

## MIDDLE-LATE MIOCENE SNAKES FROM THE PANNONIAN BASIN

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**Abstract.** The fossil record of Astaracian–early Vallesian (MN 6–MN 9) snakes is reviewed based on information derived from sixteen localities, situated on or adjacent to the former Pannonian Sea margins. The studied deposits yielded both Scolecophidia and Alethinophidia (Boidae, Colubridae, Elapidae, Viperidae). Indeterminable Scolecophidia were present in most localities, their remains consisting of trunk vertebrae only. The only Boidae recorded is a small-sized Erycinae snake (*Albaneryx* cf. *volynicus*) from Felsőtárkány 2, N-Hungary, which represents an important link between West- and East-European members of the genus. *Coluber pouchetii*, a member of the “large-sized colubrids” with still unresolved relationships, apparently was widely distributed across the European continent, whereas *Coronella miocaenica*, *Hierophis* cf. *hungaricus* and *Natrix* cf. *rudabanyaensis* possibly were newcomers from the Asiatic continent. Small-sized Elapidae, resembling the North-American genus *Micrurus*, were recorded on the basis of presacral vertebrae only. *Macrovipera* sp., from the “Oriental vipers group” is known from the Tauț and Vârciorog localities, W-Romania, whereas the vipers from the “*V. aspis* group” are known from Mátraszőlős 3, Subpiatră 2/1 and Felsőtárkány-Felnémet 2/3. The first occurrence of the “*V. berus* group” in Central Europe is reported from Felsőtárkány (1, 2 and 3/10 localities). The Astaracian–early Vallesian snake faunas of the Pannonian Basin were already dominated by modern colubrids (Natricinae and Colubrinae). Increasing faunal influence from the Asiatic continent is presumed to have started during the early Vallesian.

**Keywords:** Serpentes, Miocene, Fossil record, Hungary, Romania

## INTRODUCTION

The evolution of snake faunas was continuously influenced by climate and environmental changes as well as by tectonic rearrangement of continental plates. A scenario for the origin and history of European Cenozoic snakes was published by Ivanov et al. (2000), outlining the major changes which led to the extinction of ancient taxa and to the emergence of extant genera and species. The modern colubrids became the main component of the snake assemblages from the Miocene onward, while after the so-called Miocene Climatic Optimum (18–14 Ma: Ottnangian–Middle Badenian) (see Böhme, 2003) the non-Erycinae Boidae disappeared completely from the fauna.

The aim of the present paper is to review the fossil record of snakes from a series of Astaracian–Vallesian microvertebrate localities within the territory of Hungary and Romania. Sixteen localities included in this study are situated on or adjacent to the former Pannonian Sea margins and the resulting faunas belong to four biostratigraphic units (MN6–MN9). Most of these sites with snake rests were discovered in the last decade or so (Hír et al., 1998; Gál et al., 1999, 2000; Hír, 2006; Venczel & Hír, 2008; Hír & Kóky, 2009). The fossil remains discussed in this paper are housed in the Municipal Museum of Pásztó, Hungary (FF, FT, M, SH), the Speleological Institute „Emil Racoviță”, Bucharest, Romania (TAU) and the Țării Crișurilor Museum, Oradea, Romania (SU, TAS, VA). Osteological nomenclature of snakes and measurements of vertebrae follows Szyndlar (1984).

Abbreviations used in the present paper: MMP: Municipal Museum of Pásztó, Hungary; ISER: Speleological Institute „Emil Racoviță”, Bucharest, Romania; MTC: Țării Crișurilor Museum, Oradea, Romania; FF: Felsőtárkány-Felnémet (N-Hungary); FT: Felsőtárkány (N-Hungary); M: Mátraszőlős (N-Hungary); SH: Sámsonháza (N-Hungary); SU: Subpiatră (W-Romania); TAS: Tășad (W-Romania); TAU: Tauț (W-Romania); VA: Vârciorog (W-Romania); CL: centrum length; CW: centrum width.

