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GEOLOGIE UND PALÄONTOLOGIE

A second contribution to the ophidian fauna (Reptilia: Serpentes) of Kohfidisch, Austria Zweiter Beitrag zur Schlangenfauna (Reptilia: Serpentes) von Kohfidisch (Burgenland, Österreich)

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(Mit 1 Tafel und 6 Abbildungen im Text)

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Zusammenfassung

Die Arbeit ergänzt die frühere Bearbeitung von BACHMAYER & SZYNDLAR (1985) der obermiozänen (MN 11) Schlangen aus Kohfidisch (Burgenland, Österreich). Die hier beschriebenen neuen fossilen Materialien umfassen Schädelknochen der früher beschriebenen Schlangenarten: Elaphe kohfidischi, Coluber planicarinatus und Natrix longivertebrata (Colubridae), Naja austriaca (Elapidae), Vipera burgenlandica sp. n. (Viperidae).

Coluber planicarinatus, bisher beschrieben als Vertreter der Gattung Nanus, wird zum rezenten Genus Coluber gerechnet. Otternreste, die bisher nur bis zur Gattung bestimmt wurden, werden jetzt als neue Art Vipera burgenlandica n. sp. beschrieben.

Summary

This paper supplements the report of BACHMAYER & SZYNDLAR (1985) on Upper Miocene (MN 11) snakes from Kohfidisch (province of Burgenland, Austria). New fossil materials, reported in the present paper, consist of cranial elements belonging to formerly described ophidian species, namely Elaphe kohfidischi, Coluber planicarinatus and Natrix longivertebrata (Colubridae), Naja austriaca (Elapidae), and Vipera burgenlandica sp. n. (Viperidae).

Coluber planicarinatus, previously described as a member of the extinct genus Nanus, is reallocated into the recent genus Coluber. Viperid remains, previously identified to generic level only, are now described as a new extinct species, Vipera burgenlandica.

Introduction

The locality of Kohfidisch, bearing abundant remains of fossil vertebrates, is situated in the province of Burgenland, southeastern Austria. The age of the Kohfidisch fauna is Late Miocene (Mammalian stage – Lower Turolian; Mammalian European continental biozone MN 11; Pontian in Paratethyan terms).

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In our previous work on the snake fauna from this site (BACHMAYER & SZYNDLAR 1985) we recognized 5 different ophidian taxa: Elaphe kohfidischi, Nanus planicarinatus and Natrix longivertebrata of the family Colubridae, Naja austriaca of the Elapidae, and Vipera sp. of the Viperidae. The description of these forms was chiefly based on vertebrae. New fossil snake material from Kohfidisch, described below, consist exclusively of cranial bones belonging to all the previously recognized forms. Examination of these elements generally has confirmed the correctness of our previous determinations, although we have amended generic allocation of one of the snakes. The new material has also enabled the description of a new extinct species of Vipera, formerly identified to generic level only.

The entire material described in this paper is housed in the Geologisch-Paläontologischen Abteilung of the Naturhistorischen Museum in Vienna.

Acknowledgments. – We thank Dr. Göran Nilson (University of Göteborg) for the loan of skeletons of recent species of *Vipera*, used in the present study for comparative purposes. The material is the property of the Natural History Museum of Göteborg (abr. GNM).

Systematic description
Order Serpentes
Family Colubridae

Elaphe kohfidischi BACHMAYER & SZYNDLAR, 1985
(Text-fig. 1; pl. 1: Figs. 1, 2)

This species was described on the basis of several hundred vertebrae coming from various parts of the column. The holotype is one mid-trunk vertebra (No. 1984/96). The new material consists of several cranial bones: 3 basiparasphenoids, 1 fragmentary parietal, 2 basioccipitals, 1 fragmentary right dentary, 1 fragmentary left dentary, and 2 fragments of right maxilla(e).

