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THE SNAKE FAUNA OF DĚVÍNSKA NOVÁ VES (SLOVAK REPUBLIC) IN RELATION TO THE EVOLUTION OF SNAKE ASSEMBLAGES OF THE EUROPEAN MIDDLE MIOCENE

HADÍ FAUNA Z DĚVÍNSKÉ NOVÉ VSI (SLOVENSKÁ REPUBLIKA) VE VZTAHU K EVOLUCI EVROPSKÝCH HADÍCH SPOLEČENSTEV STŘEDNÍHO MIOCÉNU

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Abstract

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The reptile assemblage of Děvínska Nová Ves (Astaracian – MN 6) is diversified, including Colubridae, Elapidae and Viperidae. Recently, the following snake taxa were reported from this site: Colubrinae B & D, Colubrinae gen. et sp. indet., *Neonatrix* sp. and Elapidae C. All the taxa (Colubridae and Elapidae) represent the modern European snake fauna which displaced 'ancient' snake fauna (including family Boidae) out of the Central European area. The last Central European occurrence of large boid snakes (Boinae or Pythoninae) is documented at the Lower/Middle Miocene transition, while 'Oriental vipers' group occurs here till the end of Middle Miocene. Representatives of cobras (Elapidae) became extinct during the Upper Miocene in Central Europe.

Key words: Serpentes, Colubridae, Elapidae, determination, evolution, Middle Miocene, Slovak Republic.

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Introduction

The locality Děvínska Nová Ves (DNV) is situated in Slovakia at the Bratislava district (Fig. 1). Some material comes from the northern slope of Děvínska Kobyla Hill (514 m a.s.l.) which is situated at the north-western suburb of Slovak capital city Bratislava, aproximately in the centre of the triangle formed by the villages Děvínska Nová Ves, Děvín and Dúbravka. The Morava river flows at the west leading into the Danube river under the thrust-outlier of the Děvín castle, the Lamač depression is situated at the east (ŠVAGROVSKÝ 1981). The material of reptiles comes from the quarry, where a rich fauna of vertebrates, mainly large mammals (ZAPFE 1949, 1950, 1951, 1952, 1960), was discovered within the caves and joints formed in the Middle Triassic dolomitic limestone and dolomite (MIŠÍK 1976). The stratigraphical age of the material falls into the lowermost part of the stage MN 6 (sensu Steininger et al. 1990). WETTSTEIN-WESTERSHEIMB (1955) described first the discoveries of fossil reptiles; however, his determination was revised by SZYNDLAR (1991a). ESTES (1969) described representatives of the subfamily Lacertilia there. A more abundant material of reptiles comes from the place called "Bonanza", which has been discovered in year 1984 by Dr. Meszároš. It

is a case of the fissure within the Lias limestone which was filled by Badenian sediments. These sediments are rich in marine and terrestrial vertebrates, less the molluscs. The fissure occurs on the eastern margin of limestone quarry in the protective wall oriented towards the railway Brno–Bratislava. The fissure has WNW–ESE direction and its width varies between 2.5 and 3 m. The visible part is about 5 m high. The fissure is filled by limestone boulders, sand and sandstone. The sides of the fissure are formed by limestone breccia with the traces of shipworms of the genus *Lithodomus* (HOLEC et al. 1987). The bivalvians *Pecten aduncus* EICHW. indicate the Middle Badenian age (MN 6). The stratigraphical assignation of the site may be seen in Fig. 2. For the profile of the fissure and the description of the fosiliferous sediments see Fig. 3. Regarding the reptiles, HOLEC et al. (1987) mention the discoveries of the genus *Ophisaurus* sp. and Serpentes indet.

Already prepared and conserved material of snakes is deposited in the following institutes:

SNM – Slovak National Museum, Bratislava

MM – Moravian Museum, Brno

DP FNSP – Palaeontological department of the Faculty of Natural Sciences, Prague

As regards the dimensions of vertebrae, only the length (CL) and width (NAW) of the vertebral centres were measured (in mm).

Fig. 1. Distribution of the Czech and Slovak localities where the Cenozoic reptile fauna has been discovered. The localities investigated by IVANOV (1997a) are indicated by figures: 1 – Litenčice, 2 – Bechlejovice u Děčína, 3 – Merkur (Tušimice) (ME), 4 – Dolnice, 5 – Komořany, 6 – Souš, 7 – Ivanovice u Brna (IB), 8 – Děvínska N. Ves (DNV), 9 – Pezinok (PE), 10 – Kremnička, 11 – Kamenica n. Hronom, 12 – Hajnáčka u Fiľákova, 13 – Mýtne Ľudany u Levic, 14 – Včeláre, 15 – Hosťovce, 16 – Ivanovce u Trenčína (I), 17 – Zlatý kůň u Koněprus, 18 – Čejč, 19 – Mladečské jeskyně (ML), 20 – Malá Dohoda – lom (MD), 21 – Stránská skála (SS), 22 – Gánovce u Popradu.