## SYSTEMATIC PART

Suborder **SERPENTES** LINNAEUS, 1758

Infraorder **SCOLECOPHIDIA** DUMÉNIL & BIBRON, 1844

**SCOLECOPHIDIA** indet.

The available material consists of trunk vertebrae (M2, M3, TAS, SU2/1, TAU, FF2/3, FT1, FT2, FT3/10), preserving various parts of the vertebral centrum, neural arch and synapophyses (Pl. I: Fig. 1). They collectively document the typical morphological features of scolecophidians, shared by the members of Typhlopidae, Leptotyphlopidae, and Anomalepididae: the neural arch is depressed dorso-ventrally and devoid of neural spine; the centrum is flattened and free of haemal keel; the subcentral foramina are present; the cotyle and the condyle are depressed dorsoventrally; the paracotylar foramina are lacking; the synapophyses are undivided and have a hemispherical shape. Accordingly, the material is not suitable for a more inclusive assignment within scolecophidians. Presently our continent is inhabited by the only European member of Typhlopidae, the European worm snake (*Typhlops vermicularis*) (Gasc et al., 1997).

Infraorder **ALETHINOPHIDIA** NOPCSA, 1923

Family **BOIDAE** GRAY, 1825

*Albaneryx* cf. *volynicus* was recorded from FT2, based on one trunk vertebra and one caudal vertebra. Both vertebrae are extremely small (Pl. I: Figs. 2, 3) approaching in morphology those of *Albaneryx volynicus*, described from the early late Miocene (MN 9) of Gritsev (Zerova, 1989). The neural spine of the trunk vertebra is somewhat longer than that of *A. volynicus*, whereas its posterior margin is pointed similarly as in the latter form (Zerova, 1989; Szyndlar, 1991a). The neural spine of the caudal vertebra MMP 2009.608/2 is distinctly higher and more widened posteriorly than that of *A. depereti* (Hoffstetter & Rage, 1972), approaching the condition seen in *A. volynicus* too.

Up to now, the fossil record of this genus included

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Sansan (MN 6), La Grive M+L7 (MN 7), La Grive L3+L5 (MN 8), France, Kleinenbach (Bavarian Molasse Basin), Germany (Böhme & Ilg, 2003) and two late Miocene localities from the territory of Eastern Europe: the late Miocene (MN 9) of Gritsev (*Albaneryx volynicus* Zerova, 1989), and the late Miocene (MN 12) of Cherevichnoie (*Albaneryx* sp.) (Szyndlar & Zerova, 1992).

#### Family COLUBRIDAE OPPEL, 1811

Within Colubridae the informal name "Natricinae" and "Colubrinae", used mostly by paleontologists as a subfamilial rank, is applied in the present paper. All Natricinae possess the hypapophysis in the precaudal vertebrae, whereas in Colubrinae the hypapophysis of the trunk vertebrae is reduced to a haemal keel.

#### "NATRICINAE"

Until now two fossil members of the genus *Natrix* were listed from the studied localities: *N. cf. rudabanyaensis* and *N. sansaniensis*.

*N. cf. rudabanyaensis* was recorded from TAU, FF2/7, FT2, FT3/2 and FT3/10 (Pl. I: Figs: 4-9). The material consists of a series of cranial bones and precaudal vertebrae. The supraoccipital crest of the prootic (MMP 2009. 611/1 from FT2) is prominent; the foramen for the maxillary ramus of the trigeminal nerve ( $V_2$ ) is relatively small and of oval shape, and it is joined anteroventrally by the foramen for the exit of the constrictor internus dorsalis nerve ( $V_4$ ) (Pl. I: Fig. 4). In the parietal from M1, the dorsal crests do not converge anteriorly the parietal posterior margin (Pl. I: Fig. 5). The vertebrae of *N. cf. rudabanyaensis* are of relatively small size (the CL of the larger specimens reaches 4 mm) and moderately elongated (CL/CW approaching 1.5). The relatively long hypapophysis projects beyond the condyle and is rounded distally. The vertebrae from the above localities approach in morphology and size those from the type locality (Pl. I: Figs. 6-9). In fact, this species was described from the early Vallesian (MN 9) locality complex of Rudabánya (N-Hungary) on the basis of precaudal vertebrae only (Szyndlar, 2005). Thus, the available cranial bones were assigned with some doubt to this species. *N. rudabanyaensis* was not recorded beyond the borders of the Carpathian Basin and it may be considered an early Vallesian invader from Asia.