Description:

Basiparasphenoid (Text-fig. 1: 1–4; pl. 1: Figs. 1, 2): The three basiparasphenoids are perfectly preserved except for the distal portions of their parasphenoid processes, which are missing. Posterior border of the bones produced into three distinct lobes. Suborbital flanges of variable size, although always well developed. Basipterygoid processes moderately developed, surmounted by well-defined and anteriorly inclined pterygoid crests. Basisphenoid crest reduced or weakly developed. Common foramina (posterior orifices of Vidian canals plus cerebral foramina) located rather far from the postero-lateral corners of the bone. Anterior Vidian foramina pierce the bone immediately before the pterygoid crests; laterally, the foramina are sheltered by bony collars. In lateral view, the suborbital flanges distinctly bend upwards. Frontal step strong. In dorsal view, the posterior border of the pituitary fossa is straight. All foramina for the sympathetic and abducens nerves clearly visible; sympathetic nerves foramina and anterior abducens nerves foramina located close to each other. Notches for sympathetic nerves moderately developed.

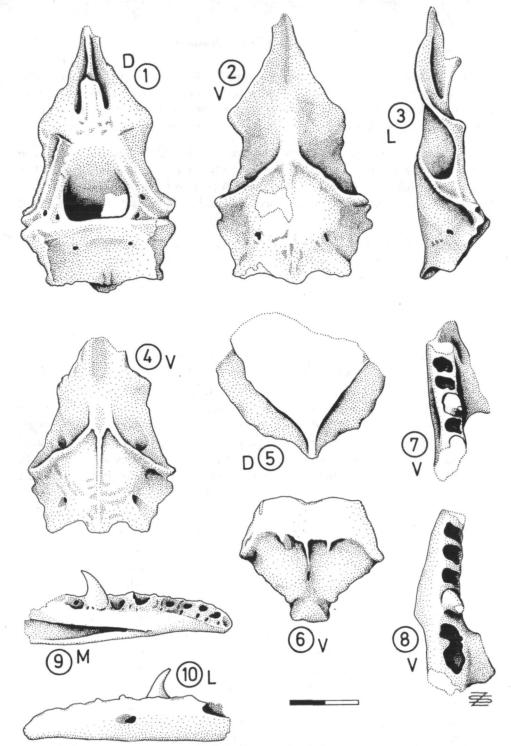


Fig. 1. Cranial bones of *Elaphe kohfidischi* Bachmayer & Szyndlar. – 1–3. basiparasphenoid (No. 1986/4/1), 4. basiparasphenoid (No. 1986/4/2), 5. parietal (No. 1986/4/3), 6. basioccipital (No. 1986/4/4), 7. anterior fragment of left maxilla (No. 1986/4/5), 8. posterior fragment of left maxilla (No. 1986/4/6), 9, 10. left dentary (No. 1986/4/7). D – dorsal, L – lateral, M – medial, V – ventral views. Scale equals 2 mm.

Parietal (Text-fig. 1: 5): The only available fragment of the parietal is from the posterior portion of the bone. Parietal foramina not visible. Dorsal surface of bone flat, devoid of furrows. The parietal crests, as characteristic for *Elaphe*, converge on each other before reaching the posterior border of the bone.

Basioccipital (Text-fig. 1: 6): The two complete basioccipitals are approximately as long as they are wide. Basioccipital crest well developed, with two distinct although small tubercles. Basioccipital process (a central lobe) indistinct. Basioccipital tubercles small. Occipitocondylar tubercle separated indistinctly off the bone.

Maxilla (Text-fig. 1: 7, 8): Two maxillary fragments come from an anterior and a posterior portion of a right maxilla (or from two maxillae of similar size). Teeth presumably isodontic. Both prefrontal and ectopterygoid processes partly missing. The latter process, twice as long as wide, was probably of regular rectangular shape. Posterior fragment of the bone provided with a dorsal constriction for maxillary ramus of pterygoid.

Dentary (Text-fig. 1: 9, 10): Two dentaries are broken posteriorly. The bones are relatively slender. The only preserved tooth in one of the bones is relatively large. The mental foramen lies at the level of the 7th tooth socket. The Meckelian groove closes completely at the level of the 6th tooth socket. These elements are allocated to the discussed species with some doubt, because elongation of the bones and small dimensions of the mental foramen suggest rather their assignment to the genus *Natrix*. Identification of the dentaries as belonging to *Elaphe* has been based on the relatively large size of the unique preserved tooth.

