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Neogene Cobras of the Genus *Naja* (Serpentes: Elapidae) of East Europe

Neogene Kobras der Gattung *Naja* (Serpentes: Elapidae) aus Osteuropa

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(Mit 3 Abbildungen im Text)

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Zusammenfassung

Fossile Überreste der Gattung *Naja* sind aus drei neogenen Fundstellen bekannt: Gritsev (Ukraine), Kohfidisch (Österreich) und Tourkobounia 1 (Griechenland). Reste aus den beiden ersterwähnten Fundstellen gehören der ausgestorbenen Art *Naja romani* an, die ursprünglich aus dem Miozän Frankreichs beschrieben wurde. Diese Art bildet einen frühen Ausläufer der Entwicklungslinie, die zu den rezenten asiatischen Vertretern der Gattung *Naja* führt. Aus dem Vorkommen von *N. romani* in den letzten sechs Millionen Jahren gehen neue Erkenntnisse über die Langlebigkeit der miozänen Ophiden-Arten hervor.

Summary

Fossil remains of the genus *Naja* are reported from three Neogene localities: Gritsev (Ukraine), Kohfidisch (Austria), and Tourkobounia 1 (Greece). Remains from the two former localities belonged to the extinct species *Naja romani* originally described from the Miocene of France. This species represented an early offshoot of the evolutionary lineage leading to the living Asiatic members of the genus *Naja*. The persistence of *N. romani* for at least six million years provides new evidence for the longevity of Miocene ophidian species.

Introduction

Among extinct European snakes, the Elapidae have perhaps the most well documented history. The fossil record of the family, which at present does not inhabit the discussed area, comes from fifteen Neogene localities. Most of the excavated material consists of isolated vertebrae only, but the cranial elements, usually well preserved, also occur quite commonly. Szyndlar and Rage (in press)

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recently reviewed the entire elapid fossil record from Europe and adjacent territories and outlined phylogenetic interrelationships among both extinct and extant cobras. They demonstrated that all but one of the European elapids belonged to the modern genus *Naja*. The latter research confirmed SZYNDLAR's (1985) opinion that living members of the genus *Naja* represented two separate phyletic lineages, currently inhabiting Africa and Asia, respectively. In the past, members of the former complex occurred in the Iberian Peninsula, while the remaining part of southern Europe was occupied by representatives of the Asiatic lineage. Most finds of European cobras come from western Europe; in the present paper we review Neogene fossils found in three East European sites in Ukraine, Austria, and Greece.

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We wish to dedicate this short article to the memory of Professor BACHMAYER in order to honour his prominent contribution to our knowledge on the Kohfidisch fauna.

Localities and material

The oldest locality of Gritsev is located in Khmelnitsky oblast', western Ukrainian SSR. According to KOROTKEVICH (1988), its fauna is of late Miocene age (Neogene European Land Mammalian Zone MN 9, Mammalian Age lower Vallesian). The squamate fauna from Gritsev was preliminary listed by ZEROVA (1987), and an erycine snake (*Albaneryx*) was described in detail by the same author (ZEROVA 1989). Snake remains belong to the following taxa: an unidentified scolecophidian, *Albaneryx volynicus* and *Bransateryx* sp. (Boidae: Erycinae), a natricine, *Coluber* sp., *Elaphe* sp. (Colubridae), *Vipera* sp. (Viperidae), and a member of the genus *Naja* (Elapidae). The latter snake was identified on the basis of a basisphenoid, a right compound bone, and ten trunk vertebrae. The material is the property of the Institute of Zoology of the Academy of Sciences of Ukrainian SSR (IZAN).

