., 2016
43.	*Naja* sp.	Sant Mamet	Spain	Middle Miocene (MN5)	Villa et al., 2024
44.	*Naja* sp.	Santiga	Spain	Late Miocene (MN9)	Villa et al., 2024
45.	cf. *Naja* sp.	DIK-1, Dikika	Ethiopia	Late Pliocene	Wynn et al., 2006
46.	cf. *Naja* sp.	Balaruc 2	France	Late Pliocene (MN16)	Bailon, 1989; Bailon, 1991
47.	cf. *Naja* sp.	Hambach 6C	Germany	Middle Miocene (MN5)	Čerňanský et al., 2017
48.	cf. *Naja* sp.	Arrisdrift	Namibia	Late Early Miocene	Rage 2003

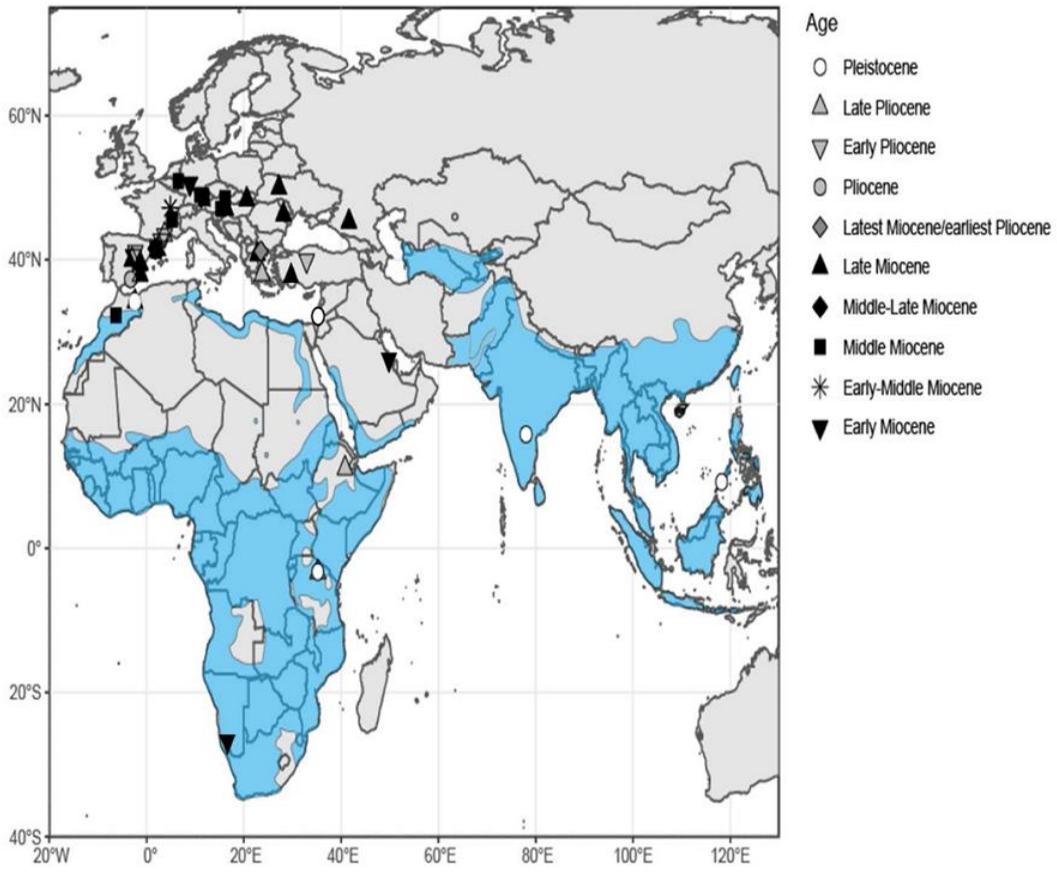

Figure 4. Distribution of *Naja spp.* **A)** Extant species (Light blue color) according to Villa et al. (2024). **B)** The age and occurrence of extinct species of Elapid snakes of prehistoric (Cenozoic) are shown in different bullet symbols based on data available on RepFocus (https://repfocus.dk/Naja.html), except for the circum-Mediterranean area, which follows Pokrant et al. (2017).

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