Grass snakes (*Natrix natrix*, *N. astreptophora*) mimicking cobras display a 'fossil behavior'

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Abstract

Mimicking venomous species is widespread among animals, especially snakes. This concerns both visual and behavioral mimicry. Raising the forepart of the body and flattening the neck are characteristic defense behaviors of cobras and mimicked by several non-venomous snake species that co-occur with them. Here we describe the cobra stance for grass snakes (*Natrix natrix* complex), whose distribution range is largely allopatric to any living cobra species. Among the various defensive behaviors of grass snakes, the cobra stance is uncommon and rarely reported, which raises the questions how effective it is and why it evolved. The fossil record indicates that cobras and grass snakes were abundant and widespread across Europe during the Miocene, where they inhabited the same habitats. They continued to be sympatric in the Mediterranean region until the Pliocene, and in the eastern Mediterranean perhaps until the Middle Pleistocene. Thus, we hypothesize that the cobra stance represents a 'fossil behavior', which developed when the distribution ranges of grass snakes and cobras broadly overlapped. The absence of cobras in most of the extant distribution range of grass snakes, and hence unfamiliarity of typical predators with these dangerously venomous snakes since the Plio-/Pleistocene, explains its rarity nowadays because displaying the cobra stance is no longer advantageous. Migrating birds from Africa, however, may still serve to some extent as target species for the cobra stance in grass snakes, supporting its survival.

Key words

Introduction

Snakes have evolved a wide variety of active and passive defensive strategies to avoid predation, which are not necessarily mutually exclusive. Defensive behaviors include deception, like feigning death or hiding the head, and aggressive behaviors, like repeated striking (Mertens, 1946). Mimicking venomous species is common in non-venomous snakes and evolved independently across several major snake taxa. This Batesian mimicry encompasses both coloration and behavior. For instance, non-venomous colubrids (e.g., *Lampropeltis elapsoides*, Akcali & Pfennig, 2014) imitate the coloration and pattern of coral snakes (*Micrurus* and *Micruroides* spp.). Another example is the Western Palearctic viperine snake, *Natrix maura*, with a viper-like dark zigzag pattern on its back (Aubret & Mangin, 2014). In addition, *N. maura* displays also behavioral mimicry by flattening and deforming its head (Valkonen *et al*., 2011; Aubret & Mangin, 2014), resulting in a triangular head shape as typical in vipers, while hissing loudly like a viper (Aubret & Mangin, 2014). A very similar head-flattening behavior is also known from *Hemorrhois ravergieri* (Werner & Frankenberg, 1982).
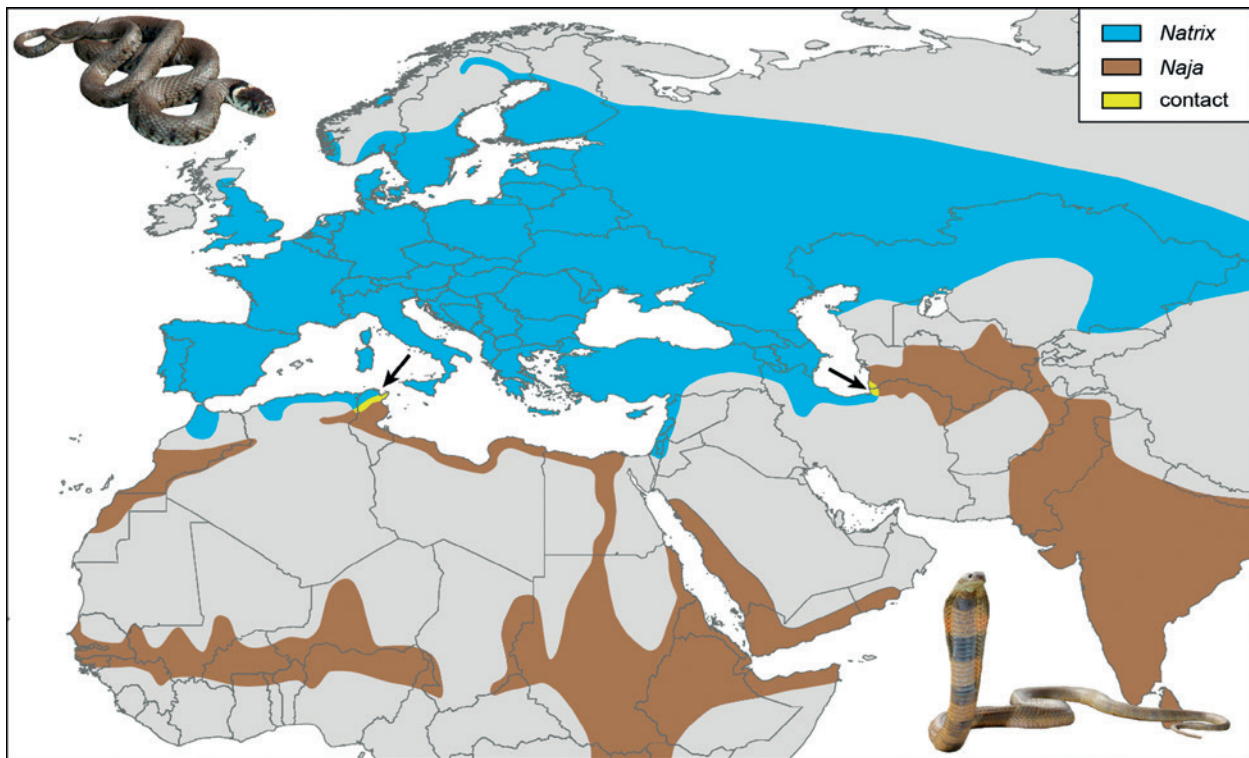
Fig. 1. Distribution ranges of grass snakes (*Natrix natrix* complex) and cobras (*Naja* spp.), combined from BANNIKOV *et al.* (1977) and SINDACO, VENCHI & GRIECO (2013). Areas of potential overlap highlighted in yellow and by arrows.

