QUATERNARY SNAKES
FROM BIHOR
(ROMANIA)

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1. INTRODUCTION

The snake remains, as indicated by numerous data are relatively common in the Neogene and Quaternary fossil bearing sediments. The great majority of them are known almost exclusively from paleokarstic deposits appropriate to preserve vertebrates and mollusks (HORAČEK & KORDOS, 1989). Other sources of fossils are known from archeological sites (mainly of Upper Pleistocene and Holocene age). However, articulated skeletons known from such deposits are extremely rare, the overwhelming part of the materials being disjointed, consisting of fragmentary vertebrae and ribs.

Unfortunately, in our country snakes have been largely excluded from paleontological studies until quite recent times. In this respect it could be mentioned that a high number of publications dealing with fossil vertebrates of Romania are focused on mammals (and mainly on micromammals), group of animals on which the biochronology of terrestrial ecosystems in the Neogene and Quaternary is based (e. g. TERZEA, 1973, 1983, 1991, 1992, 1994, 1995; TERZEA & JURCSÁK, 1969, 1976; JURCSÁK et al., 1982, 1984, a. o.). Except for few papers on fossil herpetofaunas, published in the first decades of the 20th century (e.g. BOLKAY, 1913; VON SZUNYOGHY, 1932), most of our knowledge of Romanian Quaternary fossil snakes are derived from studies published in the late fifteen years (e. g. VENCZEL, 1987, 1989, 1991, 1992, 1997, 1999) and are mainly restricted to the territory of Bihor County (W-Romania), an extremely rich area in paleokarstic deposits.

Snakes are poikilothermal animals with relatively reduced mobility, reflecting accurately the existing ecological conditions. Due to this the ophidians may be extremely useful in the reconstruction of terrestrial paleoenvironments of different geological ages (BAILON, 1991). Furthermore their fossil record promote better understanding of paleofaunistic and paleobiogeographic events during Neogene and Quaternary times, and implicitly the origin of the modern European snake fauna. The morphological and micromorphological studies on ophidian cranial bones provide valuable data on ranges of intraspecific variations, and even may contribute to the establishing of the evolutional tendencies of the studied species (SZYNDLAR, 1991c).

The present work is a simplified and updated version of my Doctoral Thesis (VENCZEL, 1995) describing the Quaternary and Holocene snake remains discovered in the territory of Bihor County, Romania. All the remains studied (more than 30000 skeletal elements) are housed in the paleontological collections of the Natural History Department of the Ţării Crişurilor Museum in Oradea.

Acknowledgements. The author is deeply indebted to a number of persons for their kind help during this study. Late paleontologist Tibor Jurcsák (Ţării Crişurilor Museum, Oradea), gave valuable information on the fossil localities of Betfia, Râpa, Galoşpetreu and Vadu Crişului, and made the fossil snake material available for study. The author held helpful discussions with Dr. Elena Terzea regarding the fossil localities of Betfia and Subpiatră. Geologist Radu Robert Huza (Ţării Crişurilor Museum, Oradea), assisted collecting the fossil materials from Subpiatră and also collected the microvertebrate materials from Chişcău 3. Dr. Ioan Ghira helped getting a number of specimens for comparative materials of the genera *Coluber*, *Elaphe*, *Coronella*, *Natrix*, and *Vipera*. Prof. Zbigniew Szyndlar (Polish Academy of Sciences, Kraków) made available for study the recent snake skeletons under his care, helped access to the relevant literature and shared many unpublished data with the author as well. Prof. Gernot Rabeder and Dr. Karl Rauscher (Institute für Paleontologie der Universität Wien) helped procuring the relevant literature and made possible the access to comparative materials in their care. Dr. Ortwine Schultz (Naturhistorisches Museum, Palaeont. Abteilung, Wien) made possible to examine the fossil snake material from Kohfidisch, while Dr. Antonia Cabela and Dr. Franz Tiedemann (Naturhistorisches Museum, Zool. Abteilung, Wien) made possible to examine recent snake skeletons from the Museum's collection. Péter Ujhelyi (Budapest) made available snake specimens from his personal collection. Dr. Olivér Dely, Dr. Zoltán Korsós (Hungarian Natural History Museum, Budapest) and Dr. Dan Cogălniceanu (University of Bucureşti) helped procuring the relevant literature. Prof. Dénes Jánossy, Dr. Gasparik Mihály (Hungarian Natural History Museum, Budapest) and Prof. László Kordos (Geological Museum of Hungary) made available the fossil materials originating from Betfia 2. Late Prof. Bogdan Stugren and Prof. Nicolae Tomescu (Babeş-Bolyai University, Cluj-Napoca) gave valuable information during this study and critically read the earlier draft of the manuscript. Ilona and Zsolt Venczel assisted me during collecting trips. The latter made the cover design also. The staff of Natural History Department of Ţării Crişurilor Museum, Oradea helped in various way during this study. The Board of Managers of the Ţării Crişurilor Museum, Oradea gave financial support in my research work and in edition of this book.

2. MATERIAL AND METHODS

2.1. The fossil materials

The snake remains studied here come from sixteen fossil localities situated in the territory of Bihor County (W-Romania)(Fig. 1). The geological age of these deposits is between Lower Pleistocene and Holocene (Fig. 2). The overwhelming part of the ophidian materials is consisted of isolated skull bones and vertebrae, collected between years 1958 – 1974 (those coming from Betfia pothole/A, Betfia 5, Betfia 7, Betfia 9/A, Betfia 10, Betfia 11, Betfia 12/A, Betfia 13, Râpa, Vadu Crişului, Galoşpetreu). The collecting trips were undertaken by the staff of Natural History Department of Ţării Crişurilor Museum in Oradea, Romania (led by paleontologist Tibor Jurcsák). Part of the excavations in the fossil locality Betfia were organized jointly with the Speleological Institute "Emil Racoviță" in Bucharest (Dr. Elena Terzea), while those at the locality Râpa, with the local Museum in Tinca (represented by Coloman Csák). The vertebrate remains obtained from the localities Betfia 1 – 6 at the beginning of the 20th century by Dr. Mihály Tóth and Dr.Tivadar Kormos, as well as those coming from the locality Betfia 5 (collected in 1941 by Dr. Miklós Kretzoi) are housed in the Hungarian Natural History Museum, Budapest and in the Geological Museum of Hungary in Budapest. The fossil remains originating from the localities Betfia pothole/B, Betfia 9/B, Betfia 9/C, Betfia 12/B, Subpiatră and Chişcău 3 were collected during years 1989 – 1999 by the members of the Natural History Department of the Ţării Crişurilor Museum (led by the author) in co-operation with the Municipal Museum in Pásztó, Hungary (led by Dr. János Hír).

The microvertebrate materials were obtained by screening and washing the sediments using screens with 0.8 – 1 mm size. Part of the material was obtained from strongly brecciated sediments (e.g. those coming from Betfia 9/B and Subpiatră) using acetic acid. The ophidian remains were selected apart from other microvertebrate remains using taxonomic criteria. The obtained material was cleaned off, dried and impregnated with solute rhodopast.

2.2. The fossil localities

Sixteen fossil localities studied in this paper are listed in order of their biochronological age (Fig. 2).

Material and methods

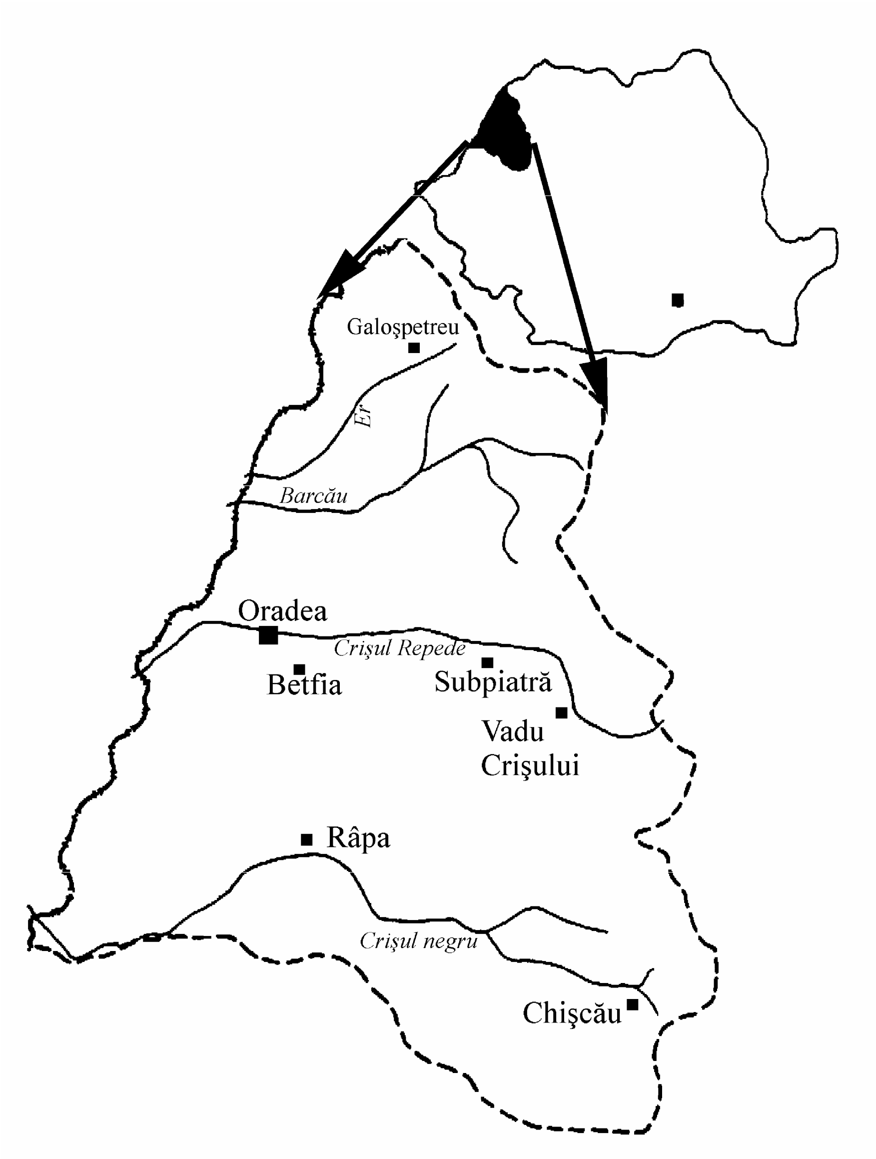


Figure 1. Location map of the studied fossil localities.

Geochronological age (m.y.)	General subdivision of the Pleistocene	Faunistical subdivision of M. Kretzoi	Cronostratigraphical subdivision	Biozones with arvicolids (after Kordos, 1992)	Biostratigraphical position of some fossil localities from Bihor
			POSTGLACIAL	Arvicola terrestris	GP, VC, VM
	SUPERIOR	TORINGIUM	WEICHSELIAN		Râpa
			EEMIAN		
0,2	MIDDLE		SAALIAN	Lagurus lagurus	
			HOLSTEINIAN	Arvicola cantiana	Chişcău-3
			ELSTERIAN		
0,4		BIHARIUM	CROMERIAN	*Lagurus transiens* *Arvicola cantiana*	
0,6				*Mimomys savini* *Lagurus transiens*	Betfia 7/4
	INFERIOR		BAVELIAN	Mimomys savini	Subpiatră
0,8				*Mimomys savini* *Mimomys pusillus* *(Dicrostonyx)*	Betfia 7/3
1,0			MENAPIAN		Chişcău-1 Betfia 7/2 Betfia 5
				Allophaiomys pliocaenicus	
1,2 1,4			WAALIAN		Betfia pothole/A Betfia 7/1 Betfia 2(1-4) Betfia 9 Betfia 11 Betfia 10
			EBURONIAN		
1,6				*Mimomys pliocaenicus* *Allophaiomys deucalion*	Betfia 13

Figure 2. Biostratigraphic position of the studied localities.