Kohfidisch, located in Burgenland (Austria), is of late Miocene age (MN 11, lower Turolian, after BACHMAYER & ZAPFE 1969). The snake fauna, described in detail by BACHMAYER & SZYNDLAR (1985, 1987), consists of five extinct species: *Elaphe kohfidischi, Coluber planicarinatus, Natrix longivertebrata* (Colubridae), *Vipera burgenlandica* (Viperidae), and *Naja austriaca* (Elapidae).The description of *Naja austriaca* was based on a basisphenoid (holotype) and a set of other cranial and axial bones. The newly discovered material, described in the present paper, contains two other basisphenoids, a fragmentary parietal, one right and one left prootics, one basioccipital, two squamosals, two left quadrates, ribs, and vertebrae. The material belongs to the Naturhistorisches Museum in Vienna (NMW).

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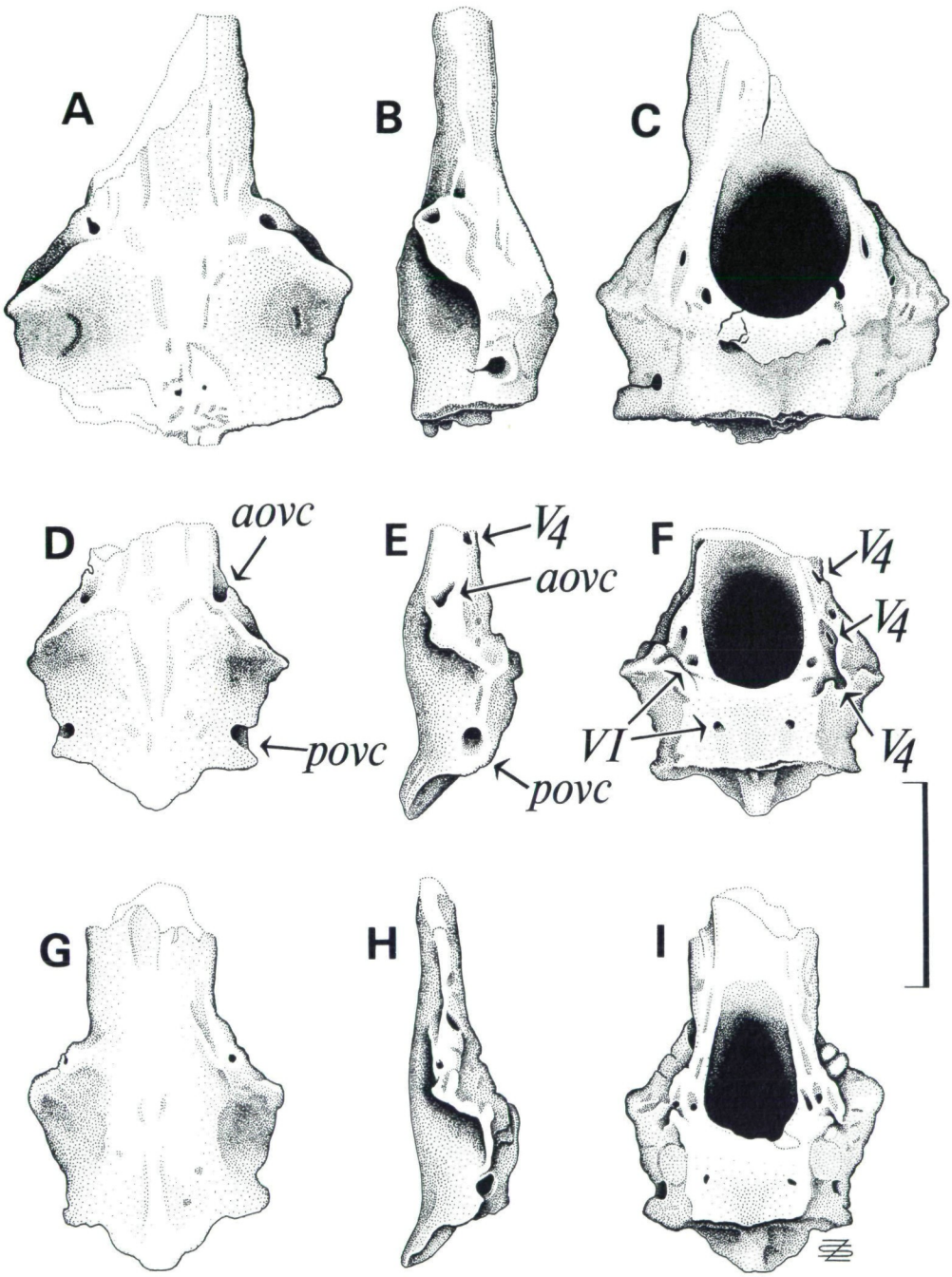