In areas where cobras occur, some species of colubrids imitate the well-known 'cobra hood', in combination with raising as much as the foremost third of their body (*Macropisthodon* sp., *Pseudoxenodon bambusicola* and *P. macrops,* POPE, 1935; *Amphiesma stolatum*, *Macropisthodon plumbicolor*, GHARPUREY, 1954; *Rhagerhis moilensis, Lytorhynchus diadema,* WERNER, 2016).

Grass snakes (*Natrix natrix* complex) are widely distributed across Europe, northwestern Africa and western Asia. In grass snakes, several defensive behaviors and strategies are known, which are displayed in different frequencies. The rarest grass snake behavior strikingly resembles the warning behavior of cobras. It consists of raising the forebody and flattening the head and neck (WALLNER, 1937; MERTENS, 1946; KABISCH, 1978; ECKSTEIN, 1993), so that the neck shape resembles the cobra hood. This behavior is, except for a single report for *Hemorrhois hippocrepis* (MERTENS, 1946), unique among European snake species and quite remarkable because the distribution ranges of grass snakes and cobras are largely mutually exclusive (Fig. 1). This raises the question why the 'cobra stance' is displayed at all by grass snakes because predators in most of their distribution range must be unfamiliar with cobras. Thus, this behavior should deliver no immediate defensive advantage. In the present study, we examine the evolutionary background of this unexpected behavior of grass snakes. If not otherwise mentioned, we understand the terms 'grass snakes' and '*Natrix natrix* complex' to refer to the two currently recognized species, *N. natrix* and *N. astreptophora* (POKRANT *et al.*, 2016).

Defensive behaviors in grass snakes

When threatened, grass snakes usually try to escape. However, they are also known to exhibit several other behaviors which are independent of sex and age (ECKSTEIN, 1993; USHAKOV, 2007). Non-escape behaviors may be classified as defensive or aggressive. Defensive behaviors include excreting a malodorous liquid from the postanal glands, flattening the head to a triangular viper-like shape (like in *Natrix maura*), regurgitating prey items, curling of the body and akinesia (often in combination with the leakage of blood from the mouth), known as death feigning (e.g., MERTENS, 1946; HEUSSER & SCHLUMPF, 1962; KABISCH, 1978, 1999; ECKSTEIN, 1993; USHAKOV, 2007). In addition, tail rattling caused by the contact of the rapidly moving tail tip and the ground is rarely displayed (ECKSTEIN, 1993).