Obr. 1. Distribuce českých a slovenských lokalit s kenozoickou plazí faunou. Čísly jsou označeny lokality studované IVANOVEM (1997a): 1 – Litenčice, 2 – Bechlejovice u Děčína, 3 – Merkur (Tušimice) (ME), 4 – Dolnice, 5 – Komořany, 6 – Souš, 7 – Ivanovice u Brna (IB), 8 – Děvínska N. Ves (DNV), 9 – Pezinok (PE), 10 – Kremnička, 11 – Kamenica n. Hronom, 12 – Hajnáčka u Fiľakova, 13 – Mýtne Ľudany u Levic, 14 – Včeláre, 15 – Hosťovce, 16 – Ivanovce u Trenčína (I), 17 – Zlatý kůň u Koněprus, 18 – Čejč, 19 – Mladečské jeskyně (ML), 20 – Malá Dohoda – lom (MD), 21 – Stránská skála (SS), 22 – Gánovce u Popradu.

Systematic part

Superfamily: Colubroidea OPPEL, 1811
Family: Colubridae OPPEL, 1811
Subfamily: Colubrinae OPPEL, 1811
Colubrinae B

1997a – Colubrinae B: Ivanov M., Hadi evropského kenozoika, p. 96, Fig. 42

Layer: Middle Badenian – Astaracian – MN 6, ? Zapfe's joint, Middle Miocene
Material: 2 trunk vertebrae (DP FNSP – DNV-p 1–2)

Trunk vertebrae (Fig. 4 A–D): Viewing from the lateral aspect the neural spine is 1.5 times longer than high, its cranial margin overhangs anteriorly and the fragmentary

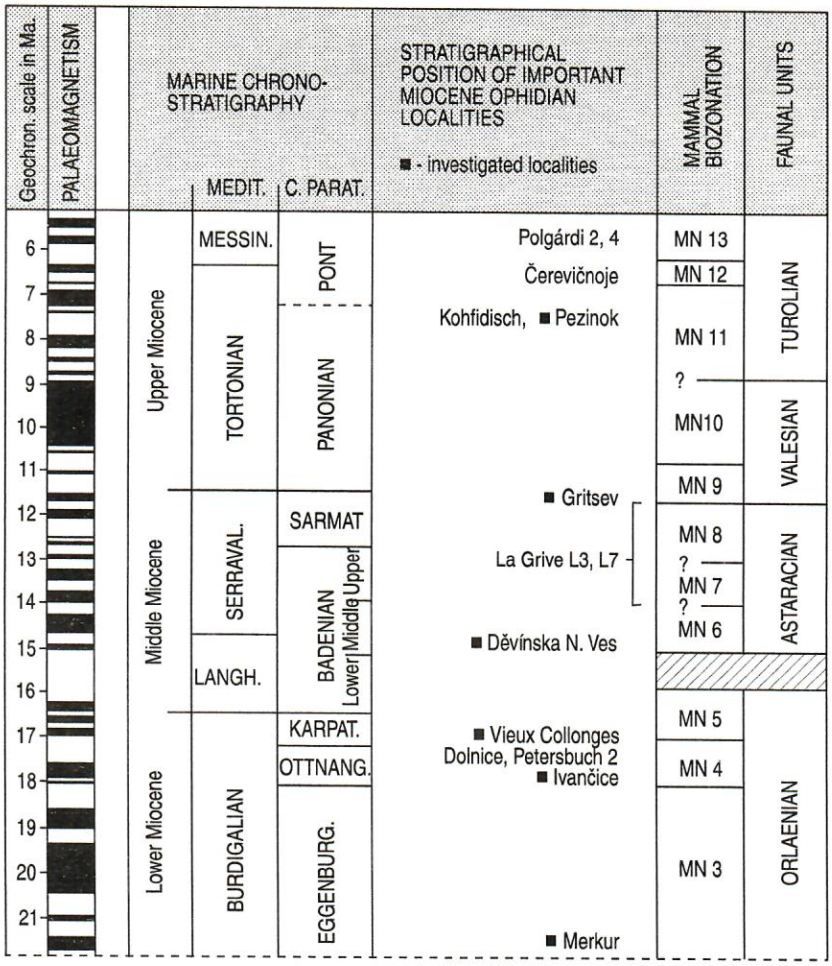

Fig. 2. Chronostratigraphic scale of the Miocene period (STEININGER et al. 1990). The sites investigated by IVANOV (1997a) are indicated by black squares; unmarked localities represent some other European Miocene sites which are interesting for palaeoherpetology.
Obr. 2. Chronostratigrafická škála použitá pro období miocénu (STEININGER et al. 1990). Studované lokality jsou označeny černým čtverečkem, neoznačené lokality představují některé další miocenní evropské lokality, které jsou z paleoherpetologického hlediska zajímavé.

caudal margin had most probably posterior overhanging. The neural spine lacks its dorsal thickness. The interzygapophyseal ridges are slightly developed, the lateral foramina are small but distinct, situated within the shallow depressions, close under the interzygapophyseal ridges. The dorsally slightly curved subcentral ridges are distinct, almost reaching the proximal margin of condyle. Both para- and diapophyses are not markedly divided, diapophyses are as large as parapophyses and they are directed laterally. The parapophyses are rounded ventrally. From the dorsal aspect, the zygosphene posseses two small lateral lobes, the medial tubercle is underdeveloped, sometimes even lacking, so the zygosphenal lip can be almost straight. The prezygapophyseal articular surfaces are irregular to roughly oval, the prezygapophyseal processes are broken-off at the base.