Fig. 1: Basisphenoids of *Naja romani* from Kohfidisch (A–C and D–F; NMW 1989/34/1 and 1989/34/2) and from Gritsev (G–I; IZAN 22–1771); ventral (A, D, G), left lateral (B, E, H), and dorsal (C, F, I) views. Scale line 5 mm. Abbreviations: aovc, anterior orifice of Vidian canal; povc, posterior orifice of Vidian canal; V_4, groove and foramina for entry and exit of cid-nerve; VI, foramina for abducens nerve.

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Tourkobounia 1, lying in the area of Athens (Greece), is of upper Pliocene age (MN 16, Villanyian; de BRUIJN & van der MEULEN 1979). The snake fauna is comprised of a scolecophidian, *Malpolon* sp. (Colubridae), two species of *Vipera* (Viperidae), and *Naja* sp. (Elapidae), the latter represented by seventeen trunk vertebrae. The material belongs to the Geological Institute of the Utrecht University (UUGI).

Morphological description

In the following description we focus on elements having taxonomic importance; the bones for which morphology is similar in all or most species of *Naja* are not described in detail.

The three available basisphenoids, both those from Kohfidisch and that from Gritsev (Text-fig. 1), display the same morphological patterns and do not differ from the holotype basisphenoid of *Naja austriaca* (cf. BACHMAYER & SZYNDLAR 1985: 89, Text-fig. 3). The parasphenoid portion is missing in all the bones. The basisphenoid portion is hexagonal in shape and becomes distinctly narrower immediately before the basipterygoid processes; the latter structures are strongly developed. The posterior orifices of the Vidian canals are located on the lateral margins of the bones (i. e., at the suture between the basisphenoid and prootic in a complete braincase). The anterior orifices of the canals lay on the ventral side of the bone, although in the close proximity to the suture between the basisphenoid and parietal. The relative shortness of the Vidian canals in one of the basisphenoids from Kohfidisch, along with its absolute size (Text-fig. 1: A–C), indicate that the bone belonged to an extremely large snake. On the dorsal side of each bone, paired foramina for the entry and exit of the abducens nerves are located around the crista sellaris in the manner characteristic of most snakes. The constrictor internus dorsalis branches of the trigeminal nerves (hereafter termed the cidnerves) entered the basisphenoid through narrow (eventually partially closed) grooves located between the lateral margins of the bone and the anterior orifices for the abducens nerves. The cid-nerves then re-entered the bone through foramina located on both sides of the pituitary fossa and left it cranial to the anterior orifices of the Vidian canals.

Two prootics from Kohfidisch come from the left and right sides of (a) braincase(s) (Text-fig. 2 A, B). The bone is subquadrate in shape; its roof possesses a strong crest for reception of the squamosal. The lateral wall contains two large cavities; the anterior for the maxillary branch of the trigeminal nerve (V_2), and the posterior housing the mandibular branch of the nerve (V_3) as well as the facial nerve; the cavities are accompanied by a number of smaller foramina. An orifice located below the V_2 cavity admitted the cid-nerve to the basisphenoid. In the right bone the foramen is located in part within the V_2 cavity. The facial nerve, leaving the V_3 cavity by a smaller (i. e., more posterior) foramen, run towards the posterior orifice of the Vidian canal within a deep groove; in the left prootic the groove is partially closed by an extension of the laterospheroid portion of the bone. The extension is pierced by the laterospheroid foramen.