Aggressive behaviors include hissing, attacks with open or closed mouth and in very rare cases biting and cobra-like lifting of the forebody and flattening the neck (WALLNER, 1937; MERTENS, 1946; KABISCH, 1978, 1999; ECKSTEIN, 1993). Often, different aggressive behaviors are shown in sequence. The most common sequence is hissing followed by akinesia. Based on 382 observations of grass snakes in Germany, it was suggested that defensive behaviors are mainly shown at lower temperatures, while aggressive behaviors are more frequent at higher temperatures. Accordingly, striking (with closed or open mouth) and the cobra stance are more likely to be displayed when temperatures exceed 27°C (ECKSTEIN, 1993). A similar shift to more aggressive behaviors with

rising temperatures was also described for common garter snakes, *Thamnophis sirtalis* (SCHIEFFELIN & DE QUEIROZ, 1991). The rarest type of aggressive behaviors observed in grass snakes was the cobra stance, which was previously documented only in six grass snake individuals (ECKSTEIN, 1993).

Over many years of field work with grass snakes, we observed this behavior only a few times (*Natrix astreptophora*: three times in southern France; *N. natrix*: once each in Istria, Croatia; Saxony, Germany; and Hungary; Fig. 2). The cobra stance has never been described for the two closely related species *N. maura* and *N. tessellata*, while all other defensive behaviors of grass snakes are also known from those species (GRUSCHWITZ *et al.*, 1999; KREINER, 2007).

When displaying the cobra posture, grass snakes are usually in an S-coiled position, and attack the enemy with repeated downwards oriented strikes with closed mouth (KABISCH, 1978; ECKSTEIN, 1993). The head is held nearly perpendicular to the body axis and the body may swing laterally. We are aware of only five descriptions of the cobra posture for grass snakes (SCHWEIZER, 1911; WALLNER, 1937; MERTENS, 1946; KABISCH, 1978; ECKSTEIN, 1993), one of which includes a photo of a large western grass snake (*N. n. helvetica*) with cobra-like hood (KABISCH, 1978) and another one depicts a grass snake with slightly erected forebody (MERTENS, 1946).

Even though the cobra stance occurs only rarely in grass snakes, its mere occurrence is surprising because cobras are largely absent from the distribution range of grass snakes (Fig. 1). There are only two small potential contact zones of cobras and grass snakes, in Tunisia and at the southeastern corner of the Caspian Sea. The genetic lineages of grass snakes occurring there are both genetically deeply divergent from the ones for which the cobra stance has been observed or described (KINDLER *et al.*, 2013), so that this cannot explain the presence of the cobra stance in the behavioral repertoire of grass snakes.

Cobra-like behaviors in snakes

The simulation of a cobra hood is displayed by a number of non-venomous or weakly venomous snake species that – except for *Hydrodynastes gigas*, *Ninia atrata,* and *Heterodon* spp. – occur at least in partial sympatry with cobras: *Rhagerhis moilensis* (MERTENS, 1946; LEÓN *et al.*, 2013; WERNER, 2016), a Western Palearctic species known as the 'false cobra' and distributed in northern Africa and the Middle East; *Pseudoxenodon macrops*, the so-called Chinese false cobra from Asia, and its Asian congener *P. bambusicola* (POPE, 1935; MERTENS, 1946; WHITAKER & CAPTAIN, 2004); *Amphiesma stolatum* of Asia (GHARPUREY, 1954); *Lytorhynchus diadema* of North Africa and the Near East (WERNER, 2016); and *Plagiopholis nuchalis* of Southeast Asia (CHAN-ARD *et al.*, 2015). In addition to these taxa, similar behaviors have also been described for *Macropisthodon* spp. (Asia), *Heterodon* spp. (North America), *Hydrodynastes gigas*

Fig. 2. Cobra stance displayed by a grass snake (*Natrix natrix*). Photo by Carolin Kindler, 27 August 2014, Dresdener Heide, Dresden-Klotzsche, Saxony, Germany.

(South America), *Argyrogena fasciolata* (South Asia), *Atretium schistosum* (South Asia), *Hemorrhois hippocrepis* (northwestern Africa, southwestern Europe), and *Ninia atrata* (southern Central America, northern South America; POPE, 1935; MERTENS, 1946; PLATT, 1969; ANGARITA-SIERRA, 2015).