Material and methods

Most of the fossil sites have been discovered in the Somleu Hill (with about ten diffe- rent fossil localities) near the small village of Betfia, Bihor County (Romania) (Fig. 3).

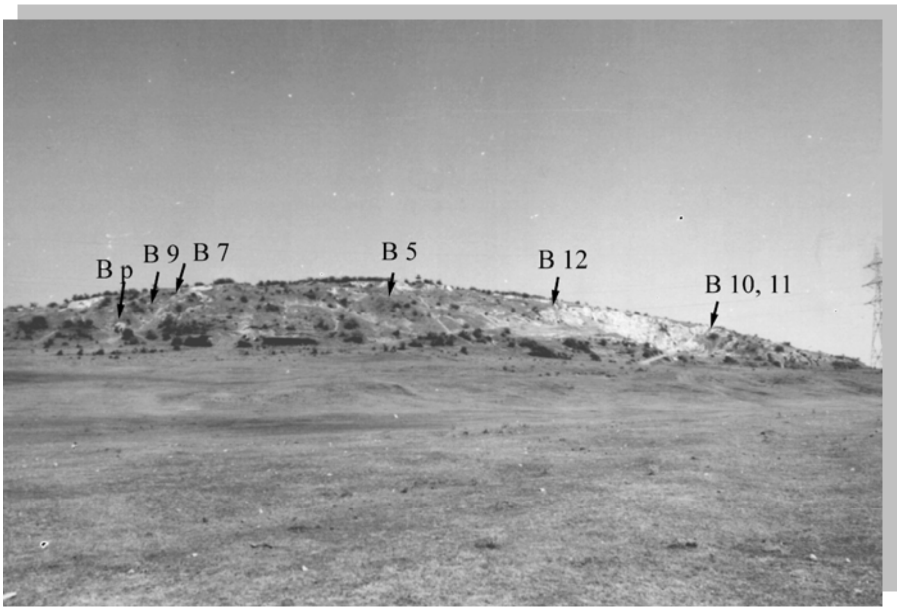


Figure 3. View of Somleu Hill, near the village of Betfia. Bp – Betfia pothole.

Betfia 13. It is situated approximately 100 m North to the Betfia pothole (at 46º 58’ 94” Northern latitude and 22º 01’ 19” Eastern longitude). E. Terzea and T. Jurcsák have excavated the fossil locality. The vertebrate assemblage among others contained: *Blarinoides mariae*, *Sorex* (*D.*) *praearaneus*, *Sorex* cf. *subaraneus*, *S. minutus*, *S. runtonensis*, *Asoriculus gibberodon*, *Petenyia hungarica*, *Beremendia fissidens*, *Crocidura kornfeldi*, *Erinaceus* sp. 1, *Talpa fossilis*, *Talpa* cf. *epsicopalis*, *Desmana thermalis* (RZEBIK-KOWALSKA, 2000a; 2000b); *Prospalax priscus*, *Trogontherium boisvilletti*, *Glis minor*, *Villanyia exilis*, *Mimomys* gr. *pliocaenicus*, *Allophaiomys pliocaenicus deucalion*, *Lagurus arankae*, *Canis* cf. *falconeri*, *Ursus etruscus*, *Equus stenonis* cf. *senezensis*. Few rarities from the faunal assemblage are: *Epimeriones dacicus*, *Sminthozapus betfianus*, and *Macaca sylvana* cf.

florentina (TERZEA, 1984, 1993, 1995; TERZEA & JURCSÁK, 1976). After KESSLER (1975) the bird fauna was made up by *Anas* cf. *crecca*, *A*. *querquedula*, *Lyrurus* cf. *tetrix*, *Francolinus čapeki*, *Tringa* aff. *totanus*, *Acrocephalus* cf. *arundinaceus* and *Turdus merula*. The ophidian materials originating from this locality are rather scanty; only fragmentary remains belonging to *Coluber viridiflavus* could be identified.

The presence of cercopithecid *Macaca*, as well as those of glirids, murids and castorids, among mammals, and *Francolinus* among birds, suggest mild climate. The environment was diversified, with forests and water courses in the vicinity of the locality. Its fossil fauna may be cotemporanous with an Eburonian interstadial, in the middle of this glacial complex (TERZEA, 1988, 1993, 1995) or may be fitted in the *Mimomys pliocaenicus – Allophaiomys deucalion* biozone (KORDOS, 1992).

Betfia 10 (Fig. 4). E. Terzea and T. Jurcsák have discovered the locality in the northeastern part of the local limestone quarry.

Figure 4. Locality of Betfia No. 10 and Betfia No. 11

Material and methods

The above authors published the following list of micromammals: *Beremendia fissidens*, *Drepanosorex margaritodon*, *Allocricetus bursae*, *Cricetus cricetus nanus*, *Muscardinus dacicus*, *Glis sackdilligensis*, *Spalax advenus*, *Pliomys episcopalis*, as well as primitive forms of *Mimomys pusillus*, *Allophaiomys pliocaenicus pliocaenicus*, *Lagurus arankae*, a.o. (TERZEA, 1988; TERZEA & JURCSÁK, 1976, 1969). RZEBIK-KOWALSKA (2000a, 2000b) gave the following list of insectivores from this locality: *Blarinoides mariae*, *Sorex* (*D.*) *praearaneus*, *Petenyia hungarica*, *Beremendia fissidens*, *Sorex minutus*, *S. runtonensis*, *Crocidura kornfeldi*, *Talpa minor* and *T. fossilis*. *Coluber viridiflavus*, *Coronella austriaca*, *Elaphe longissima*, and *Natrix tesselata* make up the ophidian fauna. Based on micromammals the age of the fauna may be defined as Lower Biharian (Early Waalian) (TERZEA, 1994, 1995) and probable may be fitted in the *Allophaiomys pliocaenicus* biozone (KORDOS, 1992).

Betfia 11. The fossil locality is situated in the northeastern part of the Betfia limestone quarry in the close vicinity of the locality Betfia 10. E. Terzea and T. Jurcsák led the excavations here. Up to present time the rodent fauna of this locality was not published yet. Regarding the insectivores, the sediments contained *Sorex* (*D.*) *praearaneus*, *Asoriculus gibberodon*, *Petenyia hungarica*, *Beremendia fissidens*, *Crocidura kornfeldi*, *Sorex minutus*, *S. runtonensis*, *Talpa minor* and *T. fossilis* RZEBIK-KOWALSKA (2000a, 2000b). According to TERZEA (1994, 1995) this faunal assemblage seems to be of the same age or slightly younger than that of Betfia 10 (Early Waalian). In this case it may be correlated with the *Allophaiomys pliocaenicus* biozone of KORDOS (1992) too. *Coluber viridiflavus*, *Elaphe quatuorlineata*, *E.* cf. *E. longissima*, *Natrix natrix* and *N. tesselata* form the ophidian fauna.

Betfia 9. The locality is situated approximately 20 m north to Betfia pothole, at 314 m altitude, presumably close to the location of the classical locality Betfia 2 (at 46º 58’ 96” Northern latitude and 22º 01’ 21” Eastern longitude) (Fig. 5). The fossil materials collected by T. Jurcsák in the late fifties and early sixties (1957–1962) from this locality were originally labeled as “Betfia 3”. Than E. Terzea and T. Jurcsák have continued the excavation of this locality and one of them (ET) considering that “the classical localities being exhausted” proposed No. 9 for this locality. The micromammals coming from this locality were first published by TERZEA (1988). The brecciated sediments yielded among others: *Talpa* cf. *fossilis*, *Crocidura kornfeldi*, *Sorex* gr. *minutus*, *Petenyia hungarica*, *Beremendia fissidens*, *Cricetus cricetus*, *Mimomys pusillus*, *Mimomys tornen-*

sis, *Pliomys episcopalis*, *Allophaiomys pliocaenicus*, *Lagurus praepannonicus*, *Hypolagus brachygnathus*, *Mustella praenivalis*, *M. palerminea*, *Canis lupus mosbachensis*. In 1994 Venczel re-excavated the locality and found a rich microvertebrate fauna (named as Betfia 9/B in order to differentiate from that excavated by E. Terzea and T. Jurcsák) with an abundant series of *Allophaiomys* molars. However the list of micromammals found in Betfia 9/B (HÍR & VENCZEL, 1997) is rather similar (with few exceptions) to that published by TERZEA (1988). In 1995 the author found a terra rossa layer (named as Betfia 9/C) under the brecciform sediment of 9/B. This lower layer produced a special fauna dominated by *Apodemus*, *Pliomys* and *Muscardinus* indicating a forested paleoenvironment.

Figure 5. Locality of Betfia No. 9 and Betfia No. 7, and posibil locations (marked with ?) of the exhausted classical locality of Betfia No. 2.

Material and methods

Based on the *Allophaiomys* remains, the localities Betfia 9/B and 9/C are somewhat older in age than Betfia 2 (HÍR, 1998; HÍR & VENCZEL, 1997, 1998a, 1998b). RZEBIK-KOWALSKA (2000a, 2000b) gave the following list of insectivores (based on materials coming from all these localities: Betfia 9/A, 9/B, 9/C): *Sorex* cf. *subaraneus*, *S. minutus*, *S. runtonensis*, *Sorex* (D.) *margaritodon*, *Asoriculus gibberodon*, *Petenyia hungarica*, *Beremendia fissidens*, *Crocidura kornfeldi*, *Crocidura* cf. *obtusa*, *Sorex* sp., *Erinaceus* sp. 2, *Talpa minor*, *T. fossilis*, *T.* cf. *episcopalis*, *T.* cf. *semsey* and *Desmana thermalis*. The later author considered that the localities Betfia 9/B and 9/C roughly are of similar ages. KESSLER (1975) listed the birds identified in this locality (noted as coming from "Betfia 3" and respectively from "breccia with microfauna"): *Anas clypeata*, *Falco subbuteo*, *Perdix perdix*, *?Otis tarda*, *?O. lambrechti*, *Asio* cf. *otus*, *Corvus* cf. *monedula*, *Garrulus glandarius*, *Turdus merula*, *Anthus* aff. *trivialis*. However new results expected from the studies of fossil birds, especially those originating from the newly excavated locality Betfia 9/C, which is extremely rich in Passeriformes among others (Gál, in prep.). The locality complex yielded among others: Scolecophidia indet., *Coluber viridiflavus*, *Coronella austriaca*, *Elaphe paralongissima*, *E. quatuorlineata*, *Natrix natrix*, *N. tesselata*, *Vipera ammodytes* and *Vipera berus*.