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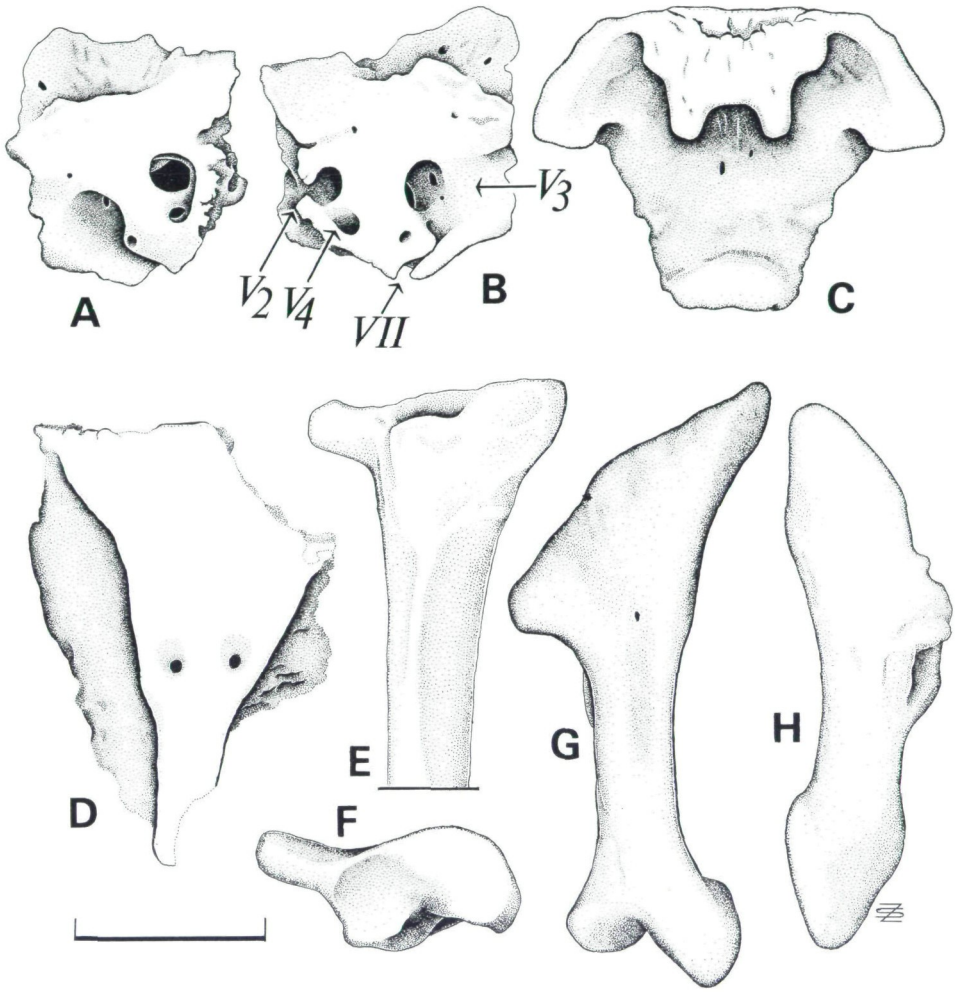

Fig. 2.: Some bones of *Naja romani* from Kohfidisch. A, right prootic in right lateral view (NMW 1989/34/4). B, left prootic in left lateral view (NMW 1989/34/5). C, basioccipital in posterolateral view (NMW 1989/34/3). D, parietal fragment in dorsal view (NMW 1989/34/3). E and F, left rib in ventral and inner views (NMW 1989/34/11). G, right quadrate in right lateral view (NMW 1989/34/9). H, left squamosal in left lateral view (NMW 1989/34/7). Scale line 5 mm. Abbreviations: V_2, cavity for maxillary branch of trigeminal nerve; V_3, cavity for mandibular branch of trigeminal nerve; V_4, foramen for entry of cid-nerve; VII, groove for facial nerve.