For taxa living at least in partial sympatry with cobras, cobra-like defensive behaviors are easily understood as Batesian mimicry and as a highly effective protection against predators. Yet, the largely mutually exclusive distribution ranges of grass snakes and cobras (Fig. 1) render the effectiveness of the cobra stance as Batesian mimicry questionable. This is also true for the completely allopatric Neotropical *Hydrodynastes gigas* and *Ninia atrata*, and completely allopatric species of the North American genus *Heterodon*. However, unlike cobras and grass snakes, *Hydrodynastes gigas* does not raise its forebody when it flattens the neck, so that a significant difference exists. This, together with the New World distribution of *Hydrodynastes gigas*, *Heterodon* species and *Ninia atrata*, suggests that their defensive behavior evolved completely independently from that of cobras. Since also rattlesnakes raise their forebody when threatened, this may have been at least the model for *Heterodon* species, which is also supported by their rattlesnake-like color pattern. In any case, the behavior of grass snakes strikingly resembles that of cobras, with a flattened neck, raised forebody and swinging body movements (pers. observ.). Therefore, the question arises how this cobra-like behavior has evolved in grass snakes
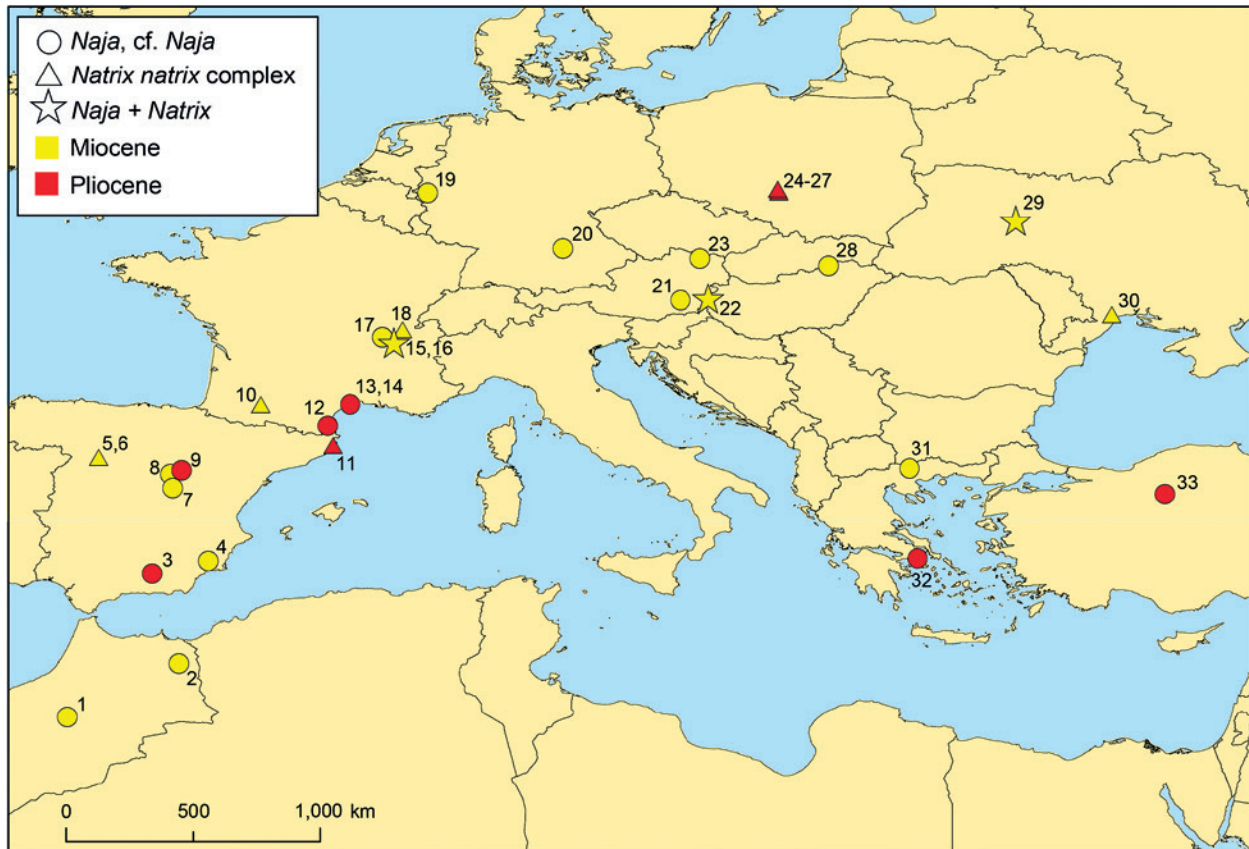
Fig. 3. Fossil records of cobras (*Naja* spp.) and grass snakes (*Natrix natrix* complex) in the Western Palearctic during the Miocene and Pliocene. For explanation of fossil sites, see Table 1.

because their predators usually have no prior experience with cobras and are naive.