Betfia 2 (1-4). The locality is the best known of all the fossil sites discovered in the Somleu Hill near the village of Betfia. It was known in the paleontological literature under the name Betfia (= Püspökfürdő). Dr. Mihály Tóth was the first who discovered the fossil site at the beginning of the 20th century, and soon he attracted Tivadar Kormos's attention (geologist at the Hungarian Royal Geological Institute in Budapest) on the extremely rich fossil vertebrate remains. The latter author visited the fossil locality first in 1904 giving a preliminary faunal list and presumed the age of the fauna of Upper Pleistocene age (!). Until 1918 he organized several collecting trips and located six fossil sites. Four of them were situated in the vicinity of Betfia pothole (however the exact location of the above mentioned localities are unknown): the locality Betfia 2 gave the main vertebrate fauna, with more than 80 vertebrate species. Unfortunately the remains found (albeit in a reduced number) in the other localities (situated in the vicinity of Betfia 2: Loc. No. 1, No. 3 and No. 4) were not separated off by those originating from Betfia 2. Subsequently KORMOS (1930, 1938) published the mammalian fauna of Betfia 2 (1-4) which served later as the stratotype of the Biharian faunas (KRETZOI, 1941, 1953; JÁNOSSY, 1979, 1986). Contributions dedicated to other vertebrate groups were published by BOLKAY (1913) (amphibians and reptiles), FEJÉRVÁRY (1917) (anurans), FEJÉRVÁRY-LÁNGH (1923) (*Pseudopus /= Ophisaurus/*), VON SZUNYOGHY (1932) (snakes), ČAPEK (1917) (birds). Based on the above publications, the fossil herpetofauna is consisted of *Pliobatrachus langhae*, *Pelobates* sp., *Bufo bufo*, *B. viridis*, *Rana esculenta* skl., *Pseudopus* (= *Ophisaurus*) *pannonicus*, *Anguis fragilis*, *Lacerta viridis*, *Coluber* (= *Zamenis jugularis*) *caspius*, *Elaphe* (= *Coluber*) *longissima*, *Natrix* (=*Tropidonotus*) *natrix*, and *N. tesselata*. It should be pointed out that HÍR (1998) reinvestigating the type material of *Allophaiomys pliocaenicus* of Betfia 2 found it rather homogenous, the distribution of the m1 morphotypes resembling closely those of Betfia 9/B. At the same time it can be mentioned that between 1966-1974 the collecting of the materials from these sites was continued by E. Terzea and T. Jurcsák who considering that "the classical localities being exhausted" gave separate numbers to the newly explored localities (respectively Betfia Loc. No. 7 and Betfia Loc. No. 9).

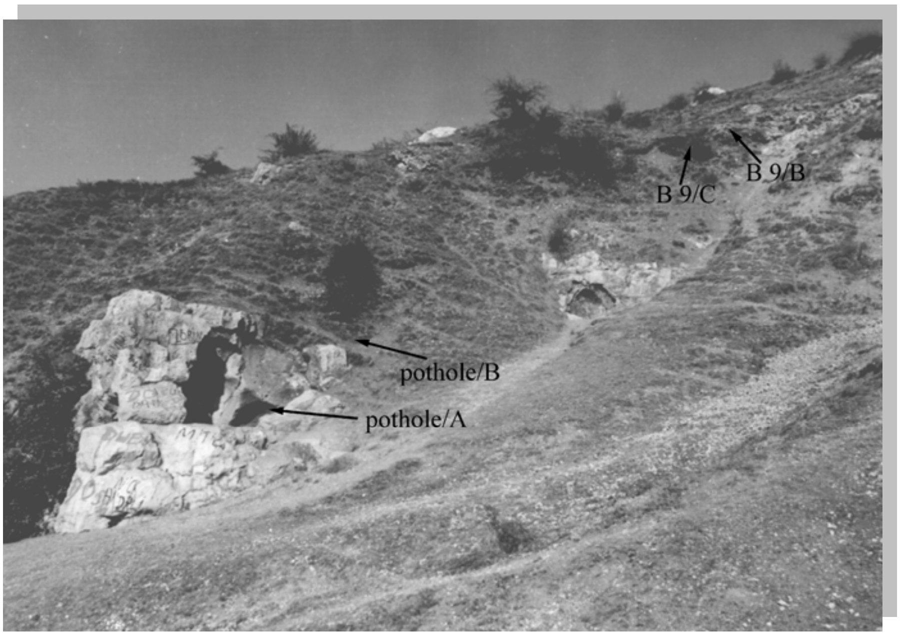


Figure 6. Locality of Betfia pothole/A and pothole/B.

Betfia pothole/A. The fossil bearing deposit was discovered in the bed of Betfia pothole (known under the local name Hudra Bradii) at – 64 m from entrance (at 46º 58' 94" Northern latitude and 22º 01' 19" Eastern longitude) (Fig. 6). The fossil materials were collected in 1958 by Tibor Jurcsák. The sediments found here were very probable redeposited from Betfia pothole/B (situated on the surface in the close vicinity of the Betfia pothole opening) after the "pothole" emergence as a result of the local limestone opencast at the beginning of 20th century. However the mammalian remains found here have never been published. Kessler (1975) gave the following list of birds: *Anas qeurquedula*, *A. strepera*, *A.* cf. *penelope*, *A. clypeata*, *Aythya nyroca*, *Falco subbuteo*, *F.* cf. *vespertinus*, *Francolinus capeki*, *Limosa limosa*, *Dendrocopos major*, *Corvus frugilegus*, *C.* cf. *monedula*, *Garrulus glandarius* and *Pyrrhocorax graculus*. *Coluber viridiflavus*, *Elaphe paralongissima*, *E. quatuorlineata*, *Natrix* sp., and *Vipera* sp. make up the ophidian fauna. The fossil vertebrate fauna of this locality as well as that from the locality Betfia pothole/B may be fitted in the biozone of *Allophaiomys pliocaenicus* of KORDOS (1992).

Betfia pothole/B. The fossil locality is situated in the proximity of Betfia pothole (2 – 3 m northeast to the pothole opening). The fossil materials coming from this locality have been collected by the author during year 1993. *Coluber viridiflavus*, *Elaphe paralongissima*, *E. quatuorlineata*, *Natrix natrix*, *N. tesselata*, *Natrix* sp. and *Vipera* sp form the snake fauna. The age of the fauna is similar with that originated from Betfia pothole/A.

Betfia 12/A. The fossil locality is situated in the northwestern part of the Betfia limestone quarry (at 46º 58' 82" Northern latitude and 22º 01' 13" Eastern longitude) (Fig. 7). T. Jurcsák has led the excavations in year 1969. The vertebrate remains originating from the sediments were consisted of snakes almost exclusively. RZEBIK-KOWALSKA (2000a, 2000b) mentioned remains of *Crocidura kornfeldi* and *Talpa minor* from this locality. In 1995 a rhinocerotid molar (probably belonging to *Rhinoceros etruscus*) has been found by V. Codrea (pers. com.). A rather frequent element here is the anguid lizard *Pseudopus pannonicus*, too. *Coluber viridiflavus*, *C.* cf. *C. gemonensis*, *Elaphe paralongissima*, *Natrix natrix*, *N. tesselata*, *Natrix* sp. and *Vipera* sp. consisted of the snakes. The age of the fauna is Lower Pleistocene (probable Waalian).

Betfia 12/B. The locality was discovered in a fissure of the limestone wall, approximately 5 m below the fossil locality of Betfia 12/A (Fig. 7). The snake fauna was made up by *Coluber viridiflavus*, *Elaphe* cf. *E. longissima*, *Natrix* sp. and *Vipera* cf. *V. ammodytes*. The age of the fauna was probable similar with that coming from Betfia 12/A.

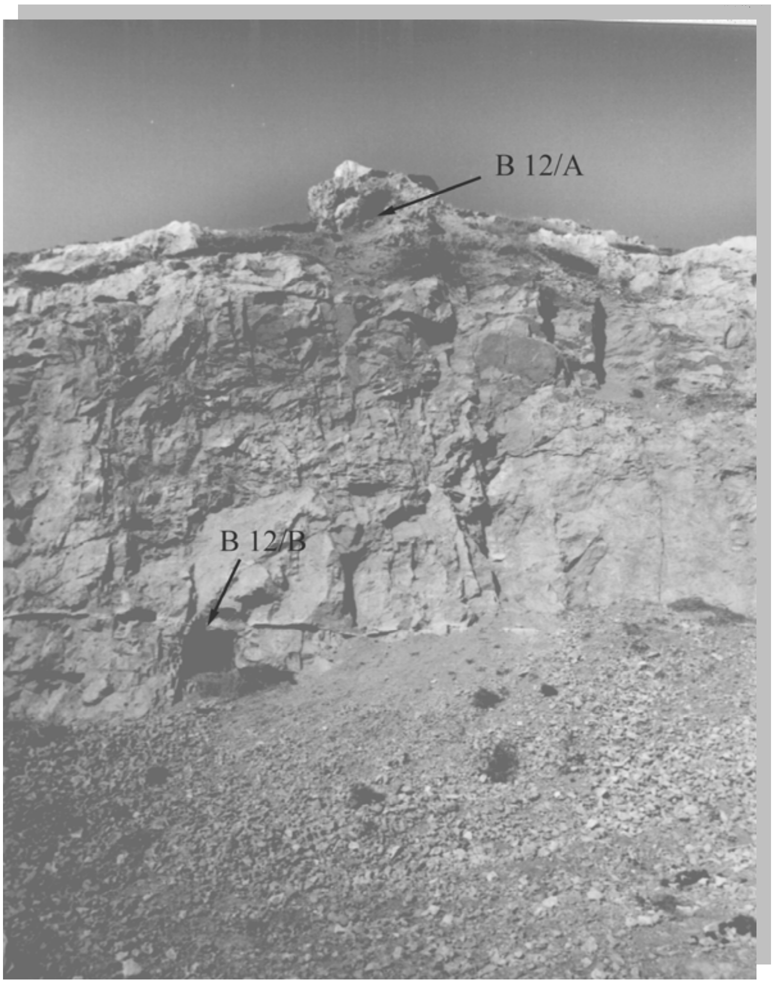


Figure 6. Locality of Betfia No. 12/A and Betfia No. 12/B

Betfia 7. The fossil locality is situated approximately 30 m north to Betfia pothole (at 46º 59’ 07” Northern latitude and 22º 01’12” Eastern longitude)

(Fig. 5). A first faunal list, resulted from excavation led by E. Terzea and T. Jurcsák, was published by these authors in 1969: *Mimomys savini*, *Pliomys episcopalis*, *Clethrionomys* sp., *Microtus* (*Pitymys*) *hintoni*, *M. arvalinus*, *Cricetus cricetus*, *Spalax* sp., *Ochotona* sp., *Lepus* sp., *Ursus? deningeri*, *Canis lupus mosbachensis*, a.o. Later studies on this faunal complex revealed that the accumulation of the sediments took place during few biochronostratigraphical units since the Waalian up to the Cromerian (TERZEA, 1993, 1994, 1995; RZEBIK-KOWALSKA, 2000a). According to the before-mentioned authors the sediments coming from this locality belong to four different phases. Betfia VII/1 may be connected with a short phase of cooling in the middle Waalian; Betfia VII/2 is little older than Betfia V and dated as Late Menapian; Betfia VII/3 is younger than Betfia V and may be placed in one of the two mild phases of the Bavelian interglacial. The faunal assemblage of Betfia VII/4 corresponds to a succesion of three climatic fluctuations, and may be correlated with Glacial A, Interglacial II and Glacial B of the Cromerian Complex (TERZEA, 1994). Unfortunately unlike the mammalian remains, the other vertebrate remains (including birds and ophidians), coming from these layers were not separated off, or were intermixed later (pers. obs.). KESSLER (1975) published the following list of birds from Betfia 7 (without specifying the exact layer of origin): *Anas strepera*, *Aythya nyroca*, *Perdix perdix*, *Tringa ?glareola*, *T. ?ochropus*, *Acrocephalus* cf. *arundinaceus* and *Anthus* aff. *trivialis?*. Regarding the snakes based on the stored material we could establish two layers only. The lower layer (or layers) probably coming from VII/1 – VII/3, included *Coluber viridiflavus*, *Coronella austriaca*, *Elaphe paralongissima*, *E. quatuorlineata*, *Natrix natrix*, *N. tesselata*, *Natrix* sp., *Vipera* berus and *V. ammodytes*, while the upper layer (probable representing VII/4) contained only remains of *Elaphe longissima*.