A basioccipital, a parietal fragment, two squamosals, two quadrates and numerous ribs from Kohfidisch (Text-fig. 2 C–H) are developed similarly to those of other cobras and do not possess important differentiating features.

Of the cranial elements belonging to the Kohfidisch fossil, described previously by BACHMAYER & SZYNDLAR (1985, 1987), the maxillae and a palatine are especially noteworthy. The venomous fangs on the maxillae are always followed by two solid teeth each. The palatine bears eight teeth, a very rare condition in *Naja*

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(usually seven teeth). Several compound bones from Kohfidisch are very similar to those of other *Naja*. The single compound from Gritsev, despite its extensive damage, displays the same morphology.

Large vertebrae from Kohfidisch were described in detail by BACHMAYER & SZYNDLAR (1985). The vertebrae examined in the present study belonged to smaller (but adult) specimens (Text-fig. 3 A–C). The only differences between them are of allometric nature: the smaller vertebrae have relatively longer centra, wider neural canals and distinctly crenate zygosphenal roofs. The ten vertebrae from Gritsev (Text-fig. 3 D–E) do not differ significantly from those from Kohfidisch; they belonged to smaller specimens.

The vertebrae from Tourkobounia 1 (Text-fig. 3 G–I) display a set of different morphological features. They differ in having relatively broad centra, relatively

