Ann. Naturhist. Mus. Wien	87	A	79–100	Wien, November 1985

Ophidians (Reptilia: Serpentes) from the Kohfidisch Fissures of Burgenland, Austria

Die Fauna der pontischen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich): Schlangen (Reptilia, Serpentes)

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(Mit 2 Tafeln und 6 Abbildungen im Text)

Manuskript eingelangt am 18. Dezember 1984

Zusammenfassung

In dieser Arbeit wurden Schlangenreste von der pontischen (MN 11) Fundstelle Kohfidisch (Burgenland, Österreich) beschrieben. Im besprochenen Material treten 5 Schlangentaxa (*Elaphe kohfidischi* sp. nov., *Nanus planicarinatus* gen. sp. nov., *Natrix longivertebrata, Naja austriaca* sp. nov., *Vipera* sp. [= *Daboia* sp.]) auf. Als Dominantformen können *Elaphe kohfidischi* sp. nov. und *Naja austriaca* sp. nov. betrachtet werden. Die hier beschriebene Schlangenfauna ist für ein etwas wärmeres als mediterranes Klima charakteristisch. Die Schlangen bewohnten ziemlich trockene jedoch unweit vom Wasser liegende Biotope.

Summary

This paper describes ophidian remains coming from the Pontian (MN 11) deposit of Kohfidisch in Austria. 5 different taxa of snakes have been recognized: *Elaphe kohfidischi* sp. nov., *Nanus planicarinatus* gen. sp. nov., *Natrix longivertebrata, Naja austriaca* sp. nov., and *Vipera* sp. (= *Daboia* sp.). *Elaphe kohfidischi* and *Naja austriaca* were dominants among the snake fauna from Kohfidisch. Assemblage of the snake fauna indicates that the locality was characterized by warm climate of at least mediterranean type or somewhat warmer. The snakes largely inhabited rather dry environment, however in the proximity of water reservoirs.

Introduction

The present article dealing with the ophidian fauna from the Pannonian locality of Kohfidisch follows descriptions of some other groups of terrestrial vertebrates given by BACHMAYER and his co-authors. So far, small mammals (BACHMAYER & WILSON 1970, 1978, 1980); proboscideans (BACHMAYER & ZAPFE 1972), anguid lizards (BACHMAYER & MŁYNARSKI 1977) and chelonians (BACHMAYER & MŁYNARSKI 1983) coming from the same locality have been described in detail.

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Contrary to the previously described faunas of Kohfidisch, usually well documented also from other fossil sites, snakes are still animals of poorly recognized history, especially with reference to the Central European Neogene. The abundant ophidian material from Kohfidisch used in this study, consisting of about 2000 bones, contains fossil remains belonging to at least 5 different extinct species. Among them, only one species has been previously known from other Neogene localities; the remaining forms are identified as new taxa.

The age of the Kohfidisch deposit was recognized by BACHMAYER & ZAPFE (1969) at Late Pannonian (= Pontian s. str.) in the Paratethyian terms or Early Pliocene. According to West European classification, recently widely introduced also in countries of Central and Eastern Europe (cf. e. g. FAHLBUSCH 1981), the age of Kohfidisch should be defined as Upper Miocene. Correlation of the Kohfidisch fauna was discussed in detail by BACHMAYER & WILSON (1970). These authors state that Kohfidisch is of the same age as Eichkogel (MEIN's biozone MN 11), slightly older than Polgárdi (MN 13) and younger than Vösendorfer (MN 10) and Montredon (MN 10) (BACHMAYER & WILSON supra cit., passim). This statement agrees with MEIN's (1975) determination that placed the Kohfidisch fauna within the MN 11 biozone.

The material described below is stored in the Geologisch-Paläontologische Abteilung of the Naturhistorische Museum in Wien. Comparative materials used in the present study belong to the Institute of Systematic and Experimental Zoology of the Polish Academy of Sciences in Cracow, Museo Nacional de Ciencias Naturales in Madrid, and Museum National d'Histoire Naturelle in Paris.

Measurements and ratios of snake vertebrae employed here were originally designated by AUFFENBERG (1963). All measurements are given in millimetres. Anatomical terminology follows that used by SZYNDLAR (1984). Figures in the text are drawn by the junior author.

Acknowledgments. – The authors are deeply indebted to Dr. Jean-Claude RAGE (Paris) for his critical comments on the part of the manuscript concerning Elapidae.

These studies were sponsored by the Foundation for Scientific Research (Fonds zur Förderung der wissenschaftlichen Forschung), Project 3880. Support was also given by the Geologisch-Paläontolog. Abteilung of the Naturhistorische Museum in Wien.

Systematic description

Family Colubridae

Elaphe kohfidischi sp. nov.

(Text-Fig. 1: 1–16, pl. 1: Figs 1–3)

Holotype: A mid-trunk vertebra (Naturhist. Mus. Wien, Geol.-Paläont. Abt., No. 1984/96).

Referred material: Several hundred vertebrae.

Name derivation: From Kohfidisch, the type locality.

Diagnosis: Typical colubrid snake with trunk vertebrae characterized by moderately long centrum, prominent and spatulate-shaped haemal keel, well defined subcentral grooves, vaulted neural arch, somewhat longer than high neural spine, straight or slightly concave zygosphene from above, moderately developed prezygapophyseal processes, prominent paradiapophyses with diapophysis and parapophysis of equal size.

Differentiating-diagnosis: Precaudal vertebrae of *Elaphe kohfidischi* resemble most those of *Elaphe longissima* and *Elaphe paralongissima,* but differ from these species by the following features: (1) from *E. longissima* – in lack of epizygapophyseal spines of atlas; lower neural spine of cervical vertebrae; concave zygosphene of largest trunk vertebrae; (2) from *E. paralongissima* – in parapophyses and diapophyses of similar length; more acute prezygapophyseal process; (3) from both *E. longissima* and *E. paralongissima* – in thin and high haemal keel of trunk vertebrae; neural canal relatively wieder; relatively longer centrum of largest trunk vertebrae (centrum length/centrum width ratio = 1.29 on average).

Description of holotype (Text-fig. 1: 1–5, pl. 1: Figs 1–3): A middle trunk vertebra, somewhat fragmentary. The antero-dorsal portion of its neural spine and lamina of the neural arch above right zygantrum are missing. In dorsal view, the vertebra is distinctly narrowed between its pre- and postzygapophyses. Centrum moderate in length, subtriangular from below, provided with prominent haemal keel, the latter structure relatively thin and high, somewhat spatulate shaped. Anteriorly, below the cotyle lips, the keel is accompanied by paired tiny tubercles. Subcentral ridges (= margo ventralis) fairly well developed posterior to the parapophyses, diminishing before the base of the condyle. Subcentral grooves well defined, especially deep on either side of the paradiapophyses. Subcentral foramina small. Neural arch rather short, vaulted, not provided with epizygapophyseal spines. Neural canal, somewhat square in outline from the front, is about the same size as the round cotyle. Neural spine relatively thin, somewhat longer than high, occupying two-thirds of the neural arch length and distinctly overhanging posteriorly. Zygosphene concave from above, provided with two tiny (but distinct) lateral lobes; in anterior view, the zygosphenal roof is straight. Prezygapophyseal articular facets elongate and oval in shape; postzygapophyseal articular facets obovate-shaped. Prezygapophyseal processes (= accessory processes) moderately developed, slightly tapering, directed antero-laterally from above. Interzygapophyseal ridges (margo lateralis) moderately developed, parallel to the axis of the centrum. Lateral foramina small. Paradiapophyses (= synapophyses) well developed, with parapophyseal and diapophyseal portions of similar size and distinct from one another; in anterior view, parapophyses are distinctly separated off the cotyle by broad subcentral grooves. Paracotylar foramina well marked, doubled on both sides of the cotyle. Condyle oval, oblique, without a distinct neck.

Basic measurements and ratios of the holotype are given in Table 1.

Description of remaining material: A single axis (Text-fig. 1: 12–14) preserved in the material has a very short centrum with its odontoid process strongly flattened anteriorly. Both intercentra and transverse processes are missing. Neural arch high, without epizygapophyseal spines. Neural spine strongly

Table 1. Measurements and ratios of holotype trunk vertebra of *Elaphe kohfidischi* sp. nov.