Betfia 5. This fossil locality is situated approximately 200 m eastward from the Betfia pothole (at 46º 58’ 97” Northern latitude and 22º 01’ 12” Eastern longitude). It has been described for the first time by KORMOS (1911). Later KRETZOI (1941) re-excavated the locality and listed among others: *Drepanosorex margaritodon*, *Mimomys* cf. *savini*, *Microtus* (*Pitymys*) *hintoni*, *Allocricetus bursae*, *Cricetus cricetus praeglacialis*, *Mustela palerminea*, *Gulo schloesseri*, *Canis lupus mosbachensis*, *Leo gombaszoegensis*, *Epimachairodus hungaricus*, *Capreolus süssenbornensis*, *Dicerorhinus etruscus*, *Alces latifrons*, *Bison schoetensacki*, a.o. The birds known from this locality are: *Palergosteon tóthi*, *Anas platyrhynchos*, *Anas* sp., *Falco tinnunculus*, *F.* cf. *subbuteo*, *Lyrurus partium*, *?Tetrao urogallus*, *Perdix jurcsáki*, *Otis lambrechti*, cf. *Asio flammeus*, *Corvus betfianus*, *Pyrrhocorax graculus vetus* and *Turdicus tenuis* (KRETZOI, 1941, 1961). The list of birds given by KESSLER (1975) is somewhat contrasting with that published previously by Kretzoi (supra cit.): *Tadorna* cf. *tadorna*, *Aquila* cf. *pomarina*, *Tetrao urogallus*, *Lyrurus* cf. *tetrix*, *Perdix perdix*, *P. jurcsáki*, *Otis ?tarda*, *O. ?lambrechti*, *Tringa* sp., *Galerida cristata*, *Corvus corax*, *C. ?corone cornix*, *C. ?betfianus* and *Passer montanus*. The fossil locality has been re-excavated later by E. Terzea and T. Jurcsák, who listed among others: *Mimomys blanci*, *M. savini*, *Pliomys lenki*, *P. episcopalis*, *Microtus* (*Pitymys*) *hintoni*, *M.* (*P.*) *arvalidens*, *M. nivalis*, *Allophaiomys pliocaenicus*, *Lagurus arankae*, *L. pannonicus*, *Homotherium moravicum*, *Dicerorhynus etruscus*, a.o. (TERZEA, 1993; TERZEA & JURCSÁK, 1969). The insectivore material was published very recently by RZEBIK-KOWALSKA (2000a, 2000b): *Sorex* cf. *subaraneus*, *Beremendia fissidens*, *Sorex minutus*, *S. runtonensis*, *S.* (*D.*) *margaritodon*, *Crocidura kornfeldi*, *Erinaceus* sp. 3, *Talpa fossilis* and *T.* cf. *episcopalis*. The ophidian fauna (material resulted from the re-excavation) was formed by *Coluber viridiflavus*, *Coronella austriaca*, *Elaphe paralongissima*, *E. quatuorlineata*, *Natrix tesselata*, *Natrix* sp. and *Vipera berus*, resembling closely the ophidian assemblage from the lower layers of Betfia VII. The age of the fauna is given by the simultaneous presence of *Mimomys savini* and *M. pusillus* (= *M. pusillus blanci*), as well as by the progressive forms of *Microtus* and *Lagurus* TERZEA (1993, 1995). According to these authors the fauna may be correlated with the *Mimomys savini - M. pusillus* biozone (Upper Menapian).

Subpiatră. The locality has been discovered in 1989 in a limestone quarry situated in the Hill of Coasta cu Pietriş approximately 200 m northeast to Subpiatră cave situated near the village of Subpiatră (Bihor county, W-Romania). During the opencast blasting a vertical carst cavity system was intersected, outspreading great quantities of fossil filled red clay sediments. The microvertebrate remains originating from this locality were studied by VENCZEL (1991, 1992), and by HÍR & VENCZEL (1991, 1992) while the macromammals by CODREA & CZIER (1993a, 1993b). Among the vertebrates we quote: *Triturus cristatus*, *T. vulgaris*, *Bombina* cf. *B. variegata*, *Pliobatrachus* cf. *langhae*, *Bufo bufo*, *B. viridis*, *Emys* sp., *Anguis fragilis*, *Lacerta* cf. *L. viridis*, *Talpa fossilis- minor* gr., *Drepanosorex savini*, *Crocidura* cf. *leucodon*, *Hystrix* sp., *Driomys nitedula*, *Allocricetus bursae*, *Cricetus* sp., *Mimomys savini*, *Pliomys episcopalis*, *P. lenki*, *Clethrionomys acrorhiza*, *Microtus* (*Pitymys*) *arvalidens*, *M. arvalinus*, *Dicerorhinus etruscus brachicephalus*, *Capreolus süssenbornensis*, a.o. *Coluber viridiflavus*, *Elaphe longissima*, *Coronella austriaca*, *Natrix natrix*, *N. tesselata* and *Vipera berus* make up the ophidian fauna. The age of the fauna based on micromammals may be correlated with the *Mimomys savini* partial zone of KORDOS (1992).

Material and methods

Chişcău 3. The fossil locality was discovered by geologist Radu Robert Huza in 1993 in a small cavern situated near the main entrance to the Chişcău cave. The samples taken from the sediments yielded among others *Clethrionomys glareolus*, *Microtus nivalis*, *M. arvalis*, *Arvicola cantiana*, *Anguis fragilis*, *Elaphe longissima*, *Natrix natrix* and *Vipera berus*. The micromammal assemblage revealed the age of the fauna, which may be correlated with the *Arvicola cantiana* biozone.

Râpa. The locality has been discovered in an open quarry on the Burzău Hill at altitude 200-210 m. As a result of the collecting trips organized by the local Museum of Tinca (led by Coloman Csák) and by Ţării Crişurilor Museum in Oradea (led by Tibor Jurcsák) a large amount of vertebrate remains have been unearthed. Among the fossil mammals we can mention *Erinaceus europeus*, *Talpa europaea*, *Sorex araneus*, *Crocidura leucodon*, *Ochotona pusilla*, *Lepus europaeus*, *Citellus citellus*, *Marmota bobac*, *Glis glis*, *Sicista subtilis*, *Spalax leucodon*, *Apodemus sylvaticus*, A. *flavicollis*, *Cricetus cricetus*, *Clethrionomys glareolus*, *Arvicola terrestris*, *Microtus gregalis*, *M. oeconomus*, *Vulpes vulpes*, *Crocuta spelaea*, *Ursus spelaeus*, *Coelodonta antiquitatis*, *Mammuthus primigenius*, *Alces alces*, a.o. (HAMAR & CSÁK, 1969; JURCSÁK et al., 1982, 1984). The bird remains partially identified by prof. D. Jánossy, were published by KESSLER (1974, 1985) and by JURCSÁK & KESSLER (1986, 1987). In the ornitofauna some were cold climate preferring forms (*Tetrao urogallus*, *Lyrurus tetrix*, *Lagopus mutus*, *L. lagopus*, *Pyrrhocorax graculus*, a.o.), while others were inhabitants of mixed deciduous-coniferous forests (e.g. *Columba palumbus*, *Turdus pilaris*, *T. viscivorus*, *Parus major*). A number of species preferred wetlands: *Anas platyrchynchos*, *A. querquedula*, *Rallus aquaticus*, *Crex crex*, *Asio flammeus*. The fossil herpetofauna for the first time was studied by FUHN & VANCEA (1961, p: 99). The above authors listed from this locality *Anguis* sp. and *Coluber* sp. Subsequently VENCZEL (1987, 1989) gave the following list of snakes: *Coronella austriaca*, *Elaphe longissima*, *Natrix tesselata* and *Vipera* sp. Based on micromammals, the age of the faunal assemblage may be correlated with a Würm I – II interstadial and fitted in the *Arvicola terrestris* biozone of KORDOS (1992).

Vadu Crişului (VC). The fossil locality is situated on the left side of the Crişul Repede Valley (near the village of Vadu Crişului) in the Devenţului Cave. The fossil bearing sediments yielded the following mammals: *Ursus spelaeus*, *U. arctos*, *Cervus elaphus*, *Rupicapra rupicapra*, *Capra ibex*, *Bison priscus* and *Castor fiber* (JURCSÁK, 1974). The vertebrate remains contained two fragmentary vertebrae of *Elaphe longissima* too. The age of the sediments have been considered as Upper Pleistocene/ Holocene.

Galoşpetreu (GP). The fossil locality is situated on Legii Hill, Northeast to the village of Galoşpetreu (Bihor County). The microvertebrate assemblage yielded among others *Pelobates fuscus*, *Rana esculenta* skl., *Marmota bobac*, *Spalax leucodon*, *Cricetus cricetus*, *Citellus citellus* (JURCSÁK, 1974). The fauna contained five vertebrae of *Vipera* sp. too. The age of the fossil fauna was considered as Holocene.

Valea Morii 1 (VM). The fossil locality is situated on the left side of the Morii Valley near the village of Aştileu at 348 m altitude (DAMM, 1998). The cave deposits yielded numerous bony fragments of small and large vertebrates, fragments of pottery and Neolithic artifacts used by *Homo sapiens*. KESSLER (1982) cited from this cave, remains of *Accipiter nisus* and *Gallus gallus*. After VENCZEL & DAMM (2000) *Salamandra salamandra*, *Triturus* cf. *cristatus*, *Bufo bufo*, *Hyla arborea*, *Rana dalmatina*, *Rana temporaria*, *Anguis fragilis*, *Lacerta* cf. *agilis*, *Coronella austriaca*, *Elaphe longissima*, *Natrix tesselata* and *Vipera* cf. *berus* formed the herpetofauna. The age of the fauna may be defined as Holocene.

2.3. The osteology of snakes

Snakes are characterized by limblessness, some forms having only vestiges of the pelvic girdle and hind limbs (e. g. typhlopids, aniliids, boids), but in the latter case without any bony connection of the vestiges of pelvic girdle and the axial skeleton (RAGE, 1984). The skull in some points is highly kinetic; some advanced snakes possess venom glands with certain alterations of the of palatomaxillary arch. The vertebral column is built up by an extremely high number of vertebrae (about 160 and 400). In the identification of snake remains both cranial and axial skeletal elements (except ribs) were used. In the following subsection we briefly describe the ophidian skeleton applied to advanced snakes and to skeletal elements with significant taxonomic importance.

2.3.1. Anatomical nomenclature

The anatomical nomenclature adopted in this work mainly follows RAGE (1984) and SZYNDLAR (1984). The interpretation of the cranial foramina mainly resulted from papers of UNDERWOOD (1967), RIEPPEL (1977, 1979), McDOWELL (1979), RAGE (1984), SZYNDLAR (1984, 1991c), RAGE & SZYNDLAR (1986).