Comments:

The morphology of the cranial bones of this snake confirms allocation of its vertebrae within the genus *Elaphe* (Bachmayer & Szyndlar 1985). Its basiparasphenoid, provided with the pterygoid crests spreading down to the lateral ends of the basipterygoid processes, is characteristic for *Elaphe*, including *E. algorensis* from the Spanish Miocene (Szyndlar 1985). Among European members of the genus *Coluber*, only *C. viridiflavus* has a basiparasphenoid similar to that of *Elaphe kohfidischi* (as well as having the posterior margin of the bone provided with three distinct lobes). Nevertheless, vertebrae of *Coluber viridiflavus* display clearly different morphological features from those of *Elaphe kohfidischi*. The pterygoid crests of remaining species of the genus *Coluber* do not reach the lateral borders of the basiparasphenoid.

The fragmentary parietal resembles those of several snakes of the genus *Elaphe*, in particular *E. longissima* (but also *Coluber viridiflavus*).

The basioccipital of *Elaphe kohfidischi* does not resemble those of European colubrid snakes. In morphology of the basioccipital crest it is somewhat similar to *E. scalaris*, but the crest of the latter is situated just after the anterior border of the bone, unlike *E. kohfidischi*.

The maxilla, with the ectopterygoid process not produced into a distinct spur on its antero-medial corner (the structure present in *Coluber*), is characteristic for the genus *Elaphe*.

Coluber planicarinatus (BACHMAYER & SZYNDLAR, 1986) (Text-fig. 2; pl. 1: Figs. 3, 4)

1985. Nanus planicarinatus sp. nov. – Bachmayer & Szyndlar, p. 84, Text-fig. 1/17–22; pl. 1, Fig. 4–6.

The description of this form, first designated as an extinct genus *Nanus*, was based on merely a few vertebrae. The holotype is one trunk vertebra (No. 1984/97). The new material assigned to these vertebrae consists of a single basiparasphenoid.

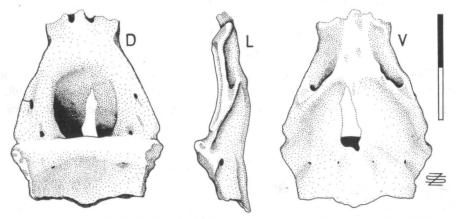


Fig. 2. Basiparasphenoid of *Coluber planicarinatus* (BACHMAYER & SZYNDLAR) (No. 1986/5). D. – dorsal, L – lateral, V – ventral views. Scale equals 2 mm.

Description:

The basiparasphenoid belonged to a small-sized, although adult snake. The bone is relatively wide and flat, with the parasphenoid process missing. Suborbital flanges presumably small. Basipterygoid processes indistinct, devoid of well-marked pterygoid crests. Basisphenoid crest absent. Common foramina small. Vidian canals relatively long – their anterior orifices located far from the common foramina. In dorsal view, the sympathetic nerves foramina and the anterior abducens nerves foramina are situated widely separated.

Comments:

In our previous work (BACHMAYER & SZYNDLAR 1985) several vertebrae of a minute snake were described as belonging to a new extinct genus, *Nanus planicarinatus*. According to our statement, the taxonomic position of this snake

was unclear, although we pointed out some similarities between *N. planicarinatus* and *Coluber najadum – C. rubriceps* group. The basiparasphenoid described above is almost identical with those of the latter snakes. Close resemblance is especially evident in the morphology of the ventral side of the basiparasphenoid: the general shape of the bone, its small size, the length of the Vidian canals, and the form of the anterior orifices of the canals. These facts entitle us to place the species *planicarinatus* in the recent genus *Coluber. C. planicarinatus* may have represented an ancestral line leading to the recent *C. najadum – C. rubriceps* group. The scantiness of available fossil materials, however, makes it impossible to set forth such a radical theory, although it was recently proved that at least a part of the living European colubrids originated from ancestors inhabiting central parts of Europe in Neogene (SZYNDLAR, in press a). The present European ranges of *C. najadum* and *C. rubriceps* are restricted to the southeastern part of the continent, thus to the south at the locality of Kohfidisch.