$PR\text{–}PO_{(L)}$	7.83		
$PR\text{–}PO_{(R)}$	8.02	CL/NAW	1.27
CL	6.57	PO–PO/NAW	1.76
PO–PO	9.12	CTW/CTH	0.93
NAW	5.19	ZW/NAW	0.87
ZW	4.52	PR–PR/PR–PO	1.22
CTH	2.84	CL/ZW	1.45
CTW	2.64	PR–PR/NAW	1.86
PR–PR	9.63		

CL – centrum length, CTH – cotyle height, CTW – cotyle width, NAW – centrum width, PO–PO – width between outer edges of postzygapophyseal articular surfaces, PR–PO – length from the anterior edge of prezygapophyseal articular surfaces to the posterior edge of postzygapophyseal articular surface, PR–PR – width between the outer edges of prezygapophyseal articular surfaces, ZW – zygosphene width.

slopes forward, posteriorly it is provided with long spinal process; anterior tip of the spine is broken.

Cervical vertebrae (Text-fig. 1: 15) have relatively long and broad hypapophysis in lateral view. Parapophyses are provided with distinct parapophyseal process, directed forward. Neural spine as high as long. Zygosphene concave from above.

Several hundred trunk vertebrae, composing a majority of the material, for the most part belonged to snakes of small size (Text-fig. 1: 6–11). As typical for snakes, vertebrae of younger specimens are relatively longer, prezygapophyseal processes more slender and their neural canal of relatively larger diameter. Besides, all trunk vertebrae closely resemble the holotype in their morphology except the shape of zygosphenal roof that shows allometric variability. In smaller specimens the zygosphene is convex in dorsal view, but in larger ones the central convexity diminishes; consequently, in the largest specimens the zygosphene is straight or (usually) slightly concave, rarely provided with a small median tubercle. Anterior edge of the neural spine, lacking in the holotype, is vertical or slightly overhanging.

Posterior trunk vertebrae differs from those of the middle of the column in having a heavy-built haemal keel, sometimes of strongly flattened ventral edge.

Cloacal vertebrae have not been found. Some caudal vertebrae (Text-fig. 1:16) have been provisionally classified to this form, their taxonomic attachment however remains unclear.

Table 2 shows measurements and ratios of a sample composed of 20 biggest mid-trunk vertebrae, including the holotype.

Comparisons: Comparison of the discussed remains with other living and Neogene European colubrids reveals that the snake from Kohfidisch is most similar to two closely related species, namely recent *Elaphe longissima* and extinct

Table 2. Measurements and ratios of trunk vertebrae of *Elaphe kohfidischi* sp. nov. (N = 20)

	OR	$\bar{X} \pm SD$
PR–PO	6.91 – 8.53	
CL	5.83 – 7.31	
PO–PO	7.62 – 10.47	
NAW	4.41 – 6.19	
ZW	3.71 – 4.47	
CTH	2.31 – 3.17	
CTW	2.41 – 3.09	
PR–PR	7.72 – 10.92	
CL/NAW	1.18 – 1.45	1.29 ± 0.08
PO–PO/NAW	1.56 – 1.97	1.78 ± 0.10
CTW/CTH	0.93 – 1.16	1.03 ± 0.06
ZW/NAW	0.72 – 0.90	0.82 ± 0.05
PR–PR/PR–PO	1.09 – 1.32	1.20 ± 0.07
CL/ZW	1.38 – 1.72	1.58 ± 0.10
PR–PR/NAW	1.61 – 2.05	1.80 ± 0.09

OR – observed range, $\bar{X}$ – mean, SD – standard deviation. For explanation of measurements see Table 1.

E. paralongissima. Basic differences among these three species are explicated below. Comparisons of *E. kohfidischi* with other snakes ate omitted; differentiating criteria of colubrid vertebrae can be found in RAGE (1984) with reference to extinct species and in SZYNDLAR (1984) with reference to living forms.

Cervical vertebrae of *E. kohfidischi* are characterized by a relatively low neural spine, approximately as high as long, similar to *E. paralongissima* and unlike *E. longissima* (including Early Pleistocene fossils from Poland) in which this structure is usually much higher than ong; both *E. kohfidischi* and *E. paralongissima* have also distinct parapophyseal processes unlike *E. longissima.* In trunk vertebrae, para- and diapophyses of *E. kohfidischi* are of similar length as in *E. longissima,* while in *E. paralongissima* diapophysis is two times shorter than parapophysis. Haemal keel of *E. kohfidischi* is somewhat similar in shape to that of *E. longissima*, although distinctly higher and thinner; the keel of *E. paralongissima* is strongly flattened and widening posteriorly. Zygosphene of trunk vertebrae of *E. kohfidischi* shows different pattern of allometric variability than in *E. longissima*, since smaller specimens of the latter form have rather crenate than convex (central lobe narrower) zygosphenal roof and in large specimens it is generally straight and not provided with distinct lobes; allometric variability of this structure in *E. paralongissima* is unknown.

Relative elongation of the vertebrae of *E. kohfidischi* seems also to be of taxonomic importance. As shown by SZYNDLAR (1984) on the basis of numerous measurements the centrum length/width ratio (CL/NAW) of the largest vertebrae of *E. longissima* from various Quaternary localities fluctuates about the value 1.15 (similarly in *E. paralongissima*), while in specimens of *E. kohfidischi* (of similar size as the former forms) this ratio is much higher (1.29 on average).

Comments: *Elaphe longissima, E. paralongissima* and *E. kohfidischi,* coming from geographically close territories, may represent an interesting example of evolutionary differentiation. *E. longissima,* presently inhabiting South and Central Europe including Austria, has been also reported from numerous fossil localities (cf. SZYNDLAR 1984, and references therein). *E. paralongissima* is known only from the type locality, i. e. Upper Pliocene (MN 16) of Węże II in Southern Poland (SZYNDLAR 1984; SZYNDLAR in MŁYNARSKI & al., in press). Some problems concerning relationsphips within these three species could be perhaps revealed after thorough examination of remains of other probably related forms coming from nearby areas, namely presumed *E. longissima* reported from the Uppermost Miocene (MN 13) of Polgárdi and Upper Pliocene (MN 16) of Beremend in Hungary (SZUNYOGHY 1932). The remains from the former locality, although identified by SZUNYOGHY (supra cit.) as just belonging to *E. longissima,* may have represented a distinct form as originally assigned by BOLKAY (1913), i. e. *E. kormosi* (BOLKAY) (cf. RAGE 1984). Unfortunately, vertebrae of these snakes have never been described and no recent revision of the ancient descriptions is available.

Nanus gen. nov.

Type species (by monotypy): *Nanus planicarinatus* sp. nov.

Name derivation: From Latin nanus – dwarf.

Diagnosis: As for the type-species.

Nanus planicarinatus sp. nov.

(Text-fig. 1: 17–22; pl. 1: Figs 4–6)

Holotype: A trunk vertebra (Naturhist. Mus. Wien, Geol.-Paläont. Abt., No. 1984/97).

Referred material: 6 trunk vertebrae.

Name derivation: From Latin planus – flat and carina – keel: planicarinatus – having flattened haemal keel.

Diagnosis: A small-sized colubrid snake differing from living European and fossil Holarctic snakes by having mid-trunk vertebrae provided with (1) very broad and flat haemal keel; (2) indistinct subcentral grooves; (3) underdeveloped subcentral ridges; (4) minute paradiapophyses.

Description of holotype (Text-fig. 1: 17–21, pl. 1: Figs. 4–6): A small-sized vertebra from the middle of the column. Centrum relatively long, somewhat cylindrical in ventral view. Haemal keel cuneate-shaped, extending from the cotyle lip posteriorly to near the condyle where it is not well defined, flattened and strongly broadened. Subcentral ridges (margo inferior) underdeveloped; subcentral grooves indistinct, restricted to the anteriormost portion of the centrum. Subcentral foramina minute, hardly visible. Neural arch elongate, weakly vaulted.