2.3.2. Anatomical terms and abbreviations

Atlas: ic1 – intercentrum I

Axis: ic3 – intercentrum III, spp – spinal process, tp – transvers process

Basioccipital: boc – basioccipital crest, bop – basioccipital process, bot – basioccipital tubercle, mc – medial crest, ot – occipitocondylar tubercle

Basiparasphenoid: aanf – anterior foramen of abducens nerve, bpp – basipterygoid process, bsc – basisphenoid crest, ca – central area, cof – common foramen, eV4 – foramen for exit of the constrictor internus dorsalis branch of trigeminal nerve (= cid nerve), cs – crista sellaris, fs – frontal step, panf – posterior foramen of abducens nerve, pfs – pituitary fossa, pspp – parasphenoid process, ptc – pterygoid crest, sfl – suborbital flange, tg – trabecular groove, tp – trabecular process, Vc – Vidian canal

Caudal vertebra: ha – haemapophysis, pl – pleurapophysis, pt – pterapophysis, scp – subcotylar process

Cervical vertebra: ak – anterior keel, c – centrum, d – diapophysis, h – hypapophysis, ir – interzygapophyseal ridge, ns – neural spine, p – parapophysis, sr – subcentral ridge

Cloacal vertebra: ct – cotyle, ls – lymphapophysis, nc – neural canal, pr – prezygapophysis

Compound bone: cp – coronoid process, lfl – lateral flange, maf – mandibular fossa, mfl – medial flange, rap – retroarticular process, saf – supraangular foramen, sf – sigmoid fossa

Dentary: cn – compound notch, mef – mental foramen, mg – Meckel's groove

Ectopterygoid: era – external ramus, ira – internal ramus, pr – posterior ramus

Exoccipital: cc – circumfenestral crest, ecd – exoccipital condyle, et – exoccipital tubercle, oc – occipital crest, pcp – parotic process, pof – postoccipital foramen, rst – recessus scalae tympani, sop – supraotic process, X,XII – vagus-hypoglossal nerve foramen

Frontal: epfp – external prefrontal process, fa – frontal aperture, ipfp – internal prefrontal process, smp – septomaxillary process, tr – trabecular ridge

Maxilla: ep – ectopterygoid process, pfp – prefrontal process

Palatine: chp – choanal process, mxp – maxillary process, vp – vomerine process

Parietal: pc – parietal crest, pf – parietal foramen, pofr – postfrontal

Prefrontal: laf – lacrimal foramen

Premaxilla: lar – lateral arm, np – nasal process, plp – palatine process, pmch – premaxillary channel

Prootic: ls – laterosphenoid, oi – otic incisure, soc – supraoccipital crest, V2 – foramen for the maxillary branch of trigeminal nerve, V3 – foramen for the mandibular branch of trigeminal nerve, VII – facial nerve foramen

Pterygoid: ep – ectopterygoid process

Quadrate: dc – dorsal crest, qc – quadrate crest, stp – stapedial process, tq – trochlea quadrati

Septomaxilla (= intranasal): anp – ascendent nasal process, dfs – dorsal fossa, fp – frontal process

Supraoccipital: oc – occipital crest, pa – posterior area, sc – sagittal crest, soa – supraoccipital area, sof – supraoccipital foramen

Trunk vertebra: cd – condyle, dp – descending part of neural arch, hk – haemal keel, lf – lateral foramen, nl – neural lamina, ns – neural spine, po – postzygapophysis, pra – prezygapophyseal articular surface, prp – prezygapophyseal process

Vomer: cv – cavum vomeris, lsp – lamina spheroidea palatina, pip – posteroinferior process, pmp – premaxillary process, psp – posterosuperior process, vf – vomerine foramen

2.3.3. The skull

The ophidians are diapsid reptiles with their cranium lightly built (an important part of chondrocranium remains unossified) and slightly modified (Fig. 8-10), sharing with other squamates (i.e. lizards) a number of derived characters (e. g. lacrimals and quadratojugals are lacking, the quadrate is streptostylic, the parietals are fused medially displaying a broad frontoparietal joint). However in snakes the skull is platytrabic (UNDERWOOD, 1967), or regarded as a semi-platytrabic condition (RAGE, 1984), whereas in all the other modern reptiles, it is tropitrabic. The occipital region contains four bones: a basioccipital, two exoccipitals and a supraoccipital. There is a single occipital condyle built up by the basioccipital and exoccipital posterior processes, while the foramen magnum is delimited only by the exoccipitals (dorsally and laterally) and by the basioccipital (ventrally). Between the exoccipital and prootic a deep recess is evidenced (the juxtastapedial fossa), delimited by the circumfenestral crest. The temporal arches are absent. The base of the brain-case is closed by an elongated and posteriorly widened bone, the basiparasphenoid. The latter is resulted from the fusion of the parasphenoid (a dermal bone, situated anteriorly) and the basisphenoid (an endochondral bone, situated posteriorly). The anterior part of the basiparasphenoid is sutured with the ventral margins of the paired frontals and of the parietal. In some snakes (e. g. *Coluber*) a frontal crest rises between the ventromedial margins of the frontals. Posterolaterally the basisphenoid part is in sutured contact with the prootic, while posteriorly with the basioccipital. The palatomaxillary arch is formed by a medial ramus (palatine + pterygoid) and by a lateral ramus (maxilla + ectopterygoid). The maxilla is jointed to the prefrontal. A premaxilla and paired nasals, septomaxillae (= intranasals) and vomers make up the snout complex. The latter is connected to frontals in a movable joint. The mandible is made up of a compound bone (supraangular + prearticular + articular), a coronoid, an angular and a dentary.

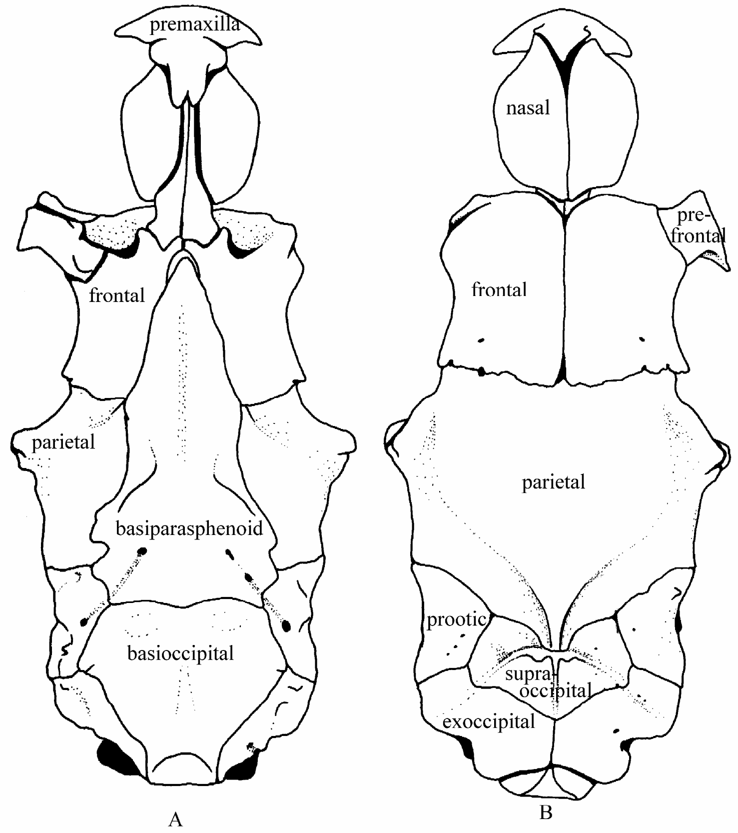


Figure 8. The ophidian neurocranium (*Lampropeltis* sp., Fam. Colubridae) in ventral- (A) and dorsal (B) views.

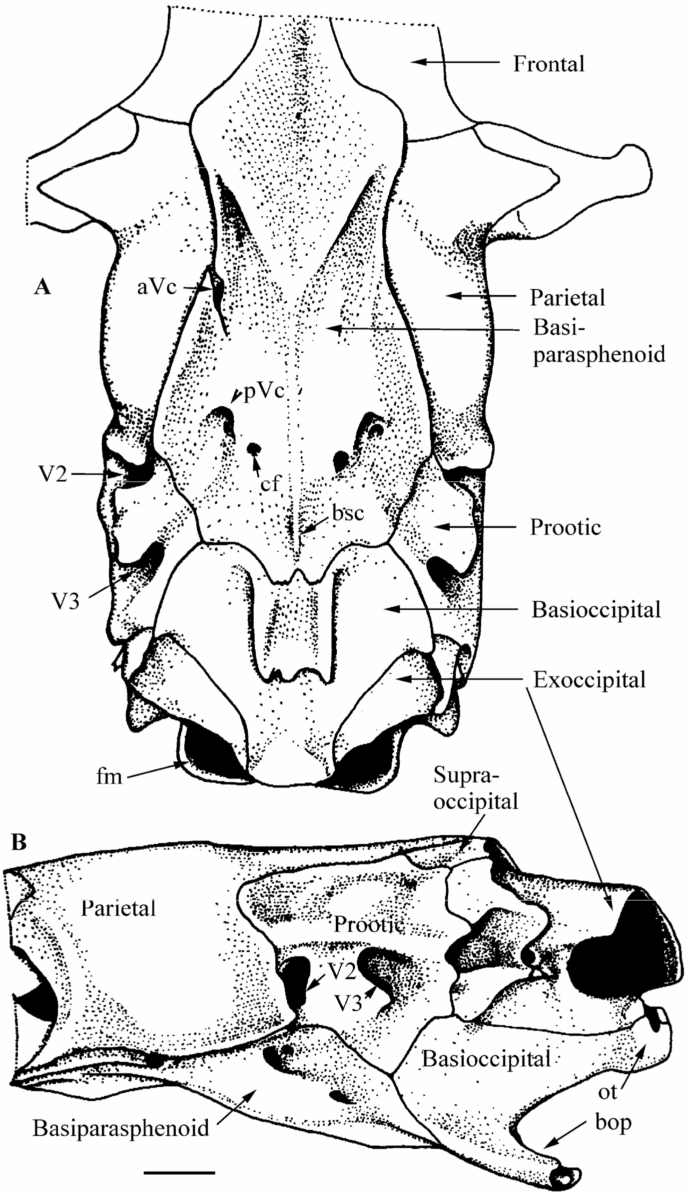


Figure 9. The neurocranium in *Vipera*, in ventral- (A) and lateral (B) views.

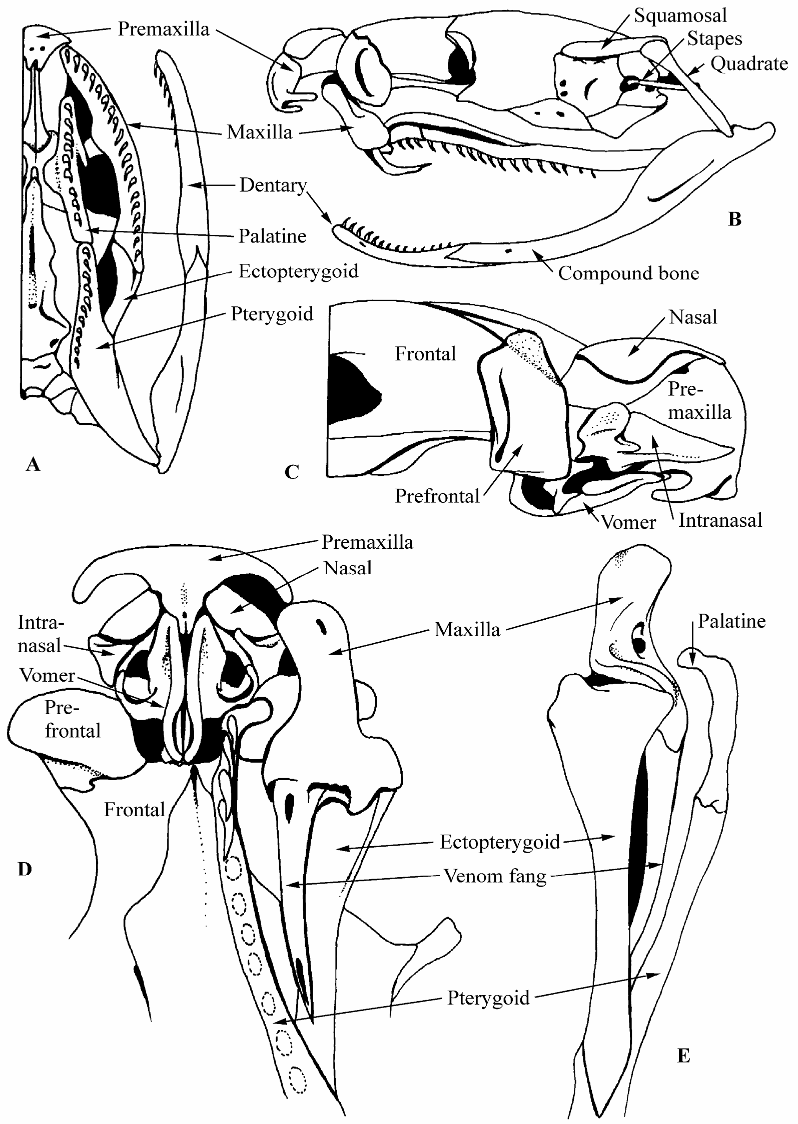


Figure 10. The skull in Colubridae (A) and Viperidae (B-E).