Based on the fossil record of Western Palearctic snakes, we hypothesize that the cobra stance has evolved when grass snakes were sympatric with cobras, i.e. in the late Neogene. In the following, we elaborate this hypothesis based on fossil evidence.

Excavating a fossil behavior

The Neogene fossil snake fauna of Eurasia is comparatively well studied and fossil sites are widespread. 'Modern' snake species, i.e. taxa that closely resemble extant snakes and are probably closely related to them, started to appear in the early Miocene (Szyndlar & Schleich, 1993; Ivanov, 2002; Szyndlar & Rage, 2003; Rage & Szyndlar, 2005; Čerňanský *et al.*, 2015). Among fossil snake taxa, both *Naja* and *Natrix* are particularly well known (Szyndlar, 1991a, b; Szyndlar & Schleich, 1993) and using molecular phylogenetic data combined with fossil evidence, the evolutionary and biogeographic history of these clades in Europe is well understood (Ivanov, 2001; Guicking *et al.*, 2006; Wüster *et al.*, 2007; Fritz *et al.*, 2012; Kindler *et al.*, 2013, 2014; Pokrant *et al.*, 2016). While *Naja* originated in Africa (Wüster *et al.*, 2007) and subsequently colonized Asia and Europe, the genus *Natrix* has its origin in Asia and then spread

across Europe (Ivanov, 2001; Guicking *et al.*, 2006). Species of *Naja* colonized Europe twice via different dispersal routes: *Naja* reached Central Europe via Asia, and independently the Iberian Peninsula via Africa during the Messinian salinity crisis (Szyndlar, 1985; Szyndlar & Rage, 1990). In contrast, the fossil record and molecular genetic evidence suggest that *Natrix* invaded Europe only once, spreading from the east to the Iberian Peninsula, whose population became isolated by the Pyrenean uplift and diverged (as *N. astreptophora*) from the populations that became *N. natrix* northeast of the Pyrenees (Fritz *et al.*, 2012; Pokrant *et al.*, 2016).

Vertebrae of *Naja* are distinctive and hence recognizable, and based on this evidence, cobras are widely reported from the European Miocene and Pliocene. The earliest European species referred to *Naja* is *N. romani* from Petersbuch 2, Germany (MN 4; Bachmayer & Szyndlar, 1985; Szyndlar & Schleich, 1993). This species, widespread in the Miocene of Central Europe, is considered to represent the 'Euroasiatic complex' of *Naja*. In contrast, *N. antiqua* and *N. iberica* from the Iberian Peninsula are considered to represent the 'African complex' of *Naja* (Szyndlar & Rage, 1990). In the Pliocene, remains of *Naja* are restricted to southern Europe, including the locality of Balaruc 2 in France (Bailon, 1989; Bailon & Blain, 2007), probably as a result of climatic cooling (Fig. 3).

The earliest European species referred to *Natrix* are early Miocene in age. Some of them (e.g., *N. sansanensis*,

Table 1. Fossil records of cobras (*Naja* spp., cf. *Naja* spp.) and grass snakes (*Natrix natrix* complex) in the Western Palearctic. Site numbers refer to Figure 3.