Natrix longivertebrata SZYNDLAR, 1984 (Text-fig. 3)

This species, widely distributed in the European Neogene, was reported from Kohfidisch on the basis of 15 precaudal vertebrae (Bachmayer & Szyndlar 1985). Of the new material from this locality a complete parietal is assigned to this species.

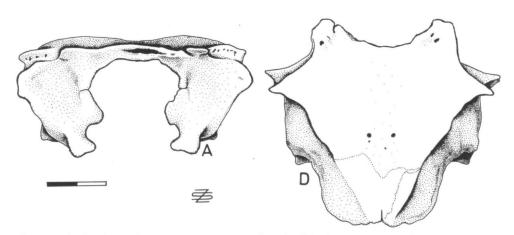


Fig. 3. Parietal of *Natrix longivertebrata* SZYNDLAR (No. 1986/6). A – anterior, D – dorsal views. Scale equals 2 mm.

Description:

The parietal has a flat dorsal surface with an indistinct medial furrow. Parietal foramina clearly visible. Parietal crests straight, not converging on each other before reaching the posterior border of the bone. The postorbitals form large subtriangular lobes in anterior view.

Comments:

This bone bears characteristic features of the genus *Natrix*, especially *N. natrix*, presently inhabiting Europe. Considering, however, that no other bones (in particular vertebrae) of *N. natrix* have been found in Kohfidisch as well as that the presence of a living snake species in the Miocene is improbable (see SZYNDLAR 1984), the discussed parietal is assigned to another member of the genus *Natrix*, namely *N. longivertebrata*. Several vertebrae clearly referable to the latter form were reported from Kohfidisch in our preceding work. Unfortunately, neither the type material of *N. longivertebrata* nor remains from other localities contain any parietal to be compared with that from Kohfidisch. Based on other cranial elements, this snake was apparently a close relative of *N. natrix* (SZYNDLAR 1984); thus, the find from Kohfidisch confirms the previous supposition.

The dentaries, temporarily assigned to *Elaphe kohfidischi* but alternatively belonging perhaps to a *Natrix*-like snake (vide supra), could also represent *N. longivertebrata*. Unfortunately, as in the case of the parietal, dentaries of *N. longivertebrata* are unknown from the type material.

Family Elapidae Naja austriaca BACHMAYER & SZYNDLAR, 1985 (Text-fig. 4)

Contrary to the other snakes formerly reported from Kohfidisch, the description of *Naja austriaca* was based on both vertebrae and cranial elements, including frontals, maxillae, fragmentary dentaries and fragmentary pterygoids (Bachmayer & Szyndlar 1985). The holotype is a basiparasphenoid (No. 1984/98). The new material consists of 3 left and 2 right compound bones, one left palatine plus a tiny fragment of a right palatine, and three fragmentary dentaries.

Description:

Compound bone (Text-fig. 4: 1-4): Several perfectly preserved compound bones, undoubtedly belonging to large-sized animals, are characterized by the medial flange being distinctly lower than the lateral flange, a feature very typical for cobras. In dorsal view, the posterior portion of the lateral flange is turned laterally. Supraangular foramen large. Articular facet (for reception of the quadrate) strongly concave, accompanied ventrally by a distinct crest. Retroarticular process of variable length, slightly curved medially in dorsal view.

Dentary (Text-fig. 4: 5, 6): Some fragmentary dentaries were reported in our previous work; a more complete bone was found in the new material. Its tooth ramus (unfortunately broken posteriorly) is provided with 9 teeth or tooth sockets. The mental foramen is located at the level of the 6th tooth. The compound notch lies next to the 7th tooth. The Meckelian groove closes completely at the level of the 4th tooth; the symphysis is partly fused anteriorly.

Palatine (Text-fig. 4: 7, 8): An almost complete left palatine bears 8 teeth or tooth sockets. Its vomerine process is relatively low and slopes slightly posteriorly; the antero-dorsal corner of the process missing. The maxillary process, situated between the maxillary nerve foramina, is very short.