Most members of Alethinophidia bear teeth on maxillae, palatines, pterygoids, and dentaries. The dentition is of subacrodont type (RAGE, 1984). The teeth are conical and curved posteriorly. The latter condition, combined with the peculiar jaw joint (which enlarges two-three times on opening by the supratemporal-quadrate system) and independently moveable toothed elements of the palatomaxillary arch, helps striking and swallowing a relatively large prey.

In isolated skull bones a number of morphologic characters may be revealed (Fig. 11-13). However not all of them could be used for the identification of particular taxa. In this respect a special attention has been paid to skull bones having greater taxonomic importance (e.g. basiparasphenoid, basioccipital, exoccipital, prootic, supraoccipital, ectopterygoid, quadrate, premaxilla, maxilla, vomer, compound bone, a.o)(VON SZUNYOGHY, 1932; UNDERWOOD, 1967; RABEDER, 1977; SZYNDLAR, 1984, 1991a, 1991b, 1991c). The fossil remains have been identified comparing them with homologous elements of recent species. In this respect we studied small series of recent skeletons of all European species, and few others distributed beyond our continent. Original descriptions of a number of extinct taxa were used too. Valuable morphological data were obtained also from a number of papers devoted to taxonomy and systematics of modern ophidian taxa (e.g. UNDERWOOD, 1967; HOFFSTETTER & RAGE, 1972; RABEDER, 1977; RAGE, 1984; BACHMAYER & SZYNDLAR, 1985, 1987; McDOWELL, 1987; SZYNDLAR, 1984; 1985, 1987, 1988, 1991a, 1991b, 1991c; BAILON, 1991; SZYNDLAR & BÖHME, 1993; SZYNDLAR & SCHLEICH, 1993; SZYNDLAR & RAGE, 1999; a.o.)

2.3.4. The vertebral column

In snakes the vertebral column may be subdivided in trunk (or precaudal) and caudal region. Except for the first vertebra (= atlas)(Fig. 13: E) in the trunk region the vertebrae bear articulated ribs, while the second vertebra (= axis)(Fig. 13: F) usually bear fused ribs. In the caudal region the ribs are always fused to the vertebrae. Furthermore in colubrine snakes the trunk region may be partitioned in cervical vertebrae (provided, except for atlas with hypapophyses)(Fig. 13: G) and trunk vertebrae in which the hypapophysis is reduced to a low ridge (= haemal keel)(Fig. 13: H).

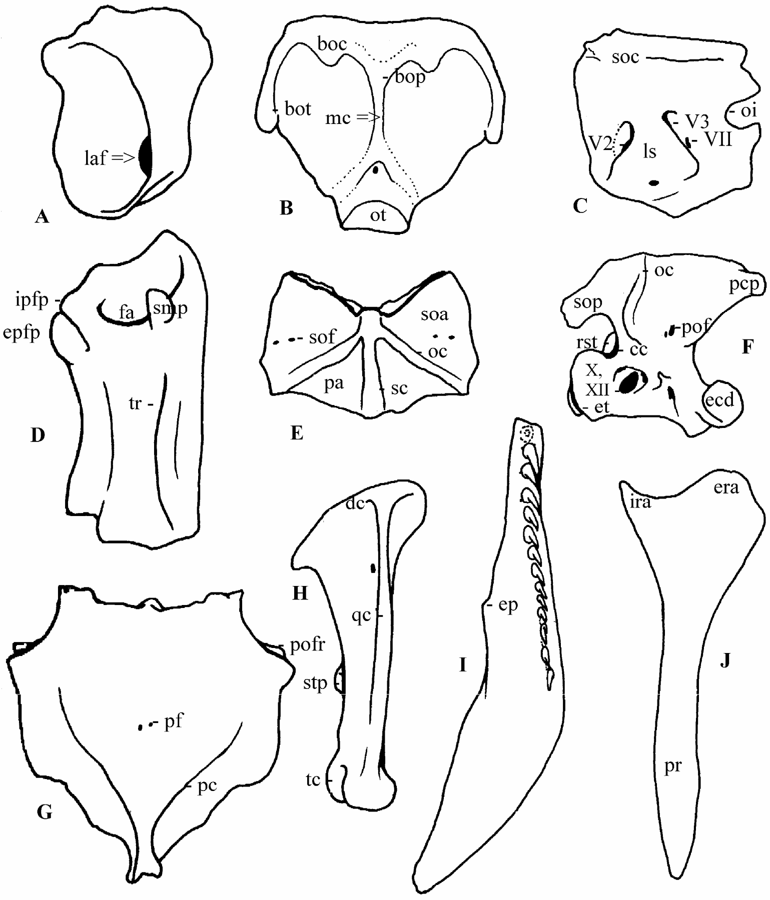


Figure 11. Disjointed cranial bones of recent *Elaphe longissima*. A: prefrontal; B: basioccipital; C: prootic; D: frontal; E: supraoccipital; F: exoccipital; G: parietal; H: quadrate; I: pterygoid; J: ectopterygoid. A – posteroventral view; B, D, I – ventral views; C, F – lateral views; E, G, J – dorsal views, H – posterolateral view.

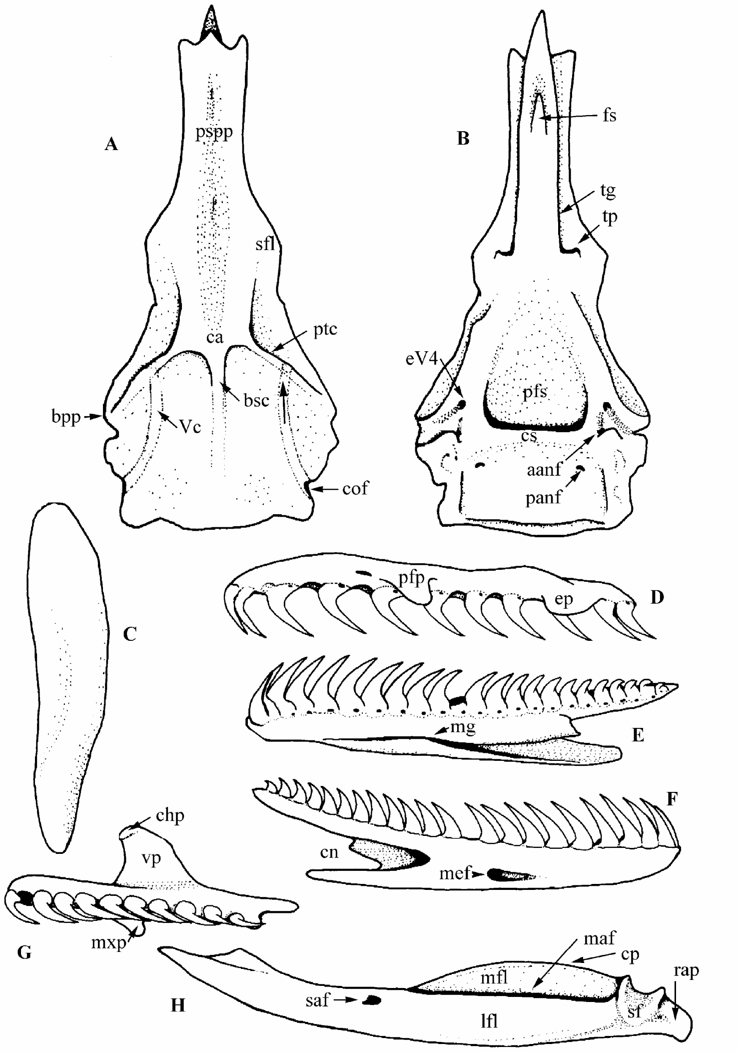


Figure 12. Disjointed cranial bones of recent *Elaphe longissima*. A, B: basiparasphenoid; C: supratemporal (= squamosal); D: maxilla; E, F: dentary; G: palatine; H: compound bone (supraangular + prearticular + articular); A, G – ventral views; B, C – dorsal views; D, E – medial views; F, H – lateral views.

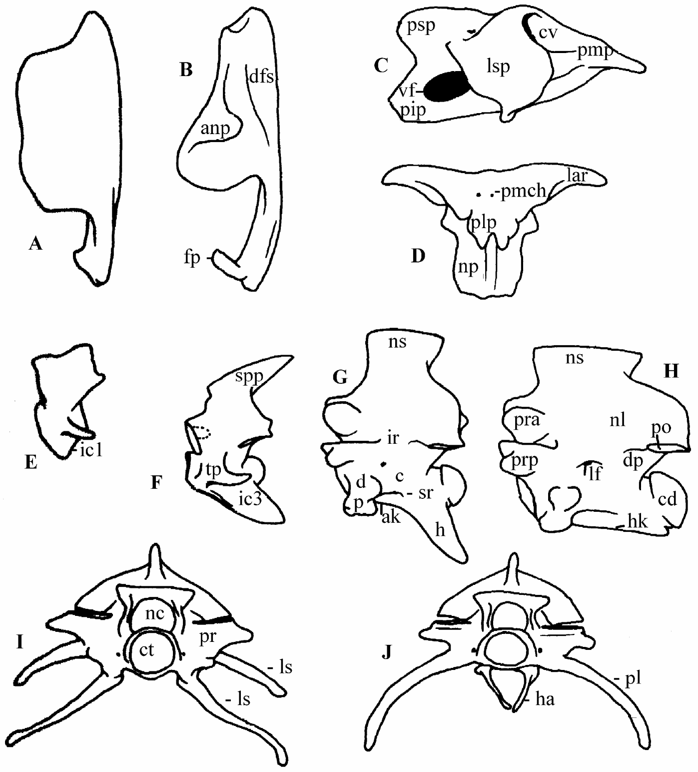


Figure 13. Disjointed cranial bones of recent *Elaphe longissima*. A: nasal; B: intranasal (= septomaxilla); C: vomer; D: premaxilla (= intermaxilla); E: atlas; F: axis; G: cervical vertebra; H: trunk (= presacral) vertebra; I: sacral (= cloacal) vertebra; J: caudal vertebra. A, B – dorsal views; C, E, F, G, H – lateral views; D – posteroventral view; I, J – anterior views.

The caudal region may be partitioned in cloacal vertebrae (Fig. 13: I) which bear forked ribs (= lymphapophyses) and caudal vertebrae (Fig. 13: J) bearing simple ribs (= pleurapophyses).