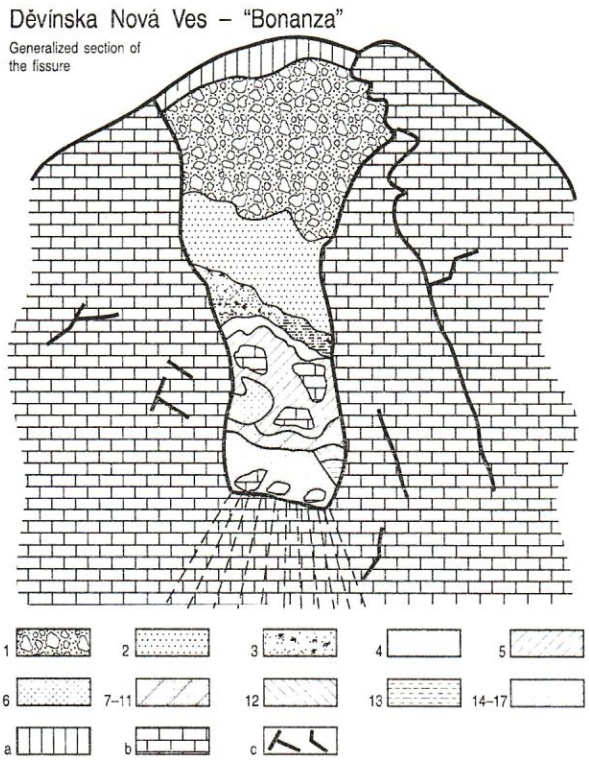

Fig. 3. Generalised section through the sediments at Děvínska Nová Ves – "Bonanza": 1 – fine limestone debris covered by a layer of brown loam (Holocene), 2 – white limey sand, 3 – disaggregating sandstone with a higher content of muscovite, 4 – solid, light yellow marlstone with a great quantity of fossils, 5 – big boulders with white limey matter, 6 – greenish sand with interbeds of white limey matter, 7–11 – layers with coarse-grained, disaggregating sandstone with no fossils to the fossiliferous marl which is very rich in fossils, 12 – white calciferous sandstone, 13 – yellowish-white sand with a great quantity of fauna, 14–17 – greenish to light sandstone, the biggest quantity of fossils are contained in the layer No. 17, a – Holocene humus-carbonate soil, b – Lias limestone, c – tectonic faults (according to Holec et al. 1987).

Obr. 3. Schematický profil sedimenty lokality Děvínská Nová Ves – „Bonanza": 1 – drobný vápencový štěrk překrytý hnědou hlínou (holocén), 2 – bílý vápenatý písek, 3 – rozpadající se pískovec s větším obsahem muskovitu, 4 – pevný, světle žlutý slínovec, velký obsah fosilií, 5 – velké balvany v bílé vápenaté hmotě, 6 – zelenavý písek s vložkami bílé vápenaté hmoty, 7–11 – vrstvy od hrubozrnnějšího rozpadajícího se sterilního pískovce po bohaté fosiliferní slíny, 12 – bílý vápnitý pískovec, 13 – žlutobílý písek s bohatým obsahem fauny, 14–17 – pískovec zelenavé až světlé barvy, největší obsah fosilií ve vrstvě č. 17, a – holocenní pokryv, b – liasový vápenec, c – tektonické porušení (podle Holec et al. 1987).

The epizygapophyseal spines are lacking. From the ventral aspect the subcentral grooves are shallow, the subcentral foramina, situated at the base of a distinct haemal keel, are very small and hardly visible. The caudal part of the haemal keel is shoulder-shaped just close to the proximal margin of the condyle (DP FNSP – DNV-p 1) or it can be almost straight (DP FNSP – DNV-p 2). The postzygapophyseal articular surfaces are irregular without lateral expansions. Viewing from the cranial aspect, the neural arch is slightly vaulted, the neural canal is rounded with a square-like cranial orifice. The lateral sinuses are more (DP FNSP – DNV-p 1) or less (DP FNSP – DNV-p 2) developed. The prezygapophyses can be slightly turned dorsally (DP FNSP – DNV-p 1). The paracotylar foramina are located at both sides of the cotyle which is rounded or slightly dorso-ventrally flattened. Metric measurements are the following – vertebra No. DP FNSP – DNV-p 1: CL = 4.84; NAW = 3.98; CL/NAW = 1.22; vertebra no. DP FNSP – DNV-p 2: CL = 4.96; NAW = 3.70; CL/NAW = 1.34.

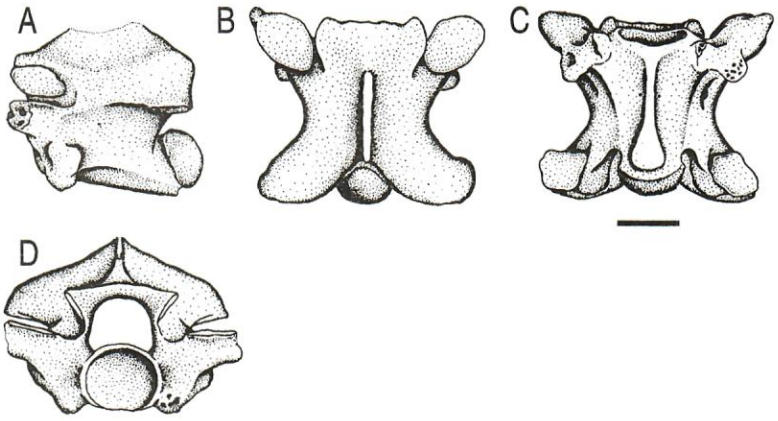

Fig. 4. Colubrinae B from the Middle Miocene of DNV. A–D: Mid-trunk vertebra (DP FNSP – DNV-p 1). A – lateral aspect; B – dorsal aspect; C – ventral aspect; D – cranial aspect (scale equals 2 mm).
Obr. 4. Colubrinae B ze středního miocénu lokality DNV. A–D: obratel ze střední části trupního oddílu (DP FNSP – DNV-p 1). A – pohled laterální; B – pohled dorzální; C – pohled ventrální; D – pohled kraniální (měřítko odpovídá 2 mm).