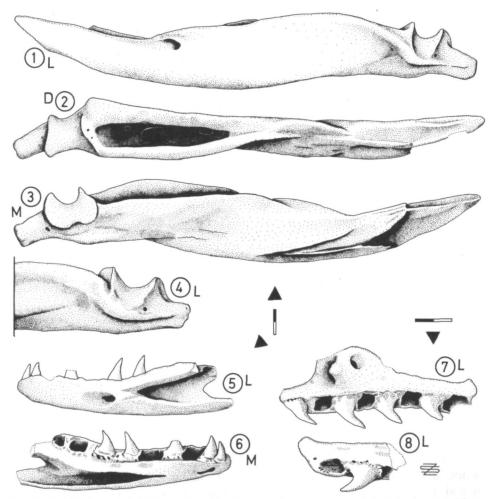


Fig. 4. Cranial bones of *Naja austriaca* BACHMAYER & SZYNDLAR. – 1–3. left compound bone (No. 1986/7/1), 4. left compound bone (No. 1986/7/2), 5, 6. left dentary (No. 1986/7/3), 7. left palatine (No. 1986/7/4), 8. posterior fragment of right palatine (NO. 1986/7/5). D – dorsal, L – lateral, M – medial views. Scale equals 2 mm.

Comments:

The new elapid material from Kohfidisch contributes little to specifying the taxonomic position of *Naja austriaca*. The newly described bones are very similar to one another in most members of the *Naja-Palaeonaja* group, and interspecific differences are expressed in details only. In the compound bone of recent species of

the genus Naja (N. naja, N. oxiana, N. haje, N. nigricollis) the posterior end of the lateral flange is extended upwards in lateral view, hence unlike fossil cobras including N. austriaca (cf. Hoffstetter 1939, pl. I: Fig. 11, Palaeonaja romani; Szyndlar 1985, Fig. 7: 1, Naja iberica). The palatine of most cobras at hand (Naja naja, N. haje, N. nigricollis, fossil N. iberica; palatine of Palaeonaja romani is unknown) bears 7 teeth, while in Naja austriaca it is provided with 8 teeth or tooth sockets. There are, however, some rare exceptions to this rule – for instance, the palatine of one specimen of N. naja (R. Hofstetter's coll.) bears 8 teeth, while N. oxiana (ex. coll. Inst. Paleobiol. Tbilisi) even has 9 teeth.

Family Viperidae

BACHMAYER & SZYNDLAR (1985) reported remains of a large-sized *Vipera*. More precise identification was not possible at that time. Recovery of new fossils containing taxonomically important cranial elements, together with access to recent comparative materials, make it possible to give a detailed description of a new extinct species.

Vipera burgenlandica sp. n.

(Text-figs. 5 and 6; pl. 1: Figs. 5, 6)

Holotype: A basiparasphenoid (Naturhist. Mus., Geol.-Paläont. Abt., No. 1986/3).

Material: 1 right compound bone, 1 left dentary, 1 basioccipital (previously described), 71 precaudal vertebrae (previously described).

Name derivation: From Burgenland, the province name.

Diagnosis: Typical member of the group of "oriental vipers" of the genus *Vipera* characterized by a relatively short and broad basiparasphenoid, compound bone bearing high medial flange, basioccipital with long basioccipital process, as well as large vertebrae provided with moderately long centrum, strongly depressed neural arch, long and acute parapophyseal processes, and relatively high neural spine and hypapophysis.

Differentiating diagnosis: It differs from V. lebetina and V. mauretanica in having a shorter basiparasphenoid, not laterally expanded posterior portion of basiparasphenoid, shorter and thinner basioccipital process, and vertebrae provided with shorter prezygapophyseal processes; from V. palaestinae in the lack of lateral processes at the level of the cerebral foramina in the basiparasphenoid and in having a much shorter basioccipital process; from V. russelli in having a much shorter basiparasphenoid, cerebral foramina piercing the basiparasphenoid much closer to its posterior border, lower medial flange of the compound bone, a much shorter and thinner basioccipital process, and vertebrae provided with a lower neural spine, longer hypapophysis and lacking of a medial notch of the zygosphene; from V. xanthina in having a somewhat thinner basioccipital process and vertebrae provided with a higher neural spine, square-shaped prezygapophyseal articular facets and a weakly developed central lobe of the zygosphene; from V. gedulyi of