Material and methods

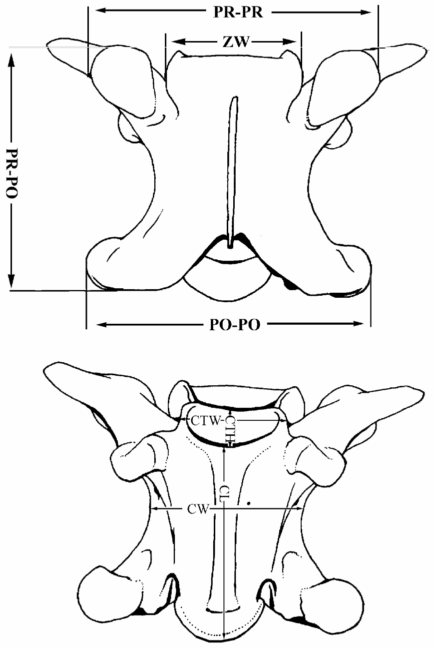


Figure 14. Measurements of trunk vertebrae used in this paper (after AUFFENBERG, 1963 and SZYNDLAR, 1984). CL – centrum length, CTH – cotyle height, CTW – cotyle width, CW – centrum width, PO-PO – width between the lateral margins of postzygapophyseal articular facets, PR-PO - length between the anterior margin of the prezygapophyseal articular facet and posterior margin of the postzygapohyseal articular facet, PR-PR – width between the lateral margins of the prezygapophyseal articular facets, ZW – zygosphene width.

Biometric measurements of vertebral column and use of bivariate ratios of measurements of snake vertebrae initiated by JOHNSON (1955) were later applied in a somewhat modified form in the identification of snake taxa

(AUFFENBERG, 1963; SZYNDLAR, 1981; MEYLAN, 1982) (Fig. 14). Out of the measurements and ratios of vertebrae given by AUFFENBERG (1963) and SZYNDLAR (1984) we usually applied on a series of well preserved middle trunk vertebrae the following ones only: centrum length (CL), centrum width (CW), and centrum length/centrum width ratio (CL/CW). The number of specimens (N), the observed ranges (OR) and mean in all species were indicated. The interpretation of the results obtained is given in the systematic part. However SZYNDLAR (1984) pointed out that satisfactory methods of identification based on numerical data only have not been demonstrated yet. Thus biometrical characters of vertebrae are of secondary significance in comparison with their morphology (SZYNDLAR, 1991b).

2.4. Identification of ophidian taxa

The morphological criteria for the identification of European snakes based on vertebrae (pictorial keys) was elaborated by SZYNDLAR (1984). Nevertheless due to intraspecific (or even interspecific) variations some morphological characters may overlap in a number of taxa. Due to this the usefulness of vertebrae in identification of particular taxa or even in phylogenetic reconstruction were strongly criticized by some authors (McDOWELL, 1987; CADLE, 1987, 1988; HECHT & LaDUKE, 1988). Thus identification of snakes based exclusively on vertebrae at least in some case may be doubtful or even an impossible task. But inverse, identification of ophidian taxa based on isolated cranial bones alone produced similar results, especially when only the outer shape of the bones were taken into consideration, instead of some useful morphological characters (as was the practice of some earlier students, e.g. using pictorial keys elaborated by VON SZUNYOGHY, 1932).

Taking into consideration all the above remarks we think that in the case of Romanian fossil snake remains which belonged (except for the extinct *Elaphe paralongissima*) almost exclusively to recent taxa (about 12 species) the identification of particular taxa based on vertebrae alone is not extremely problematic. However we faced some difficulties in the case of the members of natricine snakes (*Natrix natrix* and *N. tesselata*) because of overlapping vertebral characters. However a combination of the vertebral morphological key characters completed with numerical data (e. g. centrum length/centrum ratio, which based on our observations, differ significantly) could facilitate proper assignment. This was the practice in the case of identification of isolated viperid remains (*Vipera berus* and *V. ammodytes*), too. Fortunately, in almost all fossil localities, the remains consisted of both vertebrae and cranial bones. Due to this in the identification of particular taxa the following steps were followed:

1. Estimation of the number of snake taxa based on trunk (or precaudal) vertebrae.
2. Co-ordination of the available isolated skull bones to the selected vertebrae.
3. Measurements undertaken on selected (measurable) middle trunk vertebrae.
4. Description of the remains paying special attention to intra-specific variations or to other aspects (e. g. malformations).
5. Paleoenvironmental reconstruction of the studied locality.

Assisting future paleontological and archeological research activities, we compiled a dichotomic key for living Romanian snakes as well as for those discovered in fossil state in our country. We were based primarily on the pictorial keys elaborated by SZYNDLAR (1984) with few alterations which resulted from our own observations. However note that the "normal practice" in the snake identification is combining the key characters found in vertebrae with the morphology of cranial bones (if they are available).

2.5. Dichotomic key to living and fossil Romanian snakes

A. Key to suborders of **Serpentes**:

1. Neural spine absent........................ **Scolecophidia** (***Typhlops***, cf. Fig. 21)
1a. Neural spine present...**Alethinophidia**

B. Key to families of **Alethinophidia**:

1. Vertebral centrum longer than wide...**2**
1a. Vertebral centrum wider than long.....................**Boidae** (***Eryx***, Fig. 15: A-D)

2. Trunk vertebrae provided with hypapophyses..**3**
2a. Trunk vertebrae without hypapophyses......**Colubridae** (**"Colubrinae"**) **►C**

3. Hypapophysis sigmoid-shaped; neural spine strongly overhangs anteriorly and posteriorly; prezygapophyseal process obtuse........**Colubridae**........ ....(**"Natricinae"**) **►D**
3a. Hypapophysis straight; neural spine overhangs only posteriorly; prezygapophyseal process acute...**Viperidae ►E**

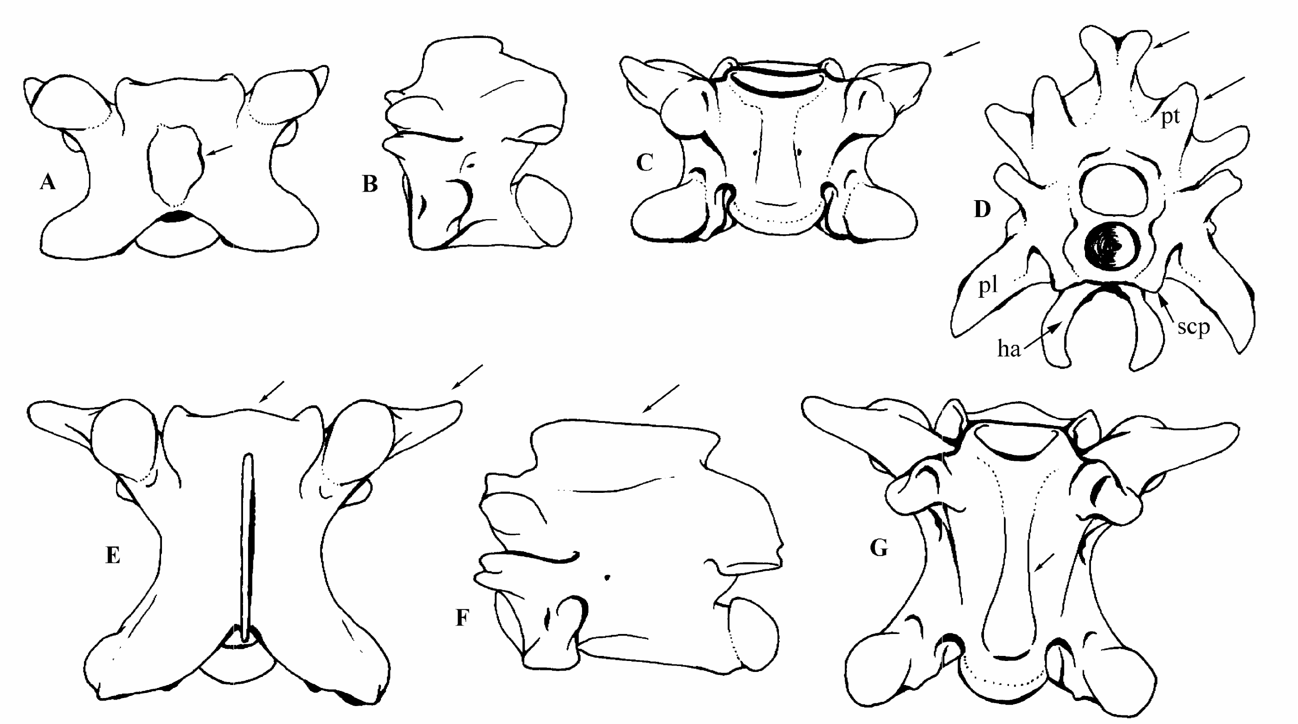


Figure 15. *Eryx jaculus* (A-D) and *Coluber najadum* (E-G).

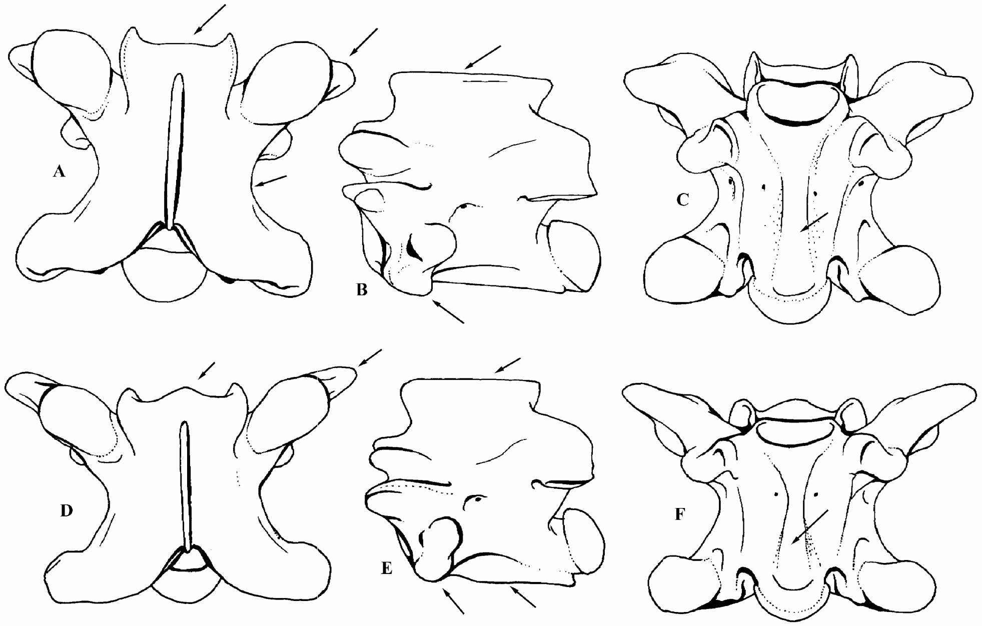


Figure 16. *Coronella austriaca* (A-C) and *Telescopus fallax* (D-F).