Site	Taxon	Country	Locality	Latitude	Longitude	MN level	Age	References
1	*Naja antiqua*	Morocco	Béni Mellal	32.34	−6.34	7	Middle Miocene	Rage (1976)
2	*Naja* cf. *antiqua*	Morocco	Guefait-1	34.24	−2.39	9/10	Upper Miocene	Blain et al. (2013)
3	*Naja* sp.	Spain	Moreda	37.44	−3.33	16	Upper Pliocene	Bailon (1992)
4	*Naja* aff. *depereti*	Spain	Librilla	37.89	−1.36	13	Upper Miocene	Alberdi et al. (1981)
5	*Natrix* sp.	Spain	Ampudia 9	41.91	−4.78	9	Upper Miocene	Szyndlar (2012)
6	*Natrix* sp.	Spain	Torremormojón 3 & 4	41.96	−4.78	9	Upper Miocene	Szyndlar (2012)
7	*Naja* sp.	Spain	Córcoles	40.49	−2.66	4b	Lower Miocene	Alférez Delgado & Brea López (1981)
8	*Naja iberica*	Spain	Algora	40.96	−2.67	13	Upper Miocene	Szyndlar (1985)
9	*Naja* sp.	Spain	Layna	41.10	−2.30	15	Upper Pliocene	Jaén & Sanchíz (1985)
10	*Natrix* cf. *longivertebrata*	France	Sansan	43.53	0.62	6	Middle Miocene	Augé & Rage (2000); Szyndlar (2012)
11	*Natrix* cf. *natrix*	France	Iles Medas	42.05	3.22	16	Upper Pliocene	Bailon & Blain (2007)
12	*Naja depereti*	France	Perpignan	42.69	2.89	15	Upper Pliocene	Hoffstetter (1939)
13	cf. *Naja* sp.	France	Balaruc 2	43.44	3.68	16	Upper Pliocene	Bailon (1989)
14	*Naja* sp.	France	Sete	43.41	3.70	15	Upper Pliocene	Szyndlar & Rage (1990)
15	*Naja* sp.	France	Isle d'Abeau	45.62	5.23	7/8	Middle Miocene	Szyndlar & Rage (1990)
16	*Naja romani*	France	La Grive-Saint Alban	45.60	5.23	7/8	Middle Miocene	Hoffstetter (1939)
16	*Natrix longivertebrata*	France	La Grive L7	45.60	5.23	7/8	Middle Miocene	Rage & Szyndlar (1986)
17	*Naja* cf. *romani*	France	Vieux Collonges	45.83	4.83	4/5	Middle Miocene	Ivanov (2000, 2001)
17	*Naja* sp.	France	Vieux Collonges	45.83	4.83	4/5	Middle Miocene	Ivanov (2000, 2001)
18	*Natrix* cf. *longivertebrata*	France	Béon 1	45.85	5.75	4	Lower Miocene	Rage & Bailon (2005)
19	cf. *Naja* sp.	Germany	Hambach 6C	50.90	6.45	5	Middle Miocene	Čerňanský et al. (2016)
20	*Naja romani*	Germany	Petersbuch 2	48.98	11.19	4	Lower Miocene	Szyndlar & Schleich (1993)
21	*Naja* sp.	Austria	Gratkorn	47.15	15.37	?	Middle Miocene	Böhme & Vasilyan (2014)
22	*Naja romani*	Austria	Kohfidisch	47.18	16.35	11	Upper Miocene	Bachmayer & Szyndlar (1985, 1987); Szyndlar & Schleich (1993)
22	*Natrix longivertebrata*	Austria	Kohfidisch	47.18	16.35	11	Upper Miocene	Bachmayer & Szyndlar (1985, 1987); Szyndlar & Schleich (1993)
23	*Naja romani*	Austria	Grund	48.63	16.06	5	Middle Miocene	Miklas-Tempfer (2003)
24	*Natrix longivertebrata*	Poland	Rębielice Królewskie I	51.00	18.85	16	Upper Pliocene	Szyndlar (1984)
25	*Natrix* cf. *longivertebrata*	Poland	Rębielice Królewskie II	51.00	18.85	16	Upper Pliocene	Szyndlar (1984)
26	*Natrix* cf. *longivertebrata*	Poland	Węże I	51.09	18.80	15	Upper Pliocene	Szyndlar (1984)
27	*Natrix* cf. *longivertebrata*	Poland	Węże II	51.09	18.80	16	Upper Pliocene	Szyndlar (1984)
28	*Naja romani*	Hungary	Rudabánya	48.37	20.62	9	Upper Miocene	Bernor et al. (2004)
29	*Naja* sp.	Ukraine	Gritsev	49.98	27.23	9	Late Miocene	Szyndlar & Zerova (1990)
29	*Natrix* cf. *longivertebrata*	Ukraine	Gritsev	49.98	27.23	9	Upper Miocene	Ivanov (2001)
30	*Natrix* cf. *longivertebrata*	Ukraine	Cherevichnoie	46.64	30.63	12	Upper Miocene	Szyndlar & Zerova (1992)
31	cf. *Naja* sp.	Greece	Maramena	41.18	23.47	13	Upper Miocene	Szyndlar (1991a)
32	*Naja* sp.	Greece	Tourkobounia 1	37.99	23.77	16	Upper Pliocene	Szyndlar & Zerova (1990)
33	*Naja* sp.	Turkey	Çalta	40.25	32.54	15	Upper Pliocene	Rage & Sen (1976)