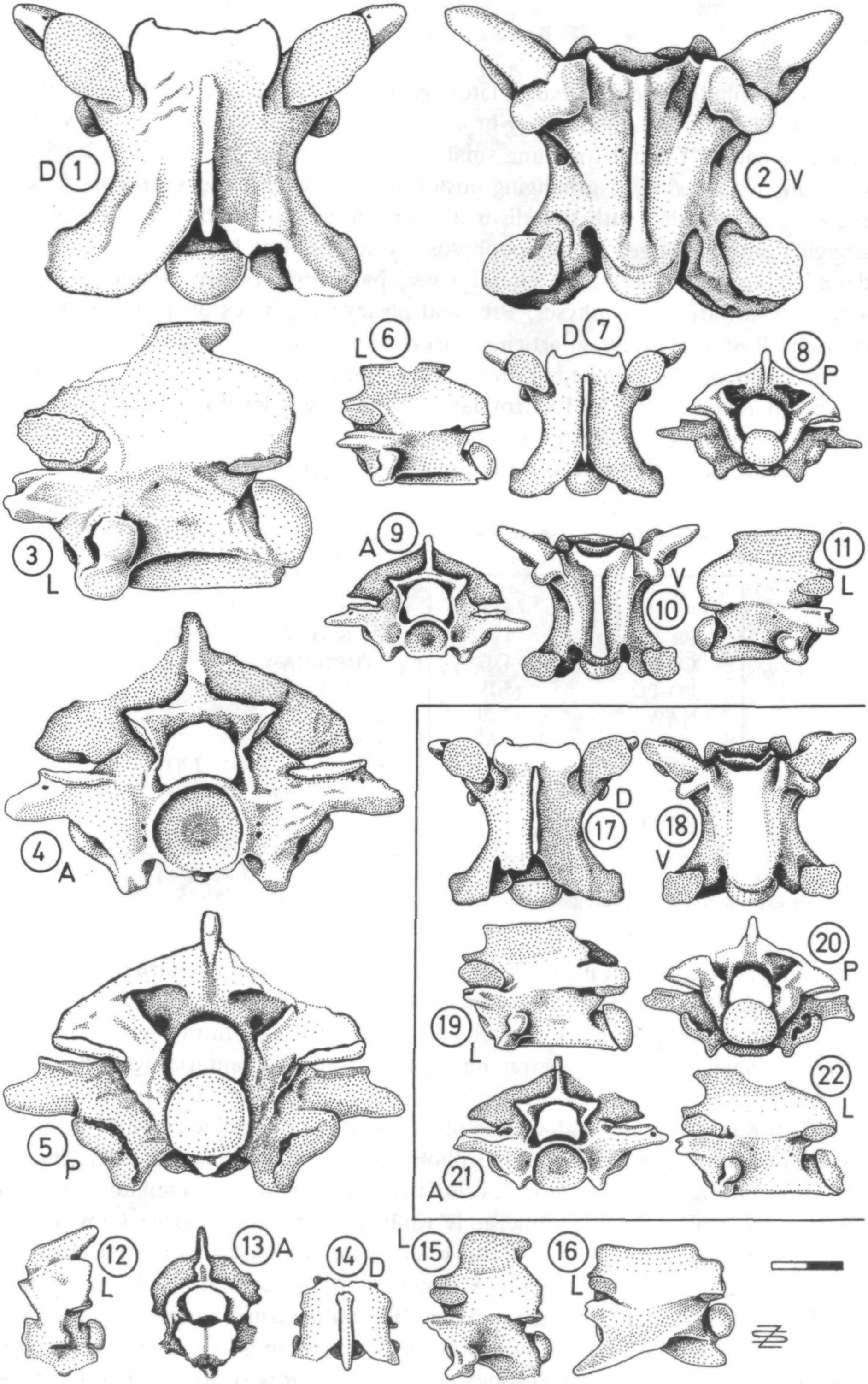


Fig. 1. 1–16. *Elaphe kohfidischi* sp. nov. – 1–5. holotype trunk vertebra (No. 1984/96), 6–10. trunk vertebra of a small specimen (No. 1984/101/1), 11. trunk vertebra of a small specimen (No. 1984/101/2), 12–14. axis (No. 1984/101/3), 15. cervical vertebra (No. 1984/101/4), 16. posterior caudal vertebra (No. 1984/101/5); 17–22. *Nanus planicarinatus* gen. sp. nov. – 17–21. holotype trunk vertebra (No. 1984/97), 22. trunk vertebra (No. 1984/102/1). A – anterior, D – dorsal, L – lateral, P – posterior, V – ventral views. Scale equals 2 mm.

Interzygapophyseal ridges (margo lateralis) moderate, parallel to the axis of the centrum. Neural canal moderately broad and high, of similar width as the slightly flattened cotyle. Lateral foramina small, but well visible. Neural spine long and very low, with slightly overhanging posterior and anterior edges. In dorsal view, zygosphene provided with two distinct lateral lobes and slightly convex (almost straight) anterior edge. Paradiapophyses (synapophyses) minute, with two well definded articular facets. In lateral view, parapophyses are distinctly shifted anteriorly towards diapophyses. Pre- and postzygapophyses distinctly projecting laterally. Postzygapophyseal articular facets square-shaped. Prezygapophyseal articular facets obovate-shaped. Prezygapophyseal processes (accessory processes) short and relatively thick. Paracotylar foramina well developed. Condyle on a moderately long neck, directed upwards.

Measurements and ratios of the holotype are given in Table 3.

Table 3. Measurements and ratios of holotype trunk vertebra of *Nanus planicarinatus* gen. sp. nov.

$PR–PO_{(L)}$	4.85		
$PR–PO_{(R)}$	4.96	CL/NAW	1.44
CL	4.03	PO–PO/NAW	1.86
PO–PO	5.19	CTW/CTH	1.07
NAW	2.79	ZW/NAW	0.94
ZW	2.63	PR–PR/PR–PO	1.18
CTH	1.64	CL/ZW	1.53
CTW	1.75	PR–PR/NAW	2.07
PR–PR	5.77		

For explanation of measurements see Table 1.

Description of remaining material: Few remaining trunk vertebrae do not differ significantly from the holotype. Some vertebrae have their neural spines provided with stronger anterior overhang (Text-fig. 1: 22). In two posterior trunk vertebrae haemal keel is a better defined than in more anterior vertebrae and subcentral grooves are deep and distinct throughout the centrum length.

Comparisons: Several species of small-sized Colubridae presently inhabiting Europe have their vertebrae morphologically similar to one another, characterized in all the forms by poor development of haemal keel, crenate or convex shape of zygosphenal roof, moderately vaulted neural arch and very low neural spine. The above remarks concern trunk vertebrae; well defined differences can be observed in axes, unfortunately there is no axis among the Kohfidisch remains that could be referred to the genus erected here. Regarding trunk vertebrae, morphology of ventral surface of the centrum seems to bear most important taxonomic information. Haemal keel of European small colubrids is always relatively narrow (although often hardly visible) except *Coluber najadum* (including its subspecies *rubriceps* sometimes regarded as a distinct species), however, even in the latter form this structure is distinctly narrower than in *Nanus*. Moreover, except the genus *Coronella*, all remaining colubrids presently inhabiting Europe have well defined subcentral grooves, the condition not observed in *Nanus*. In morphology of the ventral side of its centrum, especially in the shape of the haemal keel, *Nanus* is somewhat similar to *Texasophis meini* RAGE & HOLMAN (1984), recently described from the French Middle Miocene (MN 7 and 8). The latter form, however, is characterized by well developed subcentral grooves and subcentral ridges (generic features – cf. HOLMAN 1977), not observed in *Nanus*. Another characteristic feature of the Austrian form are minute paradiapophyses, distinctly smaller than homologous structures observed in all forms discussed above.

Comments: Taxonomic position of this minute snake from Kohfidisch, considering morphological distinction of its vertebrae and scarcity of the examined material, remains unclear. The form can be referred to the artificial subfamily Colubrinae s. l. (Colubridae without hypapophyses on trunk vertebrae), but it is unrealisable to indicate clearly features of relationship of this snake with other colubrid genera.

Natrix longivertebrata SZYNDLAR, 1984
(Text-fig. 2)

Material: 15 precaudal vertebrae.

Vertebrae of this extinct species, found among the Kohfidisch material, closely resemble those of *Natrix longivertebrata* coming from the type-locality, Upper Pliocene (MN 16) of Rębielice Królewskie I in Poland.