Discussion:

Due to the presence of the haemal keel in trunk vertebrae, the material belongs unquestionably to the subfamily Colubrinae. The vertebrae of the morphotype Colubrinae B belonged to a relatively large colubrid snake. Scantiness of the fossil material did not enable more precise determination. It cannot be excluded that the vertebrae could belong to the genus *Elaphe* which is documented by the low ratio CL/NAW. On the contrary, the division of para- and diapophyses is not clearly developed, which supports the assignation to the genus *Coluber*. Contrary to the morphotype Colubrinae A (Ivanov 1997a), vertebrae of the morphotype Colubrinae B are more massive and larger.

Subfamily: Colubrinae Oppel, 1811
Colubrinae D

1997a – Colubrinae D: Ivanov M., Hadi evropského kenozoika, p. 97, Fig. 44

Layer: Middle Badenian – Astaracian – MN 6, "Bonanza" – layer No. 13, Middle Miocene
Material: 2 trunk vertebrae (SNM – DNV 2–3)

Trunk vertebrae (Fig. 5 A–E): Viewing from the lateral aspect, the neural spine is very low, about 4 times longer than high. Its cranial margin overhangs posteriorly, the caudal margin is vertical or overhangs very slightly anteriorly. The interzygapophyseal ridges are distinct, lateral foramina are small, situated in depressions. The subcentral ridges are very short. The para- and diapophyses are slightly divided to each other, parapophyses are somewhat larger than diapophyses. From the dorsal aspect, the diapophyses are directed postero-laterally. The condyle is situated at a long neck. Viewing from the dorsal aspect, both the lateral lobes of the zygosphenal lip and the medial tubercle are clearly developed. The prezygapophyseal articular surfaces are oval, the prezygapophyseal processes are short, reaching about 1/3 of the length of prezygapophyseal surfaces. The epizygapophyseal spines are lacking. Viewing from the ventral aspect, the haemal keel is strikingly broad and low, distinct especially in the anterior part of vertebra, in the direction of the condyle the haemal keel becomes lower. Both the subcentral ridges and subcentral grooves are indistinct, the subcentral foramina are very small and inconspicuous. The postzygapophyseal articular surfaces are approximately round. Viewing from the cranial aspect, the neural arch is flattened dorso- ventrally, the neural canal is round-square to round. Small paracotylar foramina are located at both sides of the dorso- ventrally flattened cotyle. The metric measurements are taken only in one vertebra (SNM – DNV 2): CL = 2.47; NAW = 1.75; CL/NAW = 1.41.

Discussion:

The vertebrae of the morphotype Colubrinae D are characterised by small dimensions and belong unquestionably to a small representative of the subfamily Colubrinae. The vertebrae of the morphotype Colubrinae D are very similar to the recent genus *Coronella*, especially *C. austriaca*, by the presence of low neural spine, flattened neural arch and the broad and indistinct haemal keel. Also *Hispanophis coronelloideus* SZYNDLAR, 1985 has similar vertebrae, but the neural arch is more vaulted and the prezygapophyseal processes are obtuse in the last mentioned species. Until now, the oldest

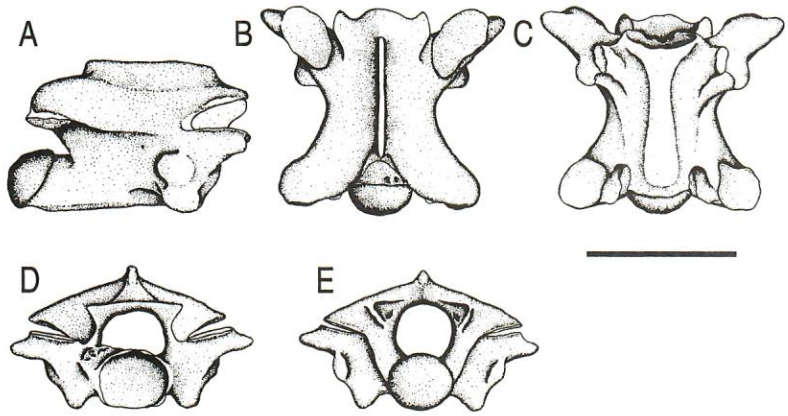

Fig. 5. Colubrinae D from the Middle Miocene of DNV. A–E: Mid-trunk vertebra (SNM – DNV 2). A – lateral aspect; B – dorsal aspect; C – ventral aspect; D – cranial aspect; E – caudal aspect (scale equals 2 mm).