*N. sansaniensis* was briefly described from M1 by Gál et al. (1999). The vertebrae are of various sizes with relatively high neural spines and provided with very long prezygapophyseal processes.

The remaining materials of Natricinae were assigned either to *Natrix* sp. or to Natricinae indet. The presence of Natricinae snakes, based on habitat preference of recent forms, indicates the existence of aquatic paleoenvironments in the vicinity of the fossil deposits.

#### "COLUBRINAE"

Four genera were identified in the studied localities: *Coronella*, *Elaphe*, *Hierophis*, and *Texasophis*.

The only remains assigned to *Coronella miocaenica* are four trunk vertebrae recovered from TAU (Venczel & Ştiucă, 2008). They closely resemble the type material from the late Miocene (MN 13) of Polgárdi 4, Hungary

(Venczel, 1998), by their relatively small size, elongated centrum, moderately flattened neural arch and by extremely short prezygapophyseal processes (the measurements of ISER Tt-0490/1: CL=3.45, CW=2.38, CL/CW= 1.45) (Pl. I: Figs. 10-12). The neural spine of *C. miocaenica* is moderately high (if compared to recent *Coronella*), and it overhangs both anteriorly and posteriorly without any thickening of the dorsal margin.

*Texasophis cf. meini* was described briefly by Gál et al. (1999) from M1 (Pl. II: Figs. 1, 2). The available material consists of five trunk vertebrae of relatively small size (the CL of the largest one is 3.6 mm and it is 1.4 times longer than wide). The neural arch is depressed and provided with a relatively long and low neural spine. The zygosphenes are narrow with straight or crenate anterior margin, whereas the prezygapophyseal processes are extremely short. The subcentral area is concave ventrally and the haemal keel is prominent with a flattened ventral surface. A taxon with a rather similar morphology to *Texasophis cf. meini* (i.e. *Telescopus bolkayi*), was described recently from the early Vallesian (MN 9) locality of Rudabánya (Szyndlar, 2005).

Remains referred to *Coluber* (named as *Coluber* sp.) were reported from the Astaracian (MN 6) site of SH by Hír et al. (1998). Of the five vertebrae assigned to this form, the largest one has a centrum somewhat longer than wide (CL = 8.08 mm, CW = 7.62 mm, CL/CW = 1.06). The haemal keel is flattened and widened posteriorly; in few of the assigned specimens it is steeply angled behind the cotylar lip. The neural arch is moderately vaulted, provided with a putatively high neural spine; the anterior margin of the zygosphenes is straight; the paradiapophyses are distinctly differentiated into parapophyseal and diapophyseal portions and are roughly of equal length. More numerous and better preserved material assignable to the above taxon was recovered from the localities of M1, M2, M3, FT3/2 and FT3/10; it consists of fragmentary basiparaspheoid, quadrate, cervical and trunk vertebrae. In fact, the vertebrae from the above localities are morphologically comparable to those described under the name *Coluber pouchetii* from the Astaracian (MN 6) of Sansan, France (Augé & Rage 2000) and cf. *Coluber pouchetii* from the early Vallesian (MN 9) of Rudabánya. However, part of the material derived from the localities of M1 and M2 was already described under the name of *Elaphe* sp. by Gál et al. (1999, 2000) (Pl. II: Figs. 3-5). After the latter authors, the assignment was based mainly on the fact that the hypapophyses of the cervical vertebrae have an anteroventral orientation (Pl. II: Fig. 3), feature observed only in some egg eating colubrids (e.g. *Dasypeltis* and *Elaphe*). On the contrary, in members of *Coluber* such morphological character was never observed (Szyndlar, 2005). Thus, the future taxonomic revision of the above forms is considered necessary.

A single small sized vertebra (CL = 3.32, CW = 3.03) derived from FT1 may be assigned to *Elaphe* sp. The centrum is short and wide (CL/CW = 1.09), whereas the haemal keel is flattened and spatulate. The zygosphenes are crenate and the paradiapophyses are markedly differentiated into parapophyseal- and diapophyseal portions; the parapophyses are distinctly longer than the diapophyses. All the above features are typical for the members of *Elaphe*.