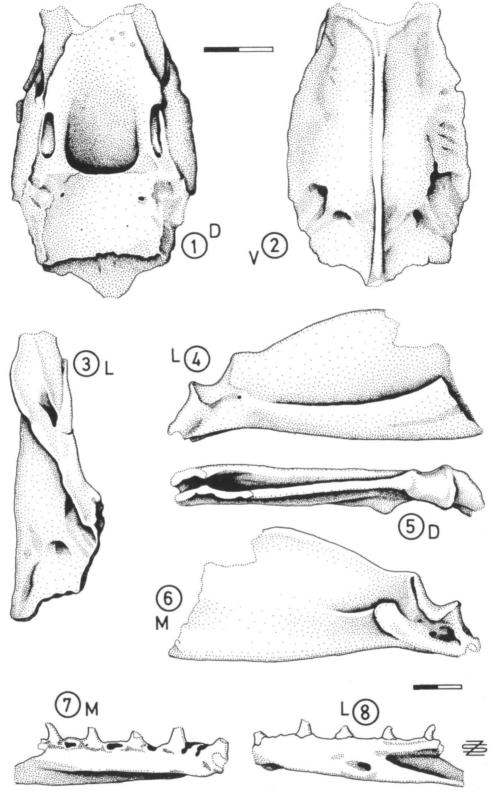


Fig. 5. Cranial bones of *Vipera burgenlandica* sp. n. – 1–3. holotype basiparasphenoid (No. 1986/3), 4–6. right compoundd bone (No. 1986/8/1), 7, 8. left dentary (No. 1986/8/2). D – dorsal, L – lateral, M – medial, V – ventral views. Scale equals 2 mm.

the Hungarian Miocene in having a much shorter basiparasphenoid and much shorter and thinner basioccipital process; from unnamed *Vipera* of the Czech Miocene in having square-shaped prezygapophyseal articular facets and a weakly developed central lobe of the zygosphene; differs from all the above species in having sympathetic nerve foramina and anterior abducens nerve foramina located in common cavities.

Description of holotype (Text-fig. 5: 1-3; pl. 1: Figs. 5, 6):

The basiparasphenoid is relatively short and wide. Parasphenoid process missing. Suborbital flanges partly damaged, but presumably of medial size. Pterygoid crests absent. Basisphenoid crest strong, extending from the posterior border of the bone up to the level of the suborbital flanges. Posteriorly, the crest probably continued into a distinct spur, unfortunately broken off in this material. As characteristic for vipers, the cerebral foramina (situated posteriorly) are distinctly separated from the posterior orifices of the Vidian canal (situated anteriorly). In lateral view, the suborbital flanges bent upward, with the anterior orifices of the Vidian canals opened below them. In dorsal view, the foramina of the sympathetic nerves and abducens nerves are located in deep common furrows on either side of the pituitary fossa. Posterior foramina of the abducens nerves also clearly visible. Notches for the sympathetic nerves indistinct.

Description of remaining material:

Compound bone (Text-fig. 5: 4-6): The fragmentary right compound bone is provided with a very high medial flange, unfortunately missing anteriorly. Lateral flange low, especially posteriorly. Retroarticular process strongly bent medially, its distal end broken off.

Dentary (Text-fig. 5: 7, 8): The unique dentary is slender, with the Meckelian groove reaching (in a symphyseal form) the anterior end of the bone. Tooth ramus broken posteriorly. Mental foramen located at the level of the 8th tooth socket. The compound notch reaches the level of the 9th tooth.

Basioccipital (Text-fig. 6: 9, 10): The bone is subtriangular with weakly developed basioccipital tubercles. Basioccipital process elongate, depressed laterally. Medial crest absend. Occipitocondylar tubercle well developed, distinctly separated off the bone.