Obr. 5. Colubrinae D ze středního miocénu lokality DNV. A–E: obratel ze střední části trupního oddílu (SNM – DNV 2). A – pohled laterální; B – pohled dorzální; C – pohled ventrální; D – pohled kraniální; E – pohled kaudální (měřítko odpovídá 2 mm).

known representative of the genus *Coronella* – *Coronella* cf. *C. austriaca* was described at the Hungarian Uppermost Miocene (MN 13) locality Polgárdi 4 (VENCZEL 1994). The morphotype Colubrinae D differs from *Coronella* cf. *C. austriaca*, described by VENCZEL (1994), by the following features: 1. The neural spine is lower – its cranial margin overhangs posteriorly, not anteriorly; 2. The prezygapophyseal processes are more pointed and somewhat longer; 3. The lateral lobes and the medial tubercle of the zygosphene are distinct, contrary to *Coronella* cf. *C. austriaca* with straight to slightly convex zygosphene (VENCZEL 1994 – p. 8, Fig. 3). Based on the similarity with both recent and fossil material of the genus *Coronella*, I consider the assignation of discovered vertebrae to this genus to be very probable. However, a more precise determination was not possible because of the scarcity of fossil material.

Subfamily: Colubrinae OPPEL, 1811
Colubrinae gen. et sp. indet.

1997a – Colubrinae gen. et sp. indet.: Ivanov M., Hadi evropského kenozoika, p. 99

Layer: Middle Badenian – Astaracian – MN 6, "Bonanza" – layer No. 13, Middle Miocene
Material: 1 cervical vertebra (SNM – DNV 1)

Cervical vertebra: The preserved vertebra is very fragmentary with broken-off neural spine at the base. The zygapophyses are also heavily damaged. A more precise determination with assignation to some morphotype was impossible.

Superfamily: Colubroidea OPPEL, 1811
Family: Colubridae OPPEL, 1811
Subfamily: Natricinae BONAPARTE, 1838
Genus: *Neonatrix* HOLMAN, 1977
Neonatrix sp.

1997a – *Neonatrix* sp.: Ivanov M., Hadi evropského kenozoika, p. 100, Fig. 46

Layer: Middle Badenian – Astaracian – MN 6, "Bonanza" – layer No. 13, Middle Miocene
Material: 3 trunk vertebrae (SNM – DNV 4–6)

Trunk vertebrae (Fig. 6 A–D): Viewing from the lateral aspect, the neural spine is relatively high, about 1.5 times longer than high. Although the cranial border of the neural spine is not preserved, its caudal margin may be seen which overhangs posteriorly. A dorsal thickness of the neural spine was not found. The interzygapophyseal ridges are well developed, the lateral foramina are striking and large, situated within shallow depressions. The subcentral ridges are distinct, slightly arched dorsally. Both para- and diapophyses are well divided, diapophyses are directed caudally, parapophyseal processes are directed antero-ventrally. The hypapophysis is low and short, it does not reach behind the caudal margin of the condyle which is situated at short neck. Viewing from the dorsal aspect, the zygosphenal lip has very distinct lateral lobes and broad medial tubercle. The prezygapophyseal articular surfaces are oval, prezygapophyseal processes are about as long as prezygapophyseal surfaces. The epizygapophyseal spines are lacking. Viewing from the ventral aspect, the subcentral ridges are well developed, the subcentral grooves are broad and shallow. The subcentral foramina are very small, hardly visible. The hypapophysis does not expand anteriorly. The parapophyseal processes are pointless distally. The postzygapophyseal articular surfaces are irregular. Viewing from the cranial aspect, the neural arch is slightly vaulted, the neural canal is square and the zygosphenal lip is straight. The small paracotylar foramina are situated

within the shallow depressions at both sides of the rounded cotyle, the subcotylar tubercles are lacking. The metrical measurements follow (N = 3):): CL: OR = 3.73–3.96; NAW: OR = 2.26–2.42; CL/NAW: OR = 1.57–1.71, mean 1.64±0.07.

Discussion:

The genus *Neonatrix* belonged to common representatives of the subfamily Natricinae in the European Tertiary. Based on the scanty fossil material, the determination is difficult and therefore the assignation at the species level is impossible. The recent investigations (SZYNDLAR – unpubl. data; see below) showed that small representatives of the family Elapidae, just very similar to small natricinae snakes, became common during the Neogene. The only characteristic feature is the neural spine which is relatively high in colubrids. However, the neural spine is often broken-off at the base and therefore the determination even at the family level can be problematic. Therefore, some ophidian palaeontologists (SZYNDLAR – pers. consult. 1996) recommend the assignation to Natricinae indet. which is less precise yet more correct.

The genus *Neonatrix* is characterised by small dimensions and short hypapophysis which does not reach behind the caudal margin of condyle. Altogether three species have been discovered in the European Tertiary: *Neonatrix europaea* RAGE & HOLMAN, 1984, *Neonatrix crassa* RAGE & HOLMAN, 1984 and *Neonatrix nova* SZYNDLAR, 1987 (RAGE & HOLMAN 1984; SZYNDLAR 1987a). The remaining species – *Neonatrix elongata* HOLMAN, 1973 and *Neonatrix magna* HOLMAN, 1982 – have been discovered in the Middle and Upper Miocene of Nebraska, Texas and South Dakota (HOLMAN, 1979, 1982). The species *N.* cf. *europaea* occurred at the Lower/Middle Miocene transition (MN 4/5) at the French locality Vieux Collonges (RAGE & HOLMAN 1984; IVANOV 1997a, 1997b). *N. nova* differs from *N.* cf. *europaea* by smaller dimensions and distinct medial tubercle on the zygosphenal lip, SZYNDLAR (1987a) considers as remaining characteristic features also the less vaulted neural arch and rounded cotyle and condyle in *N. nova*. However, I assume that similarly developed structures may also be seen in *N. europaea*. *N. crassa* differs from *N.* cf. *europaea* by the convex zygosphenal lip, *N. crassa* differs further