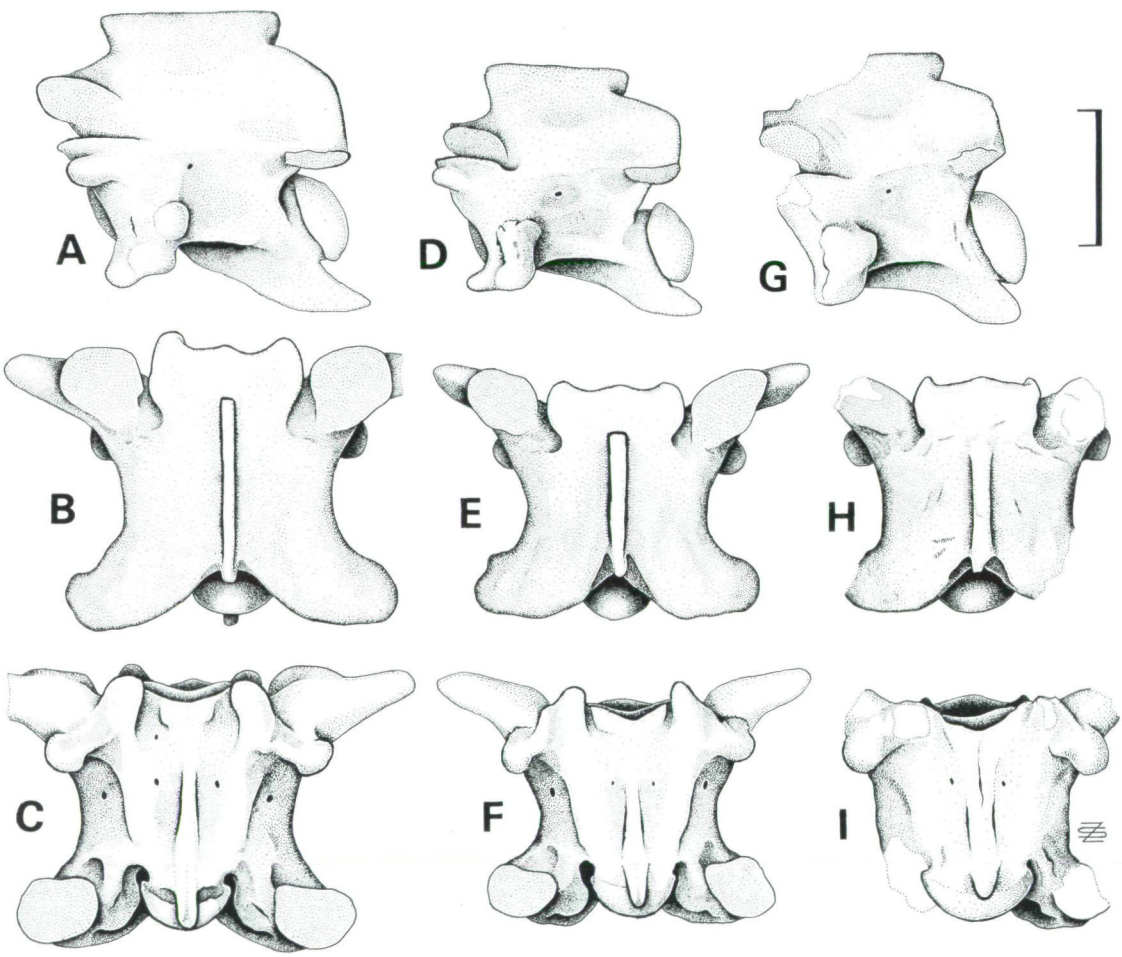

Fig. 3.: Mid-trunk vertebrae of *Naja romani* from Kohfidisch (A–C; NMW 1989/34/12) and from Gritsev (D–F; IZAN 22–1776) and of *Naja* sp. from Tourkobounia 1 (G–I; UUGI uncat.); left lateral (A, D, G,), dorsal (B, E, H), and ventral (C, F, I) views. Scale line 5 mm.

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short and obtuse hypapophyses as well as convex (not crenate) zygosphenes in dorsal view. All vertebrae are damaged.

Discussion

The vertebrae from Tourkobounia 1 undoubtedly belonged to a different species than those from Gritsev and Kohfidisch. Unfortunately, proper identification to the specific level cannot be demonstrated. In some details (especially the zygosphenal roof), they resemble vertebrae of the Asiatic *N. naja* but also those of some African forms, e. g., *N. melanoleuca.*

As previously mentioned, there are no significant differences between the remains from Gritsev and Kohfidisch, and then they are regarded the same species. The fossil from Kohfidisch was originally described as a new extinct species, *N. austriaca,* by BACHMAYER & SZYNDLAR (1985); these authors pointed out close similarities between *N. austriaca* and *Palaeonaja romani*. The latter form, coming from the Middle Miocene (MN 7/8) of La Grive-Saint Alban in France, was described on the basis of numerous cranial and axial elements by HOFFSTETTER (1939); from the same locality he also described, based exclusively on large trunk vertebrae, another fossil species, namely *P. crassa.* SZYNDLAR & RAGE (in press) recently synonymized *Palaeonaja* with the modern genus *Naja* and demonstrated that vertebrae of *P. crassa* belonged to large specimens of *N. romani.* BACHMAYER & SZYNDLAR (1985) did not study the type material of *N. romani* but based their opinion exclusively on HOFFSTETTER's illustrations (1939: Plates I and II). Detailed examination of the new collection from Kohfidisch and its comparison with the type material from La Grive-Saint Alban, undertaken in the present study, indicate that both forms are closely similar to each other. *N. austriaca* is then synonymized here with *N. romani.* Some differences between *N. austriaca* and *N. romani,* observed in vertebral morphology by BACHMAYER & SZYNDLAR (1985), resulted from the fact that only very large vertebrae of the Austrian form were considered. Smaller vertebrae, described in the present paper, are comparable with those of *N. romani* form the type locality. On the other hand, the large vertebrae from Kohfidisch closely resemble those attributed previously to *crassa.* These facts prove that the vertebral column of fossils from both La Grive-Saint Alban and Kohfidisch display the same pattern of allometric variability.