In the trunk vertebrae (Text-fig. 2: 1–5) all diagnostic features of the species

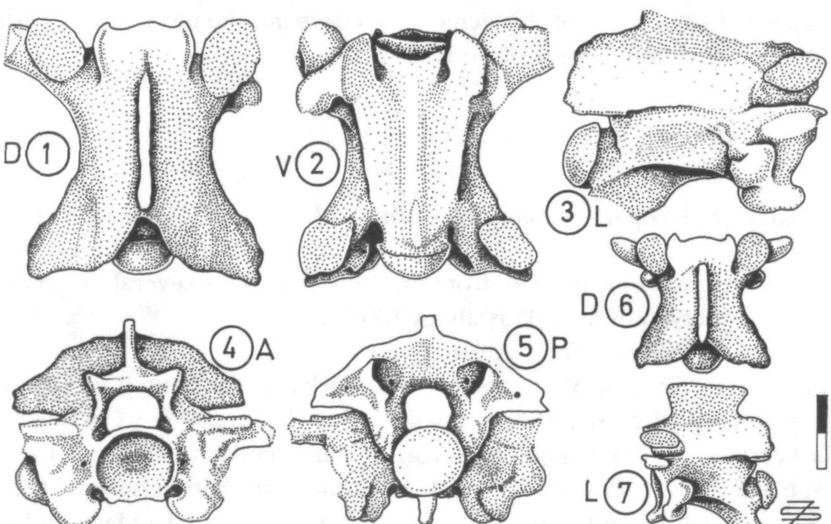


Fig. 2. Vertebrae of *Natrix longivertebrata* SZYNDLAR. – 1–5. Trunk vertebra (No. 1984/103/1), 6, 7 – cervical vertebra (No. 1984/103/2). A – anterior, D – dorsal, L – lateral, P – posterior, V – ventral views. Scale equals 2 mm.

can be seen (cf. SZYNDLAR 1984: p. 72). Centrum is usually strongly elongate; in one specimen its length/width ratio exceeds value 2.00. Neural arch is weakly vaulted. Neural spine, preserved in only two specimens, is relatively low, with prominent anterior overhang and its dorsal edge sloping posteriorly. Hypapophysis, if present, is sigmoid-shaped with relatively long ventral edge. Parapophyseal process strongly developed, projecting distinctly outside the cotyle lip. Subcentral ridges well developed. Also a single cervical vertebra (Text-fig. 2: 6, 7) does not differs significantly from those known from the type-locality.

Remains of this form have been also found in some other Neogene sites: Upper Pliocene (MN 16) of Rębielice Królewskie II, Late/Upper Pliocene (MN 15–16) of Węże I, and Upper Pliocene (MN 16) of Węże II in Poland (SZYNDLAR 1984; SZYNDLAR in MŁYNARSKI & al., 1985) as well as Middle Miocene (MN 7) of La Grive L7 in France (RAGE & SZYNDLAR, in press). All these forms, because of some morphological differences, have been classified as *Natrix* cf. or aff. *longivertebrata*. The snake from Kohfidisch, as clearly seen from the preserved bones, seems to be more similar to the type material than those from all remaining localities.

Family Elapidae

Remains of a large-sized elapid dominate among the ophidian material from Kohfidisch. The remains represent a member of the so-called "*Naja*-group", including the recent genus *Naja* and extinct genus *Palaeonaja* (see comments for details). Comparison with both recent and fossil West Palearctic cobras reveals that the Kohfidisch fossils belonged to a distinct form, well differentiated from other known species. It is described here as a new species of the genus *Naja*. Nevertheless, because of similarities of this genus to *Palaeonaja*, the newly erected form is compared below with members of both genera.

***Naja austriaca* sp. nov.**

(Text-figs 3–5, pl. 1: Figs 7–9, pl. 2: Figs 10–13)

Holotype: Basiparasphenoid (Naturhist. Mus. Wien, Geol.-Paläont. Abt., No. 1984/98).

Referred material: Two frontals, four maxillae, several fragments of dentaries and pterygoids as well as about 1000 vertebrae.

Name derivation: From Austria.

Diagnosis: Typical *Naja* characterized by basiparasphenoid provided with prominent pterygoid crests, Vidian canal leaving this bone on its external side, maxilla bearing two non-venomous teeth, dentary similar to those of the allied species, frontals short, as well as strongly built and very short vertebrae, the latter bearing prominent subcentral ridges, long hypapophysis, broad and vaulted neural arch, low neural spine, straight zygosphene from above, paradiapophyses provided with short and robust parapophyseal processes, and long prezygapophyseal processes.

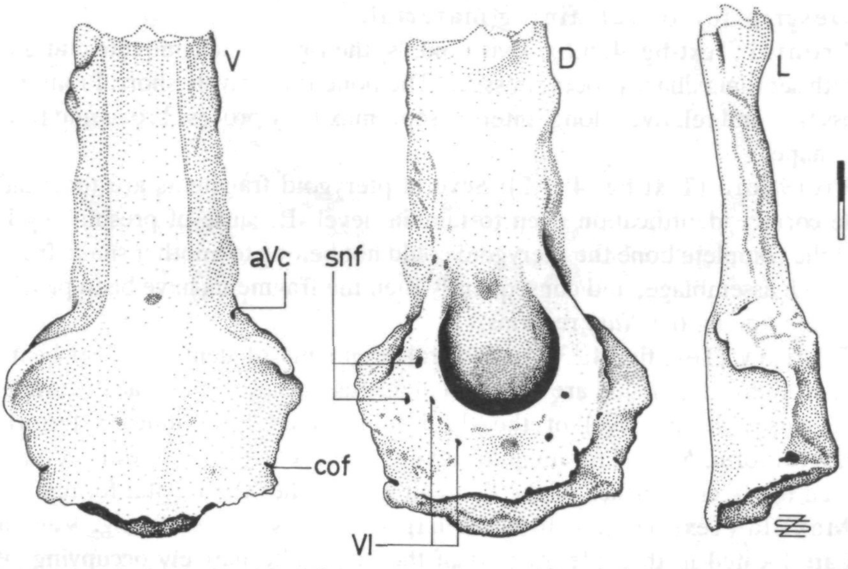


Fig. 3. Holotype basiparasphenoid of *Naja austriaca* sp. n. – Abbreviations: aVc – anterior orifice of Vidian canal, cof – common foramen, snf – sympathetic nerve foramina, VI – abducens nerve foramina. D – dorsal, L – lateral, V – ventral views. Scale equals 2 mm. (No. 1984/98).

Differentiating-diagnosis: *Naja austriaca* differs from other species of the genera *Naja* and *Palaeonaja* in the following individual features – lack of a common depression for nerve foramina on dorsal side of the basiparasphenoid; round-shaped pituitary fossa; atlas provided with depressed odontoid process and very short posterior intercentrum; directed laterally epizygaphophyseal processes of the 3rd vertebra; concave zygosphene in cervical vertebrae.

Description of holotype (Text-fig. 3, pl. 1: Figs 7, 8): The bone is heavy built, not arched in lateral view. Parasphenoid portion of the bone (parasphenoid process) missing at the level of the frontal step, the latter structure located behind suborbital flanges. Basipterygoid processes well developed, provided with strong pterygoid crests*). Basisphenoid crest weakly defined. Posterior border of the bone provided with a small central lobe. Common foramen located on the lateral margin of the bone, near its postero-lateral corner; location of the foramen indicates that carotid artery (accompanied by the palatine branch of the facial nerve) entered into the braincase between the basiparasphenoid and prootic as typical for the family Elapidae. Anterior orifice of Vidian canal situated immediately before the pterygoid crest on the lateral border of the bone. Pituitary fossa of regularly round shape. Sympathetic nerve foramina and anterior orifices of abducens nerves on the dorsal side of the bone not located in common depressions as typical for other elapids and most snakes in general, but directly on a flat surface laterally to the pituitary fossa. Sympathetic nerves did not leave the bone by lateral notches, but by individual (posterior) foramina. Right (anterior) sympathetic nerve foramen absent.

*) The term pterygoid crest used here means a lamina surmounting the basipterygoid process.

Description of remaining material:

Frontal (Text-fig. 4: 5,6): Two frontals, the right bone complete and the left one with septomaxillary process missing. The bone is relatively short. Premaxillary process thin and relatively long, internal septomaxillary process broad and triangular in shape.

Pterygoid (Text-fig. 4: 1,2): Several pterygoid fragments are too small to enable correct identification even to familial level. Because of presumably large size of the complete bone the pterygoid could not belong to another snake from the Kohfidisch assemblage, and consequently then the fragments have been provisionally placed among the *Naja* remains.

Dentary (Text-fig. 4: 3, 4): Several fragments of dentaries also bear low taxonomic information and are deprived of any useful specific characters. Meckel's groove closes at the level of the third tooth, but it continues anteriorly in symphyseal form. Mental foramen located at the level of the 6th tooth. Compound notch on the lateral surface of the bone almost reaches the mental foramen.

Maxilla (Text-fig. 4: 7–10): The largest bone is 12.5 mm long. Venomous fangs are located in the anterior part of the bone, alternatively occupying either inner or outer tooth-sockets. The only completely preserved fang (length ca. 7 mm) on a fragmentary maxilla is provided with a continous groove throughout its anterior surface. Posteriorly, the bone has two non-venomous teeth (or tooth-sockets). The basic feature well differentiating the Kohfidisch cobra from some other species is a plane lamina covering dorsally the prefrontal process. The lamina, being a part of articular surface for the ventral end of the prefrontal, is relatively large and shifted far forwards. Prefrontal process of *N. austriaca* is developed as in other cobras. Ectopterygoid process is relatively narrow at its base, occupying the space between both non-venomous teeth.