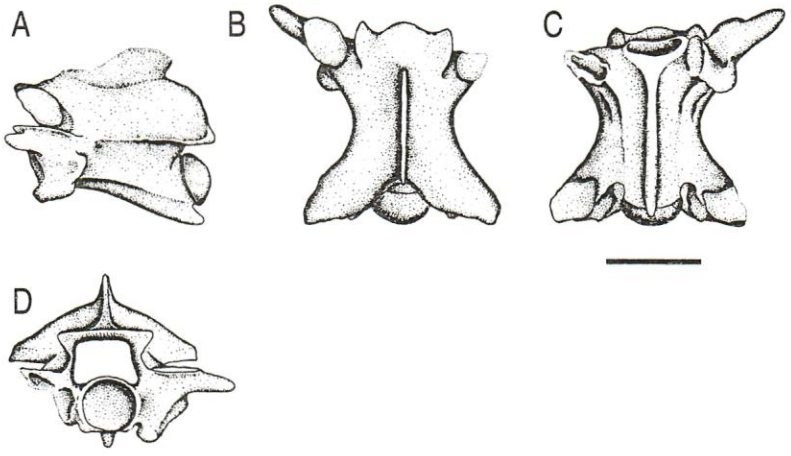

Fig. 6. *Neonatrix* sp. from the Middle Miocene of DNV. A–D: Trunk vertebra (SNM – DNV 4). A – lateral aspect; B – dorsal aspect; C – ventral aspect; D – cranial aspect (scale equals 2 mm).
Obr. 6. *Neonatrix* sp. ze středního miocénu lokality DNV. A–D: trupní obratel (SNM – DNV 4). A – pohled laterální; B – pohled dorzální; C – pohled ventrální; D – pohled kraniální (měřítko odpovídá 2 mm).

from the North American species *N. elongata* and *N. magna* by the better developed hypapophysis and longer prezygapophyseal processes (RAGE & HOLMAN 1984).

Neonatrix sp. with long prezygapophyseal processes and well developed (however short) hypapophysis is very similar to any of the two known European species. *Neonatrix* sp. conforms to *N. europaea* by the high neural spine and absence of subcotylar tubercles. On the other hand, it conforms to *N. crassa* by a distinct medial tubercle of the zygosphenal lip, caudally directed diapophyses and slightly vaulted neural arch. *Neonatrix* sp. from Děvínska Nová Ves (MN 6) is characterised by mixing of the features of both known West European species. Because of the limited number of fossil material, it was not possible to investigate the degree of intraspecific morphological variability. Therefore, I avoided a more precise determination.

Superfamily: Colubroidea OPPEL, 1811
Family: Elapidae BOIÉ, 1827
Elapidae C

1997a – Elapidae C: Ivanov M., Hadi evropského kenozoika, p. 137, Fig. 64

Layer: Middle Badenian – Astaracian – MN 6, Zapfe's joint, Middle Miocene
Material: DNV: 1 trunk vertebra (MM 5/83 01 923.930)

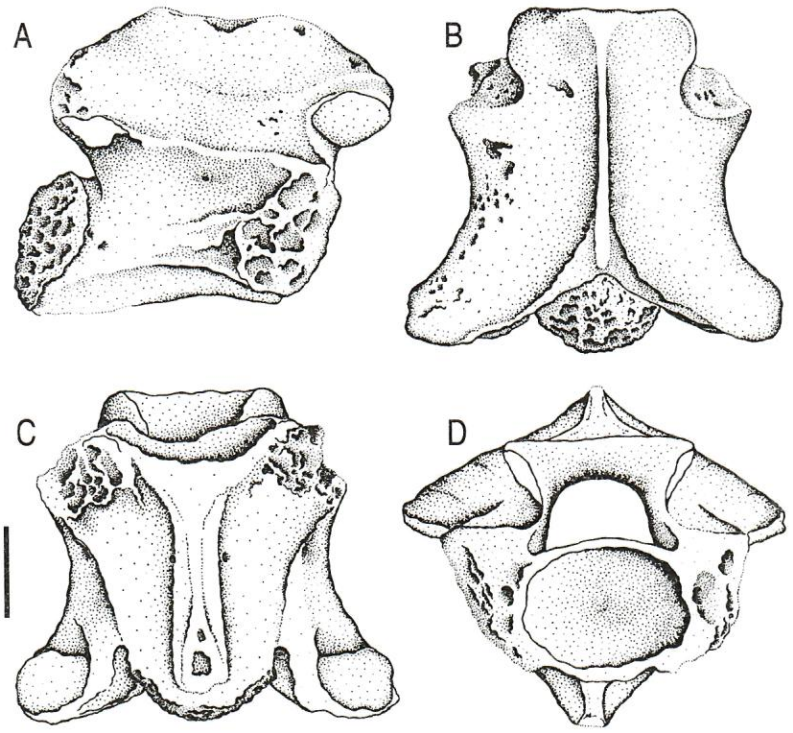

Fig. 7. Elapidae C from the Middle Miocene of DNV. A–D: Trunk vertebra (MM – 5/83 01 923.930). A – lateral aspect; B – dorsal aspect; C – ventral aspect; D – cranial aspect (scale equals 2 mm).
Obr. 7. Elapidae C ze středního miocénu lokality DNV. A–D: trupní obratel (MM – 5/83 01 923.930). A – pohled laterální; B – pohled dorzální; C – pohled ventrální; D – pohled kraniální (měřítko odpovídá 2 mm).