N. romani belonged clearly to the Asiatic stock of the genus *Naja.* The Asiatic and African members of the genus, including both living and fossil species, may be easily differentiated from each other on the basis of a set of characters of the basisphenoid. In the Asiatic cobras the basisphenoid is distinctly narrowed before the basipterygoid crests, the Vidian canals are relatively short and their anterior orifices are located on the ventral side of the bone; in the African cobras the basisphenoid is not narrowed, the canals are relatively long and their anterior orifices lie on the dorsal side of the bone (SZYNDLAR & RAGE, in press). UNDERWOOD (1967) observed that intracranial location of the anterior orifice of the Vidian canals, i. e., on the dorsal side of the basisphenoid, is a primitive condition among

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caenophidians; he also recognized relatively long canals to be primitive. RIEPPEL (1979) confirmed UNDERWOOD's observations with reference to henophidians and suggested the parallel evolution of these features in these two ophidian groups. SZYNDLAR & RAGE (in press) also expected that the corresponding characters displayed in the basisphenoid of the African *Naja* are symplesiomorphic, while those observed in the Asiatic members of the genus are synapomorphic. It should also be noted that the characters of the basisphenoid of *Naja* are fixed, contrary to those found in other regions of the posterior braincase that are highly polymorphic. These facts suggest that the two different types of the basisphenoid appeared at an early stage of history of the genus *Naja*.

Another feature that facilitates the differentiation of the Asiatic and African complexes of the genus is location of the vestibular window (SZYNDLAR 1985); the African cobras have the window situated between the prootic and exoccipital (as in most snakes), while that of the Asiatic species is located exclusively within the exoccipital and has no contact with the prootic (except for the East and Sotheast Asiatic taxa). No exoccipitals have been found in Kohfidisch or Gritsev. The only known exoccipital of *N. romani* from the Miocene of France, however, displays the „Asiatic" condition.

A feature highly characteristic for *N. romani* from Kohfidisch is that the facial nerve, on its way between the V_3 cavity and the posterior orifice of the Vidian canal, was disclosed from outside. This character is very rare among living cobras (observed in some specimens of *N. oxiana*) but is visible in *N. iberica* from the Miocene of Spain (SZYNDLAR 1985). Similarly, the entry of the cid-nerve into the prootic, in the form of a foramen not connected with the suture between the prootic and parietal, very rarely occur in recent cobras (observed in a single specimen of *N. nigricollis*) but it was present in *N. iberica*. These features seem to be of plesiomorphic nature and probably display ancestral conditions (SZYNDLAR & RAGE, in press).

Another feature differentiating modern species of *Naja* is the number of solid maxillary teeth. According to BOGERT (1943), reduction of the tooth number is an advanced condition and we agree with his opinion. Regarding living forms, the African species have two (rarely three) teeth, while the Asiatic species have one or no tooth. All available maxillae of *N. romani*, both from Kohfidisch and from La Grive-Saint Alban, are provided with two teeth each. This suggests that *N. romani* belonged to an early offshoot of the Asiatic lineage and indicates that reduction of teeth observed in this lineage was a relatively modern phenomenon.

Concluding, *N. romani* represented an old evolutionary branch that appeared at an early stage of history of the genus *Naja*. However, this event took place after the split of the genus into the Asiatic and African complexes.

The similarity of abundant fossil remains, especially cranial elements, from both La Grive-Saint Alban and Kohfidisch suggests that *N. romani* persisted in invariable form for at least six million years. Considering the presence of vertebrae reported as *N. romani* in the French Lower Miocene (MN 4; HOFFSTETTER 1939), this period may have been even much longer.

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Up to now, the only fossil ophidian species of well-documented long stratigraphic range was *Natrix longivertebrata,* reported from Middle Miocene and Upper Pliocene European localities (RAGE & SZYNDLAR 1986). *Naja romani* provides new evidence that such a longevity of snake species may not have been rare phenomena in the Miocene. Indeed, constant tropical conditions of European climate characteristic for that epoch (cf. e.g. STEININGER et al. 1985) were probably beneficial to reptiles and detained mass extinctions of ophidian species, the process common in post-Miocene times.

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