*Hierophis cf. hungaricus* was already described from the late Middle Miocene (MN7+8) of Tauț, Romania on

the basis of a quadrate and 35 trunk vertebrae (Venczel & Ştiucă, 2008). Further material was recovered from FF2/3 and FF2/7 (Venczel & Hír, in prep.). The trunk vertebrae from TAU are slightly larger (CL = 4.05-5.9, CW = 2.84-4.63, CL/CW = 1.23-1.45, n = 10) than those from FF2/3 and FF2/7 (CL = 3.02-3.1, CW = 2.07-2.1, CL/CW = 1.44-1.48, n = 4). The neural arch is moderately vaulted, sometimes provided with small epizygapophyseal spines; the zygosphene is convex dorsally with distinct crenate anterior margin; the paradiapophyses are of minute size with the parapophyseal and diapophyseal portions of roughly the same length; the prezygapophyseal processes are flattened dorsoventrally of variable length and usually with an acute tip (Pl. II: Figs. 6, 7). The subcentral area has a slightly concave surface, whereas the haemal keel is flattened (more prominent in the posterior presacral region). The material from M1, described briefly under the name *Coluber* sp. by Gál et al. (1999), approaches in morphology the remains from the above-mentioned localities, probably representing the same taxon.

Several fragmentary vertebrae were assigned to Colubrinae indet. or Colubridae indet., which probably may have belonged to several small-sized colubrid genera.

#### Family ELAPIDAE BOIE, 1827

*Micrurus gallicus* was reported from SH. The material consists of nine fragmentary presacral vertebrae with an elongated centrum and with a somewhat depressed neural arch. The hypapophysis is prominent and pointed distally; it projects posteriorly below the condyle. The neural spine is low and long, overhanging anteriorly and posteriorly. The parapophyseal and diapophyseal portions of the paradiapophyses are of equal length; the parapophyseal processes are relatively short and directed forwards. The anterior margin of the zygosphene is crenate with two lateral lobes and with a medial larger one. Other elapid material, consisting of few fragmentary vertebrae is known from FT2 and FT3/2 (Venczel & Hír, in prep.).

All the above remains represent small-sized Elapidae. The only large-sized elapid snake, genus *Naja*, is known from the early Vallesian (MN 9) locality of Rudabánya (Szyndlar, 2005).

#### Family VIPERIDAE OPPEL, 1811

Within vipers usually three groups or complexes are distinguished based on the size and morphology of presacral vertebrae: the "Oriental vipers group", the "*Vipera aspis* group" and the "*Vipera berus* group" (Szyndlar, 2005).

A large-sized maxilla and few vertebrae, representing the "Oriental vipers group" (*Macrovipera*), were discovered recently from the Astaracian (MN 7+8) locality of VA1 (Pl. II: Figs. 8, 9). The maxilla is distinctly larger when compared to European vipers (e.g. to *V. ammodytes*); it preserves two tooth positions (Pl. II: Figs. 9, 10). The dorsal process is relatively high and curved medially. In posterior view, the fossa for the ectopterygoid articulation is relatively deep, delimited dorsally by a transversal crest. The foramina for the dental canal are situated on the medial side of the bone at the base of the dorsal process (two foramina in a deep common fossa). A bony crest is developed on the anterior side of the dorsal process. On the lateral side of the latter, near its apex, a small foramen is observed. A presacral vertebra was described under the

name *Macrovipera* sp. from TAU (Venczel & Ştiucă, 2008). It is of relatively large size (CL = 8.18, CW = 6.64, CL/CW = 1.23), provided with putatively high neural spine and relatively long and straight hypapophysis (Pl. II: Fig. 10). Morphologically the specimens approach those described from the late Miocene (MN 11) of Kohfidisch, Austria (Bachmayer & Szyndlar, 1985, 1987) and Polgárdi (MN 13), Hungary (Venczel, 1994, 1998).

*Vipera* sp. ("*V. aspis* group") was recorded from FF2/3, FT3/10, M3 and SU2/1, the material consisting of isolated and fragmentary presacral vertebrae. The neural arch is depressed dorsoventrally; the neural spine in all the specimens is broken off. The hypapophysis is straight, long and posteroventrally oriented. The anterior margin of the zygosphene is crenate; the prezygapophyseal processes are extremely short, with pointed tips. The paradiapophyses are differentiated into diapo- and parapophyseal portions; the parapophyseal processes with their tips obtuse distally project anteroventrally. The centrum in a presacral vertebra from SU2/1 is moderately elongated (CL = 4.24, CW = 2.92, CL/CW = 1.45) (Venczel, 2007), whereas that of a larger specimen from M3 (Pl. II: Fig. 11) is comparatively shorter (CL = 5.16, CW = 4.16, CL/CW = 1.24).