N. merkurensis) may not be ancestral to extant *N. natrix* and *N. astreptophora* (Rage & Augé, 1993; Szyndlar & Schleich, 1993; Ivanov, 2002). In contrast, the lineage *N. longivertebrata* (including *N.* aff. *longivertebrata*), first documented in the early Miocene of Béon 1 (Rage & Bailon, 2005) and middle Miocene of Sansan and La Grive L7 in France (Rage & Szyndlar, 1986; Augé & Rage, 2000; Szyndlar, 2012), is considered to be a direct ancestor of extant *N. natrix* and *N. astreptophora* (Szyndlar, 1991a). On the Iberian Peninsula, pre-Pleistocene *Natrix* fossils are late Miocene *Natrix* sp. (López Martínez & Sanchíz, 1982 cited in Szyndlar, 2012), Pliocene *N.* cf. *maura* from Higueruelas (Badiola et al., 2007), and most importantly late Miocene (MN 16) *Natrix* cf. *natrix* (Bailon & Blain, 2007; whose species concept included *N. astreptophora*). Molecular genetics suggests

that the ancestors of extant *N. astreptophora* were present there since the middle or late Miocene (Fritz et al., 2012; Pokrant et al., 2016). Remains of *N. natrix* are particularly abundant in the Pleistocene of Central and Eastern Europe (e.g., Szyndlar, 1984; Ivanov, 2007).

The Central European lineage of *Naja* overlapped broadly with the *Natrix natrix* complex during the Miocene and both co-occurred in three geographically and temporally widely separated localities (Fig. 3): La Grive L7/Isle d'Abeau, France (MN 7/8, about 13–11 million years ago = mya); Kohfidisch, Austria (MN 11, about 9–8 mya); and Gritsev, Ukraine (MN 9, about 11–10 mya). There is no direct evidence that grass snakes and cobras co-occurred in the Pliocene of Central Europe, when the Central European *Naja* lineage became restricted to southern Europe and the Mediterranean, nor in the Miocene or

Pliocene of the Iberian Peninsula, although the inferred divergence time of *N. astreptophora* (FRITZ *et al.*, 2012; POKRANT *et al.*, 2016) and fossil occurrences suggest they could have; in particular, the localities of Balaruc I and Iles Medas are closely spaced. Thus, the last documented co-occurrence of grass snakes and cobras is in Central Europe in the late Miocene, over 8 mya. A longer period of over-lap (before MN 7/8 and after MN 11) between *Naja* and grass snakes seems probable, particularly in the Pliocene of the circum-Mediterranean region.

Similarities between fossil *Natrix* and *Naja* species, and their recent counterparts, probably also extend to their habitat requirements. In the case of *Naja*, dry habitats were most likely preferred, although the extant *Naja haje* is also reported to live often adjacent to small water bodies (TRAPE *et al.*, 2009). In *Natrix* the case is more complex and species-dependent. Like in recent grass snakes, it can be speculated that a wide variety of habitats was colonized, which span from the immediate neighborhood of ponds, creeks and rivers to habitats very distant from water. The fossil species *Natrix longivertebrata* was—next to typical freshwater habitats—found in dry habitats as well, suggestive of a syntopic occurrence with *Naja romani*. While RAGE & SZYNDLAR (1986) found that surprising, it perfectly makes sense with our current knowledge about the ecology of extant grass snakes, in particular of *Natrix astreptophora*, which is much less dependent on water compared to *N. natrix* (KABISCH, 1978, 1999; GALÁN *et al.*, 1990; KREINER, 2007; GLANDT, 2015).

Evolution of behavioral mimicry within *Natrix*

It seems plausible that, if morphology and ecology of extant species resemble that of extinct ones, behavior does so, too. In other words, we can assume that cobras had already developed their characteristic threatening behavior in the Miocene and that this behavior was mimicked by the ancestors of modern *Natrix* species. If modern cobras inherited defensive behavior from their ancestors, *Natrix natrix* and *N. astreptophora* are likely to have inherited their cobra-style strategy from their ancestors.

Neither dice snakes (*Natrix tessellata*) nor viperine snakes (*N. maura*) developed such a behavior, although they also coexisted with cobras in the same timeframe (GUICKING *et al.*, 2006). A possible explanation for this phenomenon may lie in the very different habitat requirements of cobras and these two species. *Natrix tessellata* and *N. maura* have a mostly aquatic lifestyle and spend a considerable amount of time inside and very close to the water. *Natrix natrix* and even more *N. astreptophora* are much less dependent on water and often found far away from any water body (KABISCH, 1978, 1999; GALÁN *et al.*, 1990). Consequently, a coexistence of cobras and grass snakes and, thus, a potential advantage for grass snakes by mimicking cobras is much more likely than for dice snakes and viperine snakes.