Among numerous vertebrae there are elements coming from almost all regions of the vertebral column. Most vertebrae, similarly to cranial elements, belonged to large-sized snakes.

Atlas remains unknown. A single axis is preserved in perfect state except missing transverse processes (Text-fig. 5: 7, 8). Odontoid process is flattened anteriorly, posterior intercentrum (hypapophysis) is very short, robust and posteriorly not protruding outside the condyle neck. Upper portion of the neural spine produced into distinct anterior and posterior expansions; tips of these expansions are obtuse.

The 3rd vertebra, following the axis, has postero-lateral corners of its neural arch produced into long and tapering epizygapophyseal spines directed aside; consequently, the neural arch has the shape of an equilateral triangle in dorsal view. In succeeding cervical vertebrae (Text-fig. 5: 9) the spines diminish. Similarly to recent *Naja* in anteriormost vertebrae paradiapophyses are strongly expanded laterally and their upper portions (diapophyses) protrude aside to the level of outer margins of the prezygapophyseal articular facets. Parapophyseal processes of cervical vertebrae are small and usually directed downwards. Hypapophysis is broad and rounded distally in lateral view, in more anterior vertebrae it is directed

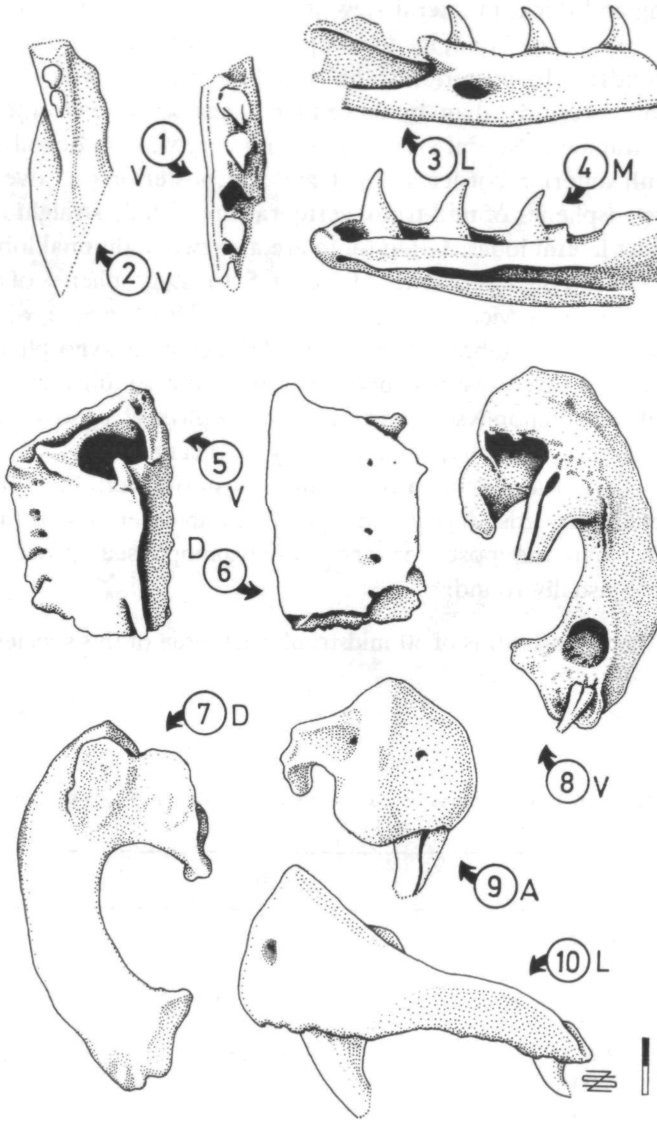


Fig. 4. Cranial bones of *Naja austriaca* sp. n. – 1 and 2. pterygoid fragments (No. 1984/104/1 and 2), 3, 4 – right compound bone (No. 1984/104/3), 5, 6. right frontal (No. 1984/104/4), 7–10. left maxilla (No. 1984/99). A – anterior, D – dorsal, L – lateral, M – medial, V – ventral views. Scale equals 2 mm.

downwards not postero-ventrally. Neural spine is relatively low. Prezygapophyseal processes are well developed in post-axial vertebrae and therefore well seen from above.

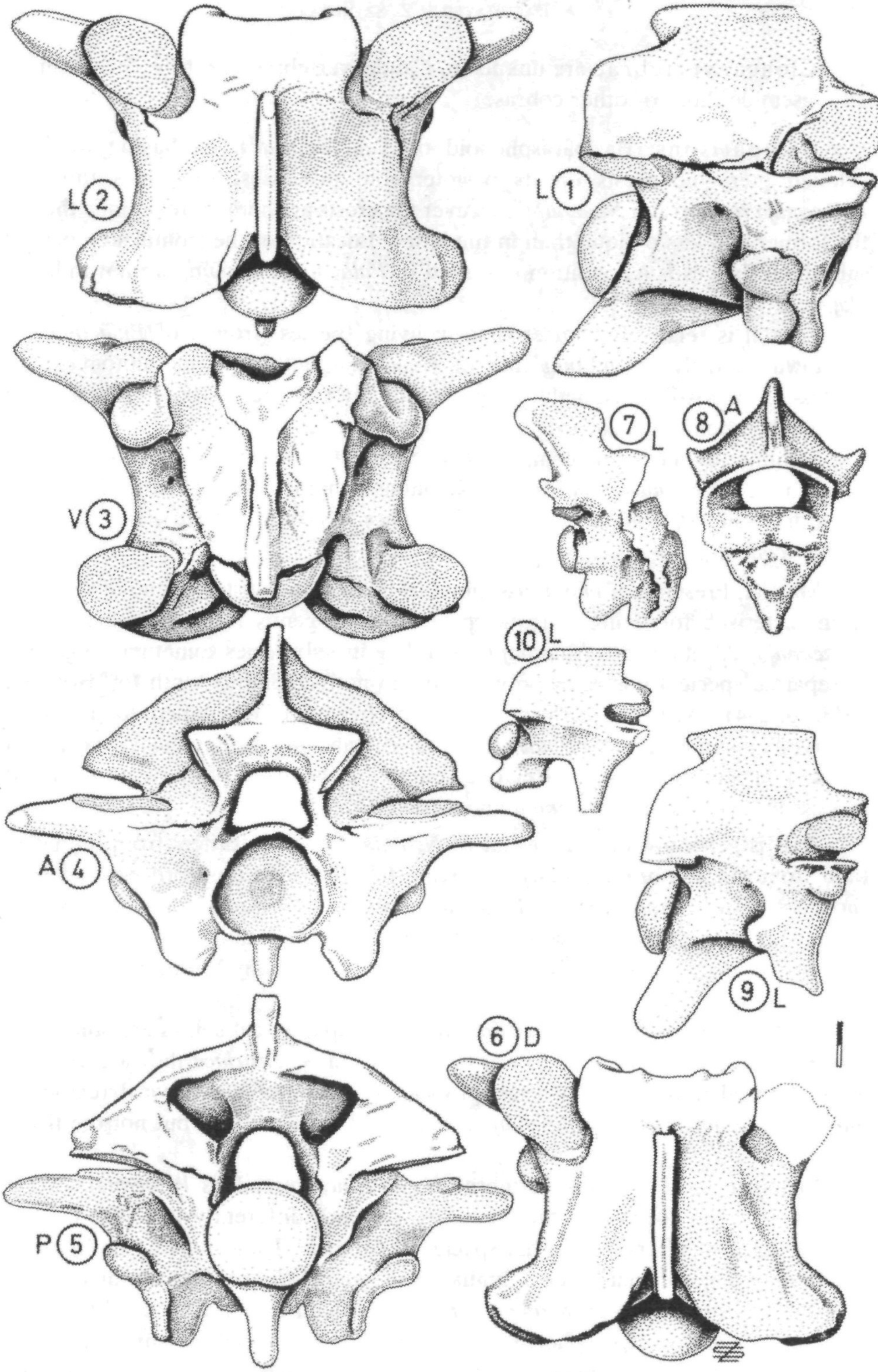
T r u n k v e r t e b r a e (Text-fig. 5: 1–5) are strongly built and relatively short; their centra distinctly wider than long. The centrum, limited laterally by strong subcentral ridges, is triangular from below, with slightly concave surface. Hypapophysis long and thick, in lateral view straight and broad, with its ventral edge parallel to the axis of the bone; its distal tip blunt, projecting posteriorly distinctly behind the condyle. In posterior trunk vertebrae hypapophyses are, however, more inclined posteriorly than in preceding bones, moreover, their distal tips become more rounded. Neural arch vaulted and very wide in dorsal view. Neural spine low, with anterior border straight and the posterior one overhanging. In dorsal view, zygosphenes of mid-trunk vertebrae are usually straight and provided with two distinct lateral lobes. Often there are also two additional lobes of minute size situated between the lateral ones (Text-fig. 5: 6). Zygosphenes of anteriormost precaudal vertebrae (cervical) are usually concave from above with no lateral lobes, but in posterior vertebrae of the precaudal region the zygosphene is crenate, i. e. provided with three distinct lobes. Paradiapophyses distinctly divided into parapophyseal and diapophyseal portions. Parapophyseal process short and robust, directed antero-ventrally, then similarly to recent species and unlike other fossil species where it looks forwards; in more posterior vertebrae parapophyseal process directed forwards. Zygapophyseal articular facets oval, these anterior more elongate than the posterior ones. Prezygapophyseal processes well developed. Cotyle usually round.