Precaudal vertebrae (Text-fig. 6: 1–8): Centrum moderately long, cylindrical in ventral view. Hypapophysis strongly developed, straight in lateral view. Relative length of the hypapophyses decreases in more posterior vertebrae. Neural arch strongly flattened. Neural spine of anterior vertebrae much higher than long, that of posterior vertebrae somewhat longer than high. Zygosphene convex in anterior view; in dorsal view, the zygosphenal roof consists of two larger lateral lobes and an indistinct medial lobe. Prezygapophyses tilted upward. The prezygapophyseal articular facets are square and elongate laterally. Prezygapophyseal processes very short. Postzygapophyseal articular facets ovaloid. Paradiapophyses

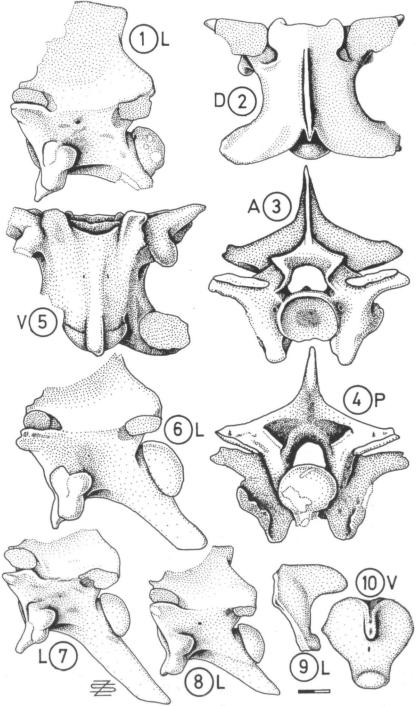


Fig. 6. Vertebrae and cranial bone of *Vipera burgenlandica* sp. n. (after Bachmayer & Szyndlar 1985). – 1–4. mid-trunk vertebra (No. 1984/106/1), 5, 6. mid-trunk vertebra (No. 1984/106/2), 7. cervical vertebra (No. 1984/106/3), 8. posterior trunk vertebra (No. 1984/106/4), 9, 10. basioccipital (No. 1984/106/5). A – anterior, D – dorsal, L – lateral, P – posterior, V – ventral views. Scale equals 2 mm.

well defined, provided with an acute process, the latter projected downward. The cotyle flattened. Condyle attached to a short neck. All vertebral foramina tiny although distinct.

Basic measurements and ratios of several trunk vertebrae are given in Table 1.

Table 1. Measurements and ratios of trunk vertebrae of Vipera burgenlandica sp. n. (N = 11)

	OR	X± SD
PR-PO	6.94 - 8.83	7.80 ± 0.64
CL	5.59 - 7.18	6.40 ± 0.49
PO-PO	8.99 - 12.16	10.02 ± 1.14
NAW	4.74 - 6.30	5.26 ± 0.46
ZW	3.82 - 4.70	4.22 ± 0.31
СТН	2.83 - 3.45	3.05 ± 0.20
CTW	3.13 - 4.04	3.53 ± 0.25
PR-PR	8.91 - 11.48	9.97 ± 0.81
CL/NAW	1.18 - 1.28	1.22 ± 0.05
PO-PO/NAW '	1.79 - 2.10	1.90 ± 0.09
CTW/CTH	1.08 - 1.29	1.16 ± 0.07
ZW/NAW	0.74 - 0.85	0.80 ± 0.04
PR-PR/PR-PO	1.19 - 1.36	1.28 ± 0.04
CL/ZW	1.44 - 1.64	1.52 ± 0.07
PR-PR/NAW	1.78 - 2.01	1.90 ± 0.07

Measurements (adpoted from AUFFENBERG 1963): CL – centrum length, CTH – cotyle height, CTW – cotyle width, NAW – centrum width, PO-PO – width between outer edges of postzygapophyseal articular facets, PR-PO – length from anterior edge of prezygapophyseal articular facet to posterior edge of postzygapophyseal articular facet, PR-PR – width between outer edges of prezygapophyseal articular facets, ZW – zygosphene width.

 $OR - observed range, \tilde{X} - mean, \pm SD - standard deviation.$

Comments:

As stated in Bachmayer & Szyndlar (1985), this snake represents a group of large-sized members of the genus *Vipera* (so-called "oriental vipers" or *Daboia*-group; "lebetina" and "xanthina" groups sensu Groombridge 1980), with a present centre of distribution in Central Asia.