*Vipera* sp. ("*V. berus* group") was recorded from FT1 (one vertebra), FT2 (one vertebra) and FT3/10 (three vertebrae). All the specimens are fragmentary, but they document collectively the most important morphological features of the "*V. berus* group". The centrum is relatively long (about 1.66 times longer than wide in one of the FT3/10 specimens), provided with a moderately long hypapophysis projecting backward beyond the condyle. The neural arch is depressed and the remnants of the neural spine indicate that it was of low height and overhanging posteriorly. Based on the above features, the vertebrae may be assigned to the "*Vipera berus* group" (Szyndlar, 1991b). In fact, the finds from the early Vallesian (MN 9) of FT represent the oldest remains of this group from the territory of Central Europe. Apart from the FT localities, the oldest record of this group comes from Gritsev (MN 9), Ukraine (Zerova, 1987; Szyndlar, 1991b).

#### CONCLUDING REMARKS

The Astaracian–early Vallesian snake faunas from the Pannonian basin are represented by taxa from at least five different groups (Scolecofiphidia, Boidae, Colubridae, Elapidae, and Viperidae). The faunas exhibit a relatively low local diversity (1-7 taxa/locality), determined by the fact that all the studied localities were deposited in marshy-lacustrine areas, yielding taxa with near-water habitat preference.

The composition of snake faunas illustrates modern patterns, dominated by colubrid snakes. A series of widely-distributed taxa were distinguished (e.g. *Coluber pouchetii*, *Natrix sansaniensis*, *Texasophis* cf. *meini*), indicating important faunal links to Western Europe. The assemblages from younger localities (MN 9) exhibit a comparatively more diverse fauna, which points to an increasing influence from Asia. The latter fact is marked by the record of *Albaneryx* cf. *volynicus*, the appearance of new Natricinae (*N. rudabanyaensis*) and Colubrinae (*Coronella miocaenica*, *Hierophis* cf. *hungaricus*, *Telescopus bolokay*) and by the first record of the "*V. berus* group".

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## PLATES

## Plate I

Fig. 1: **SCOLECOPHIDIA** indet.: trunk vertebra from FT2. Figs. 2, 3: *Albaneryx* cf. *volynicus*: trunk vertebra from FT2 (2); caudal vertebra from FT2 (3). Figs. 4-9: *Natrix* cf. *rudabanyaensis*: prootic from FT2 (4); parietal from M1 (5); presacral vertebra from M3 (6), presacral vertebra from FT2 (7) presacral vertebra from TAU (8, 9); Figs. 10-12: *Coronella miocaenica*: trunk vertebra from TAU.

1, 2, 5, 9, 10 – dorsal views; 3 – anterior view; 4, 6-8, 11 – lateral views; 12 – ventral view. Scale = 1 mm (Figs. 1-4); scale = 2 mm (Figs. 5-12).

## Plate II

Figs. 1, 2: *Texasophis* cf. *bohemicus*: trunk vertebra from M1. Figs. 3-5: *Coluber pouchetii*: fragmentary cervical vertebra from M1 (3); trunk vertebra from M3 (4, 5). Figs. 6, 7: *Hierophis* cf. *hungaricus*: trunk vertebra from TAU.

Figs. 8-10: *Macrovipera* sp.: maxilla from VA (8, 9); presacral vertebra from TAU (10). Fig. 11: *Vipera* sp. (“*Vipera aspis* group”): presacral vertebra from M3. Fig. 12: *Vipera* sp. (“*Vipera berus* group”): presacral vertebra from FT3/10. 1, 3, 10, 11, 12 – lateral views; 2, 5, 7 – ventral views; 4, 6 – dorsal views; 8 – posterior view; 9 – anterior view. Scale = 1 mm (Figs. 1-3); scale = 2 mm (Figs. 4-12).

PLATE I