Trunk vertebra (Fig. 7 A–D): The only preserved vertebra is very fragmentary with broken-off prezygapophyses, synapophyses, neural spine and hypapophysis. Viewing from the lateral aspect, the interzygapophyseal ridges are well developed, close under them small but distinct lateral foramina are situated within depressions. The subcentral ridges are well developed especially in the cranial part of the vertebra, extending from the synapophyses to the proximal margin of condyle where they become low. The condyle is situated at a short neck, its caudal margin is heavily damaged. Viewing from the dorsal aspect, the zygosphenal lip is straight, the lateral lobes are indistinct. The epizygapophyseal ridges are underdeveloped. Viewing from the ventral aspect, the basis of hypapophysis is broad, the subcotylar tubercles are absent. The subcentral grooves are very broad and shallow, the subcentral foramina are distinct. The postzygapophyseal articular surfaces are irregular but they are damaged. Viewing from the cranial aspect, the neural arch is slightly vaulted, the neural canal is rounded with lateral sinuses. The paracotylar foramina are situated at both sides of the cotyle which is slightly flattened dorso-ventrally.

Discussion:

The vertebra is characterised by the short and broad centre. The presence of the hypapophysis in trunk vertebra enable the assignation to the family Elapidae. The vertebra resembles to the morphotype *Naja* sp. 1 to a certain extent (IVANOV 1997a) but it differs by the more strongly built hypapophysis and less vaulted neural arch. Nevertheless, I assume that this is also a case of some of the representative of the genus *Naja*. The morphotype Elapidae C differs from the morphotype Elapidae B (IVANOV 1997a) by the low ratio CL/NAW (a more precise value was not found because of incomplete material). It means that Elapidae C is similar rather to some of the representatives of African cobras. Because of the incomplete material, a more precise comparison could not be done.

Evolution of the European snake fauna during the Middle Miocene

The Middle Miocene snake fauna of Central and East Europe is very scarce. With the exception of the locality Děvínska Nová Ves, the Middle Miocene snake fauna was described only from the Polish localities Przeworno (MN 6) and Opole 2 (MN 7) (SZYNDLAR 1984, 1991a, 1991b). The representatives of families Colubridae (Natricinae + Colubrinae) and Elapidae have recently been described at Děvínska Nová Ves (IVANOV 1997a, 1997b), the presence of Viperidae is documented by SZYNDLAR (1991b).

The fossil representatives of the primitive suborder Scolecophidia are very rare (they are unknown from the area of Central Europe) and the taxonomic value of their vertebrae is low.

The representatives of the family Boidae gradually disappeared from the Central European area during the Middle Miocene. The last occurrence of a large member of Boidae (morphotype Boidae D) – Boinae or Pythoninae – has been described at the Moravian locality Ivančice near Brno, the stratigraphical age falls into the time span MN 4 – ?MN 6 (IVANOV 1996). The small members of Boidae – Erycinae – survived in Central Europe till the end of the Middle Miocene as it was documented at the German site Steinheim a. A. (MN 7+8) (RAGE in SZYNDLAR 1994). The representatives of Boidae are unknown since the beginning of the Upper Miocene within the Central European area.

Although only several snake vertebrae have been described at Děvínska Nová Ves, the diversity of the snake assemblage is relatively high. Several snake vertebrae discovered were still articulated with each other (Děvínska Nová Ves – "Bonanza") and were partially enclosed within the sandstone. The preparation would be problematic and the

visible characteristic features are not sufficient for a precise determination. I assume that vertebrae could belong to a small colubrid snake which is very similar to the morphotype Colubrinae D.

The morphotypes Colubrinae B & D represent quite different members of the subfamily Colubrinae. If the vertebrae of morphotype Colubrinae B belong to the genus *Elaphe*, it could represent one of the oldest discovery of this genus within the European area – an older discovery – cf. *Elpahe* sp. is known only from the German site Oggenhausen (MN 5/6) (SZYNDLAR & BÖHME 1993; SZYNDLAR & SCHLEICH 1993). Similarly, the morphotype Colubrinae D represents a member which is very similar to the genus *Coronella*. Until now, the oldest representative of this genus – *Coronella* cf. *C. austriaca* – was described from the Uppermost Miocene (MN 13) at the Hungarian locality Polgárdi 4 (VENCZEL 1994).

The genus *Neonatrix* sp. (subfamily Natricinae) is a typical representative of assemblage migrating into Europe from the area of North America. These representatives penetrated into West Europe as early as at the Lower/Middle Miocene transition (MN 4/5) as it was documented at the French locality Vieux Collonges (IVANOV 1997a, 1997b). Colubridae from Vieux Collonges (MN 4/5) belong obviously to the descendants of the migration wave preceding closely the ingression 4 (sensu MARTINI 1990) into the Rhine Graben (IVANOV 1997b).