Measurements and ratios of 30 mid-trunk vertebrae of this species are given in Table 4.

Table 4. Measurements and ratios of trunk vertebrae of *Naja austriaca* sp. nov. (N = 30)

	OR	$\bar{X} \pm SD$
PR–PO	9.80–12.73	
CL	9.53–10.80	
PO–PO	14.70–17.03	
NAW	10.46–12.30	
ZW	6.63– 8.86	
CTH	4.09– 5.66	
CTW	4.22– 5.08	
PR–PR	14.85–16.82	
CL/NAW	0.82– 0.99	0.90 ± 0.04
PO–PO/NAW	1.33– 1.55	1.43 ± 0.04
CTW/CTH	0.83– 1.10	0.98 ± 0.06
ZW/NAW	0.61– 0.75	0.69 ± 0.03
PR–PR/PR–PO	1.26– 1.62	1.37 ± 0.08
CL/ZW	1.22– 1.41	1.31 ± 0.06
PR–PR/NAW	1.33– 1.54	1.43 ± 0.05

OR – observed range, $\bar{X}$ – mean, SD – standard deviation. For explanation of measurements see Table 1.



g. 5. Vertebrae of *Naja austriaca* sp. n. – 1–5. trunk vertebra (No. 1984/105/1), 6. trunk vertebra (No. 34/105/2), 7, 8. axis (No. 1984/105/3), 9. cervical vertebra (No. 1984/105/4), 10. anterior caudal tebra (No. 1984/105/5). A – anterior, D – dorsal, L – lateral, P – posterior, V – ventral views. Scale equals 2 mm.

Cloacal vertebrae are unknown. Caudal vertebrae (Text-fig. 5: 10) generally resemble those of other cobras.

Comparisons: Basiparasphenoid of *Naja austriaca,* by having well developed pterygoid crests on its basipterygoid processes, resembles those of *Palaeonaja romani* and *Naja naja*, however the crests are here more oblique than in the former and less oblique than in the latter. Location of the frontal step behind suborbital flanges is a condition observed in *Palaeonaja romani* and not in living *Naja.*

Frontal is relatively shorter than in living species (frontal of *Palaeonaja* is unknown), mostly resembling that of *Naja naja,* although the septomaxillary process of the fossil is distinctly longer and the internal premaxillary process much shorter than homologous structures in living species.

Dentary, by having its compound notch situated near the mental foramen, is similar to that of *Palaeonaja romani.* Remaining characters are identically defined in both fossil *(P. romani)* and living species of cobras *(Naja naja, N. haje, N. nigricollis).*

Maxilla. Presence of two non-venomous teeth at the posterior end of the bone is characteristic for living African species of the genus *Naja* as well as fossil *Palaeonaja;* Asiatic cobra *Naja naja* (including its subspecies sometimes regarded as separate species) possesses only one or no non-venomous tooth (cf. BOGERT, 1943: p. 294). Articular surface for the prefrontal is developed to a degree observed only in *N. naja;* in *Palaeonaja* and African *Naja* the lamella is smaller and situated farther posteriorly. Relative length of the base of the ectopterygoid process in less than in *Palaeonaja* and African *Naja.*

Axis is generally similar to that of *N. naja,* however, differs from the latter (and from other cobras as well) by having flattened odontoid process and very short posterior hypapophysis (in *Palaeonaja romani* this structure is especially long and protrudes far behind the condyle). Moreover, anterior and posterior tips of the neural spine in the axis of *Naja naja* are acute, whereas in *N. austriaca* they are obtuse.

In the 3rd vertebra of recent *Naja* the epizygapophyseal spines are somewhat shorter and always directed backwards, whereas in *N. austriaca* they are directed aside. In well developed prezygapophyseal processes of the cervical region *N. austriaca* resembles fossil *Palaeonaja romani* and *Naja antiqua,* but not the living *Naja.*

In shortness of its trunk vertebrae *N. austriaca* resembles *Palaeonaja crassa* and *P. depereti,* however, other features are here differently developed. *Naja austriaca* clearly differs from other species of *Naja* and *Palaeonaja* in the shape of the anterior zygosphenal border. Similar as in *Naja austriaca* intracolumnar variation can be observed in *Palaeonaja romani,* although its cervical vertebrae have crenate not concave zygosphenes. In recent *Naja* the vertebrae throughout the column have their zygosphenes distinctly crenate. Zygosphenes of *Palaeonaja crassa* and *P. depereti* (both forms known only from mid-trunk vertebrae) are not provided with lateral lobes. Also hypapophysis of *Naja austriaca* seems to be relatively longer and directed posteriorly to a lesser degree than in other species. Neural spines, including the spines of cervical vertebrae, are relatively lower than in other cobras. Prezygapophyseal processes are much longer than in other species of *Naja* and *Palaeonaja* except *P. romani.*

Comparison of vertebral size of *Naja austriaca* with dimensions of complete skeletons of living *N. naja* shows that total length of the greatest specimens from Kohfidisch could reach 270 cm. It should be mentioned here that for fossil *Palaeonaja,* HOFFSTETTER (1939) estimated smaller dimensions despite larger size of their vertebrae; HOFFSTETTER's method of this calculation were not disclosed.

Comments. The elapid remains described above are a first fossil find of cobras in Central Europe. Previous descriptions of these snakes from the area of Western Palearctica were restricted to the Mediterranean region. Except *Naja antiqua* RAGE (1976) from the Middle Miocene (MN 7) of Beni Mellal in Morocco and *Naja* sp. from the Middle Pleistocene of Chios in the Aegean Sea (SCHNEIDER 1975), all remaining fossils were attributed to an extinct genus, *Palaeonaja* HOFFSTETTER (1939). The type-species of the latter genus, *P. romani* HOFFSTETTER (1939) from the Middle Miocene (MN 7–8) of La Grive–St. Alban, France, was described on the basis of an almost complete skeleton, therefore it was possible to compare this form in detail with living members of the genus *Naja.* Based exclusively on trunk vertebrae, HOFFSTETTER (supra cit.) gave also descriptions of another two other species of *Palaeonaja* from France: *P. crassa,* a sympatric form with the type-species and *P. depereti* from the Middle Pliocene (MN 15) of Perpignan. Presence of this genus was reported later from some other South European sites.

Taxonomic distinction of the genus *Palaeonaja* was questioned by BOGERT (1943) who considered intergeneric differences between *Naja* and *Palaeonaja* not to be greater than interspecific differences among particular members of the living genus *Naja.* Although taxonomic validity of the genus *Palaeonaja* has been widely accepted by later students, HOFFSTETTER's (1939, passim) prescription enabling explicit separation of the two genera is not satisfactory. According to RAGE (1984; pers. comm., 1984) the most important diagnostic features of *Palaeonaja* are less height of prefrontal and less length of dentary in comparison with *Naja.* In our case these criteria obviously cannot be applied because of lack of prefrontal and complete mandible in the Kohfidisch material.

Indeed, the elapid remains described in the present paper are characterized by a mixture of features found also in recent *Naja* and fossil *Palaeonaja.* By presence of two non-venomous teeth on its maxilla *Naja austriaca* resembles both *Palaeonaja romani* and African living members of the genus *Naja.* On the other hand, in morphology of its basiparasphenoid the species from Kohfidisch is similar enough to *Palaeonaja romani* and *Naja naja,* but differs from the African cobras. The maxillary dentition, however, is rather an indication of the more primitive state of this character in European fossils in comparison with *Naja naja* than it is evidence of their close relationship with African forms (as stated by BOGERT 1943: p. 294, with reference to *Palaeonaja romani*). Some problems concerning taxonomy of

European cobras will be solved after examination of abundant elapid remains from the Uppermost Miocene (MN 13) of Algora in Spain (SZYNDLAR, in press).

Family Viperidae

Vipera sp. (= *Daboia* sp.)