Yet, definition of the taxonomic position of the Kohfidisch fossil with respect to the remaining species of the discussed group is a difficult task. The vertebrae of Vipera burgenlandica closely resemble those of West Asiatic V. lebetina and V. palaestinae as well as Northwest African V. mauretanica (the latter form sometimess regarded as a subspecies of V. lebetina). Vertebrae of Turkish V. xanthina and a Lower Miocene Vipera from Bohemia are characterized by a strong central lobe of the zygosphene, orbicular prezygapophyseal articular facets, and some other distinct features, and display a different morphological pattern (SZYNDLAR, in press b). V. russelli from South and Southeast Asia has vertebrae dissimilar to those of the above mentioned snakes. Vertebrae of this species are provided

with a neural spine much higher than the hypapophysis and a notched zygosphene and are hence unlike other members of the genus *Vipera*.

The basiparasphenoid of Vipera burgenlandica, taking into consideration the morphology of its posterior portion, most closely resembles those of recent V. xanthina and V. palaestinae, but also that of V. gedulyi from the Hungarian Miocene (cf. Bolkay 1913, pl. XII: Fig. 11)*). The resemblance among the basiparasphenoids of these snakes consists mainly of the general shape of the bone, while nerve and carotid foramina are situated similarly in particular species. The posterior area of the basiparasphenoid of V. lebetina (including V. mauretanica) is distinctly widened laterally. The taxonomic importance of the only feature distinguishing V. burgenlandica from its living relatives altogether, i. e. location of foramina for the sympathetic nerves and anterior foramina for the abducens nerves in common concavities, is uncertain. These foramina are usually separated from each other by bony bars in living "oriental vipers", but in one of the examined specimens of V. mauretanica (GNM 10637) this bar is lacking (although only on the right side of the basiparasphenoid). Having at hand only the unique basiparasphenoid of V. burgenlandica, we cannot exclude intraspecific variability of this feature.

The remaining bones of Vipera burgenlandica differ little from those of other "oriental vipers". The basioccipital process of the basioccipital bone of the discussed snakes is relatively much longer than in the other members of the genus Vipera. The only significant difference among particular species of "oriental vipers" consists of length, thickness, and shape (in lateral view) of this process. The basioccipital of V. burgenlandica is most similar to that of V. xanthina and to a lesser degree to V. lebetina, but it differs significantly from that of Miocene V. gedulyi, the latter having an exceptionally long and thick basioccipital process (cf. Bolkay 1913, pl. XII: Fig. 12).

Bones of the lower jaw are almost identical in all "oriental vipers". In general shape as well as in the proportions between the height of the medial and lateral flanges, the compound bone of V. burgenlandica closely resembles those of other species except V. russelli, the latter provided with a relatively higher medial flange. The dentary of V. russelli, with the mental foramen lying at the level of the 6^{th} tooth and the compound notch approaching the 7^{th} tooth, also differs from those of other related species. The dentary of the other "oriental vipers", including V. burgenlandica, has the mental foramen at the level of the 7^{th} or 8^{th} (rarely 6^{th}) teeth and the compound notch by the 9^{th} tooth.

In conclusion, Vipera burgenlandica display features characteristic for the living species V. lebetina, V. palaestinae, and V. xanthina, but not V. russelli. Although elucidation of relationships between this snake from Kohfidisch and two other Miocene vipers from Central Europe (V. gedulyi and that from Bohemia) is

^{*)} Vipera gedulyi is not a close relative of East European V. ammodytes (as stated in the literature); it belongs to the group of "oriental vipers". The taxonomic status of V. gedulyi will be discussed in detail elsewhere (SZYNDLAR, in prep.).





impossible because of the small number of homologous bones, it is obvious that these three extinct forms represented distinct species, well differentiated from one another.

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Explanation of plate

Plate 1. Basiparasphenoids of some snake species from Kohfidisch.

- Fig. 1. Elaphe kohfidischi BACHMAYER & SZYNDLAR, ventral view, 7.3×. NHMW 1986/4/1.
- Fig. 2. Ditto, dorsal view, 7.2×.
- Fig. 3. Coluber planicarinatus (BACHMAYER & SZYNDLAR), ventral view, 8.8×. NHMW 1986/5.
- Fig. 4. Ditto, dorsal view, 8.8×.
- Fig. 5. Vipera burgenlandica sp. n., ventral view, 6×. NHMW 1986/3 (Holotypus).
- Fig. 6. Ditto, dorsal view 6×.