The only discovered vertebra represents a member of subfamily Elapidae – Elapidae C. This vertebra belongs most likely to a cobra of the genus *Naja*, however, because of incomplete material a more precise determination was impossible. The history of the occurrence of cobras in Europe reaches to the Lower Miocene, the morphotype Elapidae A, discovered at the Czech Lower Miocene (MN 3a) locality Merkur (IVANOV 1997a, 1997b), could represent the oldest known member of Elapidae in Europe. Very interesting is the fact that, in this case, the first European cobras could belong to small elapids which are similar to the genus *Micrurus* or *Maticora* occupying recently the areas of South Asia and South America. The small cobras – *Micrurus gallicus* – survive in Europe demonstrably up to the final Middle Miocene (RAGE & HOLMAN 1984; RAGE & AUGÉ 1993; IVANOV 1997a, 1997b). The morphotype Elapidae C, discovered at Děvínska Nová Ves (MN 6), represents obviously a representative of another wave of immigrants of vertebrate fauna in Central Europe. The history of large elapids in Central Europe reaches up to the Upper Miocene – the species *Naja romani*, described already from the Lower Miocene (MN 4) of the German locality Petersbuch 2 (SZYNDLAR & SCHLEICH 1993), was discovered even within the Upper Miocene (MN 11) at the Austrian locality Kohfidisch (BACHMAYER & SZYNDLAR 1985, 1987). Large cobras penetrated into the West European area in a high degree at the Lower/Middle Miocene transition (IVANOV 1997a).

The Middle Miocene European representatives of the family Viperidae are represented by the genus *Vipera*. *Vipera* sp., discovered at Děvínska Nová Ves (SZYNDLAR 1991b), belongs to the 'European vipers' group of the uncertain complex. Several vertebrae may determine it as a member of the complex '*aspis*' (sensu GROOMBRIDGE 1986), like the vertebrae from the Polish Middle Miocene (MN 7) site Opole 2 (SZYNDLAR in MŁYNARSKI et al. 1982; SZYNDLAR 1984, 1991b). The 'Oriental vipers' group (sensu GROOMBRIDGE 1986) had appeared in the Central European area since the Lower Miocene (MN 4) – *Vipera platyspondyla* from the Czech locality Dolnice near Cheb (SZYNDLAR 1987a) – till the final Middle Miocene, which is documented at Steinheim a. A. (SZYNDLAR & SCHLEICH 1993). 'Oriental vipers' survived in South-eastern Europe till the Upper Pliocene (SZYNDLAR 1987b, 1988). It cannot be excluded that the representatives of 'Oriental vipers' penetrated into South-eastern Europe only from Asia but later –

for instance *Vipera maxima* from the Spanish Middle Pliocene (MN 15) locality Layna (SZYNDLAR 1988) – most probably also from Northern Africa across the Gibraltar. The Spanish Plio- Pleistocene representatives of 'Oriental vipers' (SZYNDLAR 1988; BAILON 1991) penetrated into the Iberian Peninsula most likely during the Messian crisis (MN 13) and they became part of the Iberian endemic fauna. 'Oriental vipers' became extinct in South-eastern Europe by the end of the Pleistocene.

Conclusion

Several taxa have recently been reported at Děvínska Nová Ves (Astaracian – MN 6) belonging to families Colubridae and Elapidae: Colubrinae B & D, Colubrinae gen. et sp. indet., *Neonatrix* sp. and Elapidae C. All the taxa (Colubridae and Elapidae) represent the modern European snake fauna.

The Middle Miocene is a period of the last occurrence of the family Boidae in the Central European area. Large representatives of Boidae (Boinae + Pythoninae) became extinct most probably at the Lower/Middle Miocene transition. Above all, the representatives of the family Colubridae were responsible for the displacement of Boidae from Central Europe and Colubridae became gradually dominant among the remaining ophidian families. The last boom of the evolution of Colubridae took place during the Upper Miocene which was documented among others by the evolution of the genus *Elaphe* (IVANOV 1997a, 1997b). The representatives of the family Elapidae survived in Central Europe over the Middle Miocene and became extinct in Upper Miocene. The representatives of Viperidae occur in the Central European area up to the present. However, 'Oriental vipers' – like Elapidae – survived there only till the terminal of the Middle Miocene.

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SOUHRN

Plazí společenstvo Děvínské Nové Vsi (Astaracien – MN 6) je diverzifikované, zahrnuje čeledě Colubridae, Elapidae a Viperidae. Z této lokality byly nedávno popsány následující hadí taxony: Colubrinae B & D, Colubrinae gen. et sp. indet., *Neonatrix* sp. a Elapidae C. Všechny taxony (Colubridae a Elapidae) jsou představiteli moderní evropské hadí fauny, která vytlačila „starobylou" hadí faunu (zahrnující čeleď Boidae) mimo oblast střední Evropy. Poslední středoevropský výskyt velkých boidních hadů (Boinae nebo Pythoninae) je dokumentován z přelomu spodního/středního miocénu, zatímco skupina „orientálních zmijí" se zde vyskytuje až do konce středního miocénu. Zástupci kober (Elapidae) ve střední Evropě vymřeli během svrchního miocénu.

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