(Text-fig. 6)

Material: one basioccipital and 71 precaudal vertebrae.

Basioccipital (Text-fig. 6: 9, 10) has subtriangular shape. Basioccipital tubercles underdeveloped. Basioccipital crest produced medially into a long and depressed laterally spur (basioccipital process). Medial crest absent. Occipitocondylar tubercle well developed, distinctly separated from the bone.

Precaudal vertebrae (Text-fig. 6: 1–8) have centra moderately long, cylindrical in ventral view. The centrum length of the largest vertebrae exceeds 7 mm. Hypapophyses strongly developed, long and straight in lateral view. Intracolumnar variation in the relative size of hypapophyses, when these are present on all precaudal vertebrae, appears to be distinct; those of cervical vertebrae (Text-fig. 6: 7) are much longer than those of mid-trunk vertebrae (Text-fig. 6: 6), while hypapophyses of posterior vertebrae (Text-fig. 6: 8) are extremely short. Subcentral grooves and subcentral ridges (margo inferior) present only in the anterior portion of the centrum. Neural arch strongly flattened and distinctly emarginated between the pre- and postzygapophyses. Neural spine thin, in anterior vertebrae much higher than long, slightly overhanging posteriorly; the spine in posterior trunk vertebrae distinctly longer than high. Zygapophyseal articular facets elongate laterally and square-shaped. Prezygapophyses are tilted sharply upward. Prezygapophyseal processes very short. Zygosphene distinctly convex from the front and crenate from above, with large lateral lobes and indistinct central lobe. Paradiapophyses well developed, provided with strong and acute-shaped parapophyseal processes, extending downwards. Cotyle strongly flattened. Condyle without a distinct neck. Lateral, subcentral and paracotylar foramina minute, but well visible.

Comparisons and comments: Viperid remains from Kohfidisch, considering the great dimensions and characteristic morphology of their vertebrae, in particular the relative length of the hypapophysis and neural spine, closely resemble large-sized members of the genus *Vipera*, expecially *V. xanthina* and *V. lebetina*. These and some other species are recently regarded as a distinct viperid genus, namely *Daboia* GRAY (cf. OBST 1983). From *V. russelli* the Kohfidisch form differs distinctly in having relatively lower neural spine and longer hypapophysis. Basioccipital of the Kohfidisch viper is very similar to that of *V. xanthina*, but has somewhat shorter basioccipital tubercle. Lack of skeletons of other species of the *Daboia* group at our disposal makes more precise identification of the Kohfidisch vipers impossible.

Present range of the species of the *Daboia* group is restricted to the areas outside Europe except some Aegean islands inhabited by *V. lebetina* and European

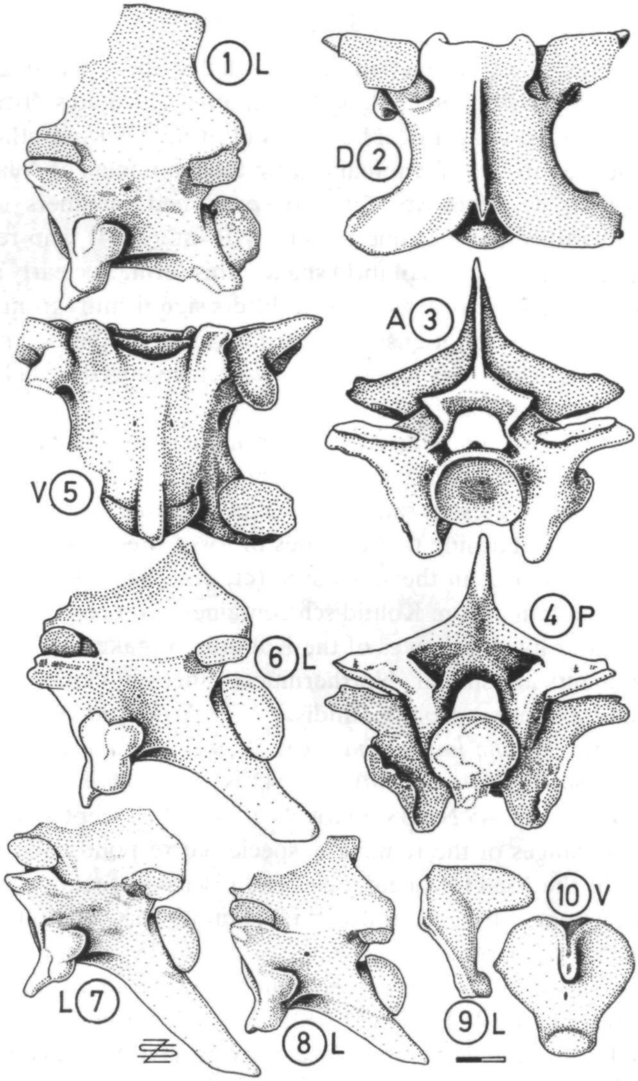


Fig. 6. *Vipera* sp. – 1–4. mid-trunk vertebra (No. 1984/106/1), 5–6. mid-trunk vertebra (No. 1984/106/2), 7. cervical vertebra (No. 1984/106/3), 8. posterior trunk vertebra (No. 1984/106/4), 9–10. basioccipital (No. 1984/106/5). A – anterior, D – dorsal, L – lateral, P – posterior, V – ventral views. Scale equals 2 mm.

territory of Turkey inhabited by *V. xanthina.* According to SAINT GIRONS (1979), during the Miocene and Pliocene ancestors of these large vipers ("grandes Vipéres plutôt meridionales") inhabited more extensive areas of our continent together with ancestors of remaining European species ("petits Vipéres plutôt septentrionalis"). Few fossils probably referable to the former group were previously reported from Miocene sites in Mediterranean countries. The present report is a first find of vipers belonging to the *Daboia* group from Central Europe.

Concluding remarks

As mentioned in the Introduction our knowledge about snakes of the Central European Neogene is still limited, thus this situation elucidates distinction of the Kohfidisch ophidian fauna against a background of faunas from other fossil sites. The only previous report of snake remains from the Pannonian of Austria, given by PAPP & al. (1954), describes vertebrae of presumed members of the family Aniliidae; this identification was questioned by RAGE (1974) who regarded these fossils as belonging actually to a colubrid snake. This form, as clearly seen from the figures (PAPP & al. 1954, pl. 6: Figs 23, 24), differs significantly from the colubrids of Kohfidisch. Other descriptions of Austrian fossil snakes concern younger localities and ophidian remains found there were recognized as belonging exclusively to living species (RABEDER 1974, 1977).

As shown by many authors, reptiles, including snakes, being ectothermic animals deriving their heat from the environment, are good indicators of past climates. Comparison of present ranges of snakes with their occurrence in the past usually enables us to determine that climates of fossil sites were either warmer or cooler than present climate in the same area (cf. e. g. SZYNDLAR 1984). Unfortunately, the ophidian fauna from Kohfidisch contained no recent species, nevertheless, we can consider living relatives of the Kohfidisch snakes, assuming that their thermal requirements are similar. Northernmost ranges of closest relatives of the three most numerous snakes from Kohfidisch (*Elaphe kohfidischi, Naja austriaca, Vipera* sp.) are: for *Elaphe longissima* – ca. 50°N (continuous range; SZYNDLAR, 1985), for *Naja naja* (or *Naja oxiana*) – ca. 42°N, for *Vipera lebetina* – ca. 43°N, and for *V. xanthina* – ca. 45°N (BANNIKOV & al. 1977). Except *Elaphe longissima* the northernmost ranges of the remaining species correspond with the latitude of the north coast of the Mediterranean Sea. The discussed snakes occur in various types of environments, but generally prefer rather dry habitats. The cobra, however, is said to be "extremely fond of water, and in the hot dry weather (. . .) is seldom found far from it" (SMITH 1943); similar behaviour is attributed to both species of vipers (ARNOLD & BURTON 1978). Thus, if environmental requirements of the fossil snakes resembled indeed those of living species, we can conclude that the site of Kohfidisch was characterized by warm climate of at least mediterranean type and relatively dry environment, but with presence of water reservoirs in its vicinity.

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Explanation of the plates

Plate 1

Fig. 1. *Elaphe kohfidischi* sp. nov., holotype trunk vertebra (Inv.-Nr. 1984/96), dorsal view, 5×.
Fig. 2. Ditto; ventral view, 5×.
Fig. 3. Ditto; lateral view, 5×.

Fig. 4. *Nanus planicarinatus* gen. sp. nov., holotype trunk vertebra (Inv.-Nr. 1984/97) dorsal view, 5×.
Fig. 5. Ditto; ventral view, 5×.
Fig. 6. Ditto; lateral view, 5×.