The high local abundance of *Naja romani* supports our hypothesis. This fossil species is extremely abundant

at Kohfidisch, where *Natrix longivertebrata* also occurs (BACHMAYER & SZYNDLAR, 1985, 1987; SZYNDLAR & SCHLEICH, 1993). Mimicking a venomous species is more effective when the dangerous species is common (DUNN, 1954; BRATTSTROM, 1955). Since grass snakes were also common then, the advantage of copying the behavior of a cobra must have been great. This is made even more likely since both taxa presumably lived together for a very long time, allowing for specific adaptations like mimicry. *Natrix longivertebrata* and *Naja romani* are in fact the two fossil snake species with the longest known stratigraphic range (SZYNDLAR & ZEROVA, 1990; SZYND-LAR, 1991b, 2005).

It is well known, however, that for the efficiency of mimicry, the model species has to be known by preda-tors, because otherwise the signal emitted by the mimic will not be recognized. As already pointed out by ALFRED RUSSEL WALLACE (1867), this is obviously true when mimic, model, and predator (the signal-receiver) live in the same environment (see also WICKLER, 1965, 1968). While this is surely the most common case, there are also other examples, like coral snake imitators, which do not live in sympatry with their model species, because they were able to extend their range beyond that of the coral snakes. For instance, the California mountain kingsnake (*Lampropeltis zonata*) shows no overlap in distribution with coral snakes at all (STEBBINS, 2003; RABOSKY *et al.*, 2016), while the closely related scarlet kingsnake (*L. elapsoides*) only partly shares distribution with its model species, *Micrurus fulvius*, which recently went extinct at several locations where now only the mimic occurs (AKCALI & PFENNIG, 2014). In our system, the model spe-cies retreated from most of the range of the mimic due to climatic reasons and the two remaining spots of possible co-occurrence (Fig. 1) harbor distinctive genetic lineages of grass snakes that diverged from other lineages at least 5.6 – 6.5 mya (FRITZ *et al.*, 2012; KINDLER *et al.*, 2013), i.e. most likely before cobras of the genus *Naja* became extinct from most of the Western Palearctic (SZYNDLAR, 2005). The last record of *Naja romani* from that area stems from the late Miocene of Kohfidisch (MN11; BACHMAYER & SZYNDLAR, 1985). Later, cobras were only found in the Mediterranean zone until the late Pliocene (MN16; BAILON, 1989; SZYNDLAR & ZEROVA, 1990) and in the eastern Mediterranean perhaps until the Middle Pleis-tocene (Chios, SCHNEIDER, 1975), i.e. in a region where also ancestors of extant grass snakes occurred.

In summary, we conclude that the cobra posture in grass snakes represents a 'fossil behavior' which origi-nated during the Miocene and Plio-/Pleistocene co-oc-currence of cobras and grass snakes. The present areas of potential contact between cobras and grass snakes are peripheral and highly localized. They refer to other genetic lineages of grass snakes (KINDLER *et al.*, 2013) than the ones for which the cobra-like behavior was re-ported. The ranges of model and mimic taxa diverged largely when cobras became extinct north of the Mediter-ranean after the Pliocene, so that the behavioral mimicry survived for a considerably long time after the model

species vanished from most of the distribution range of grass snakes. In this context, the question arises why the cobra stance still belongs to the behavioral repertoire of grass snakes because the efficacy of mimicry is expected to decline with the disappearance of the model (Ruxton *et al.*, 2004). First of all, the rareness of displaying the cobra stance suggests that grass snakes are in the process of losing this behavior. Yet, one factor might support the preservation of this behavior. The cobra stance may still yield some advantage against migratory birds that prey on grass snakes. Several bird species known to feed on grass snakes (storks, migratory raptors and herons; Kabisch, 1978, 1999) overwinter in Africa, where cobras are abundant in many regions. Thus, against those birds, mimicking cobras is most likely still effective and this may counteract the complete evolutionary loss of the cobra stance in grass snakes.

Note added in proof

Natrix natrix helvetica and related subspecies from Italy and France have recently been recognized as the distinct species *Natrix helvetica* (Kindler *et al.*, 2017).

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