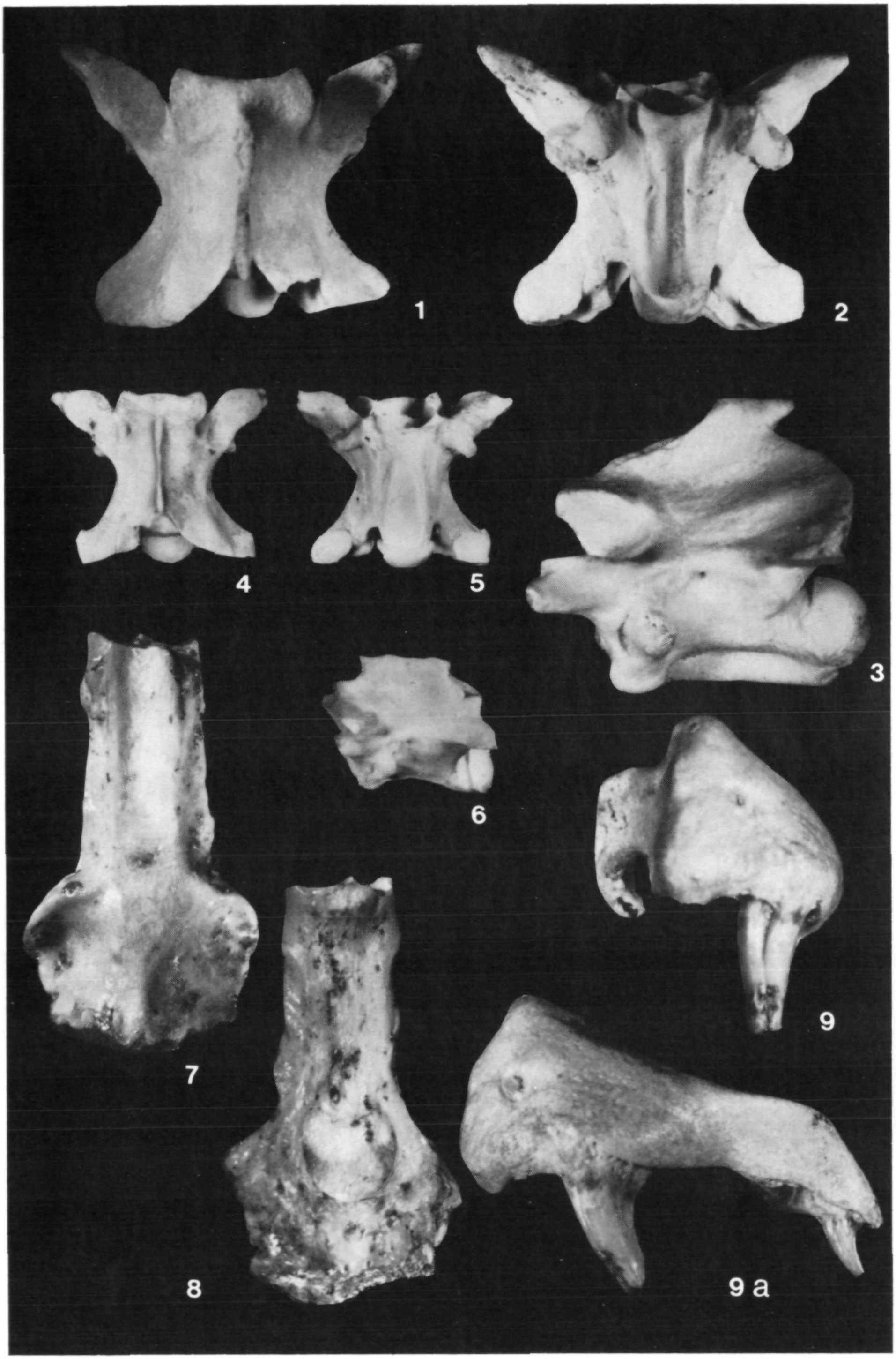
Fig. 7. *Naja austriaca* sp. nov., holotype basiparasphenoid (Inv.-Nr. 1984/98), ventral view, 5×.
Fig. 8. Ditto; dorsal view, 5×.

Fig. 9. *Naja austriaca* sp. nov., left maxilla, anterior view, 5×.
Fig. 9a. Ditto; lateral view, 5×.

Plate 2

Fig. 10. *Naja austriaca* sp. nov., left maxilla, anterior view, 4½×.
Fig. 11. *Naja austriaca* sp. nov., trunk vertebra, lateral view, 4×.
Fig. 12. Ditto; dorsal view, 4×.
Fig. 13. Ditto; anterior view, 4×.

All figured specimens are deposited in the Geologisch-Paläontologische Abteilung of the Naturhistorisches Museum in Wien.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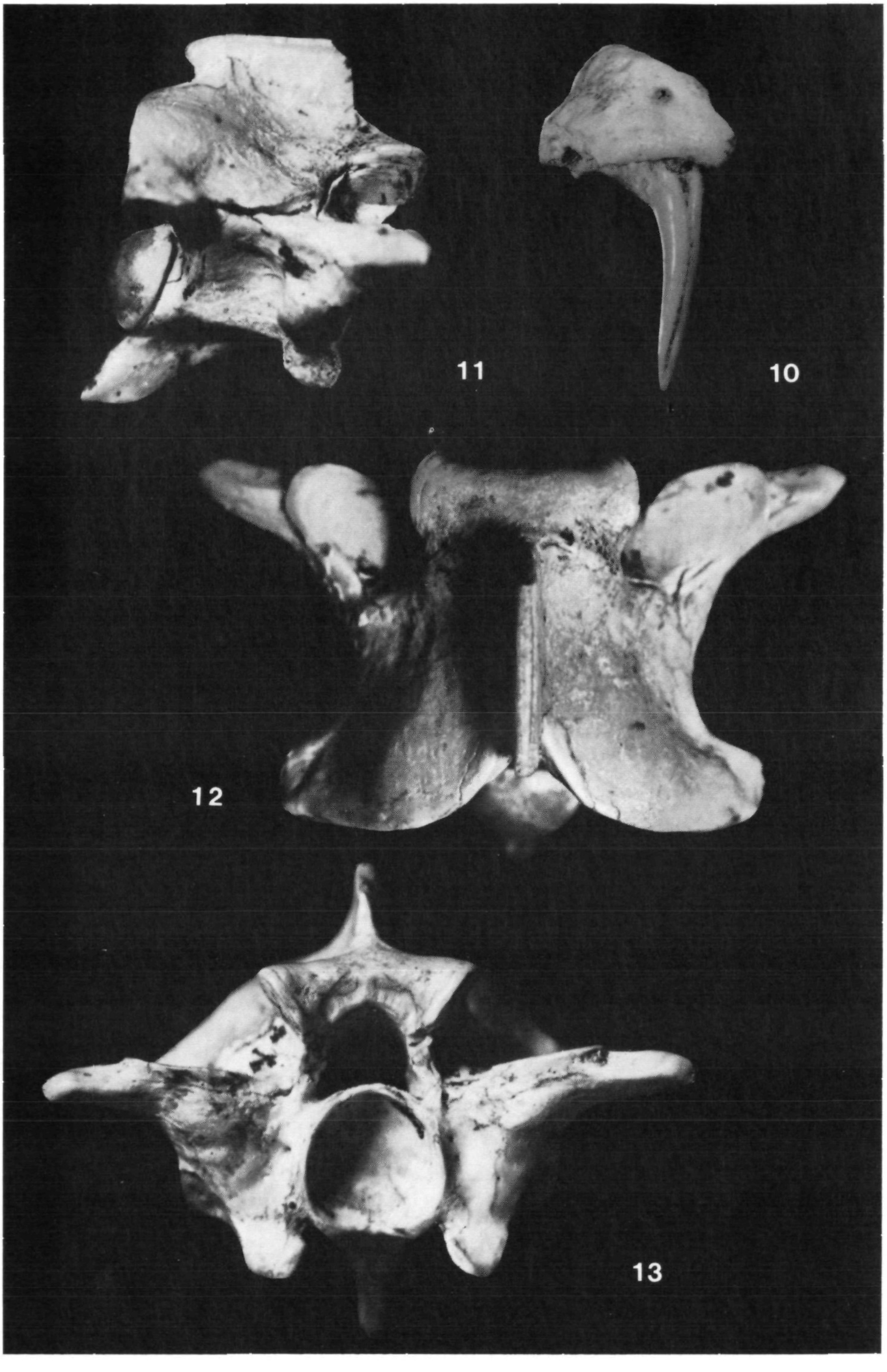
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