C. Key to **"Colubrinae"**

1. Centrum length never reach 5 mm..**2**
1a. Centrum length longer than 5 mm...**6**

2. Neural arch depressed, neural spine of low height..**3**
2a. Neural arch vaulted, neural spine high..**4**

3. Prezygapophyseal processes about ¼ the length of prezygapophyseal facets: ***Coronella austriaca*** (Fig. 16: A-C)
3a. Prezygapophyseal processes about ½ the length of prezygapophyseal facets: ***Telescopus fallax*** (Fig.16: D-F)

4. Prezygapophyseal process short and acute: ***Elaphe situla***
4a. Prezygapophyseal process long..**5**

5. Zygosphenal roof convex: ***Coluber gemonensis*** (cf. Fig. 28: F-M)
5a. Zygosphenal roof straight: ***Coluber najadum*** (Fig. 15: E-G)

6. Haemal keel flattened.. **7**
6a. Haemal keel raised.. **8**

7. Zygosphene concave**,** prezygapophyseal processes short, hypapophyses of cervical vertebrae projected anteroventrally: ***Elaphe quatuorlineata*** (Fig. 18: A-C)
7a. Zygosphene straight, prezygapophyseal processes long, hypapophyses of cervical vertebrae projected posteroventrally: ***Coluber viridiflavus*** (Fig. 17: D-F)

8. Prezygapophyseal process equals the length of prezygapophyseal articular facet...**9**
8a. Prezygapophyseal process distinctly longer than prezygapophyseal articular facet: ***Malpolon monspessulanus***.

9. Prezygapophyseal process obtuse: ***Elaphe longissima*** (Fig. 18: D-F)
9a. Prezygapophyseal process acute: ***Coluber caspius*** (Fig. 17: A-C)

Material and methods

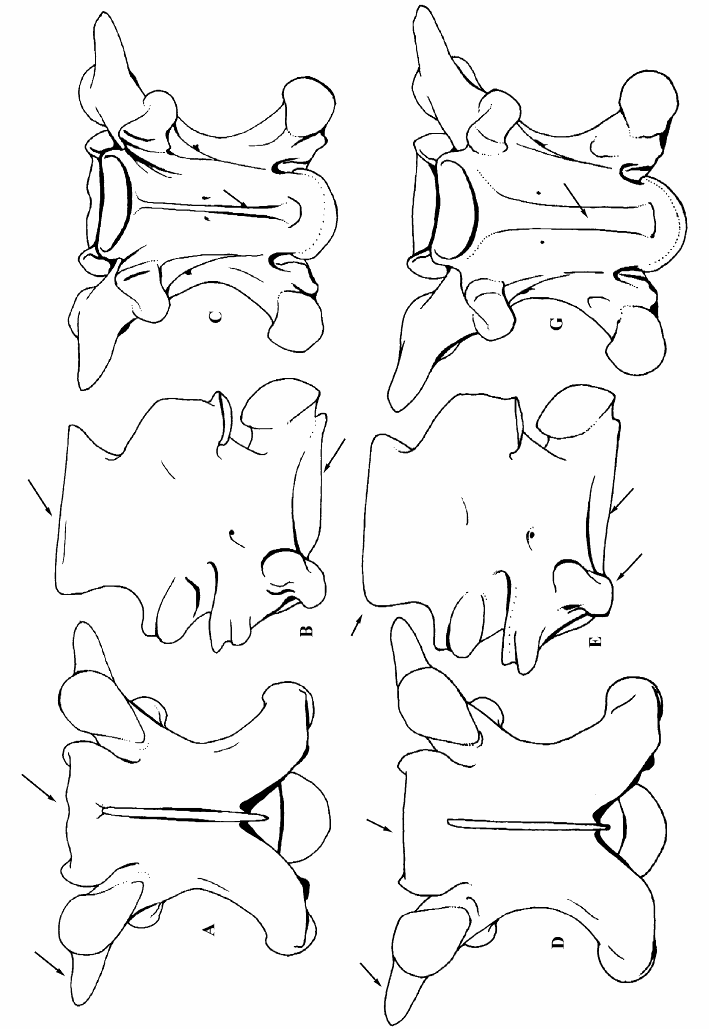


Figure 17. *Coluber caspius* (A-C) and *C. viridiflavus* (D-F).

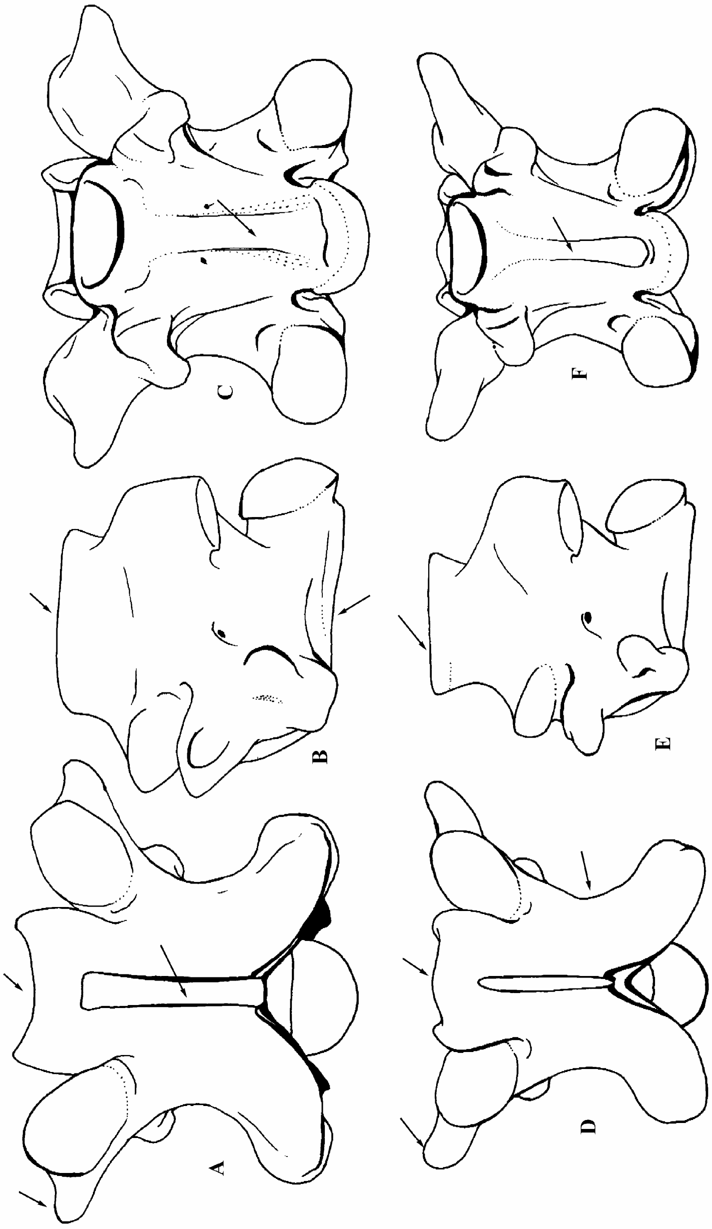


Figure 18. *Elaphe quatuorlineata* (A-C) and *E. longissima* (D-F).

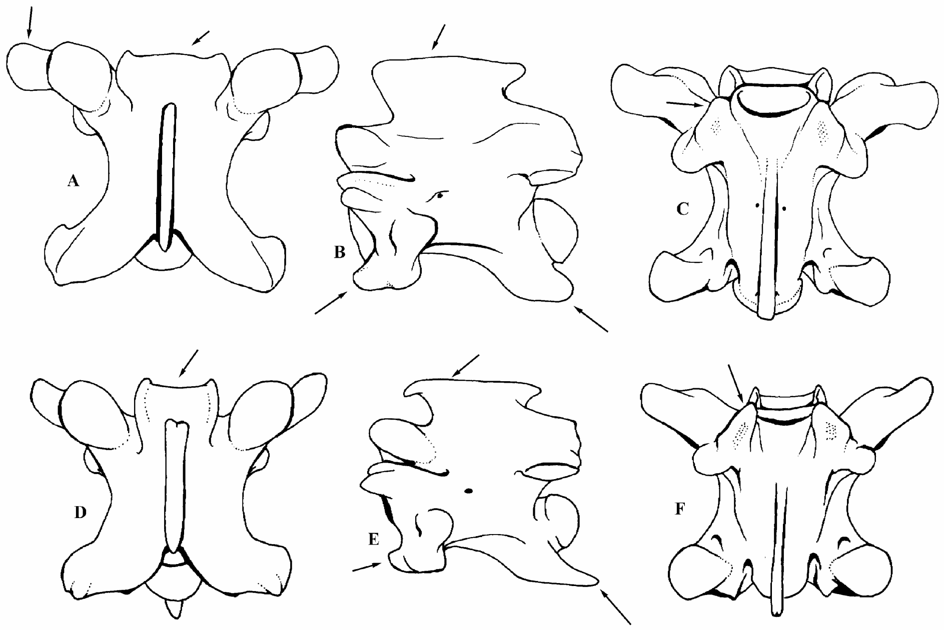


Figure 19. *Natrix natrix* (A-C) and *N. tesselata* (D-F).

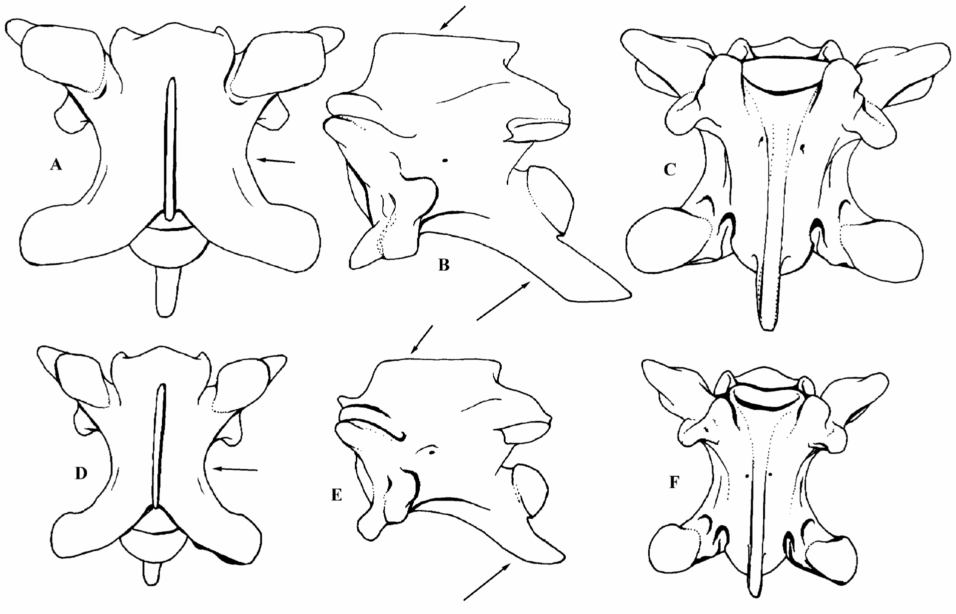


Figure 20. *Vipera ammodytes* (A-C) and *V. berus* (D-F).

D. Key to **"Natricinae"**:

1. Hypapophysis and parapophyseal process obtuse: ***Natrix natrix*** (Fig. 19: A-C)
1a. Hypapophysis and parapophyseal process acute: ***Natrix tesselata*** (Fig. 19: D-F)

D. Key to **Viperidae**:

1. Hypapophyses of cervical vertebrae longer than vertebral centrum; CL/CW ratio lesser than 1.6: ***Vipera ammodytes*** (Fig. 20: A-C)
1a. Hypapophyses of cervical vertebrae shorter than vertebral centrum; CL/CW ratio more than 1.7...**2**

2. Pleurapophyses and haemapophyses of caudal vertebrae of same length: ***Vipera ursinii***
2a. Pleurapophyses distinctly longer than haemapophyses: ***Vipera berus*** (Fig. 20: D-F)

3. SYSTEMATIC DESCRIPTION

Order **Serpentes** LINNAEUS, 1758

Suborder **Scolecophidia** Dumeril et Bibron, 1844

Scolecophidia indet.

Material: Betfia 9/C: 4 trunk vertebrae (MTC. No. 21426)

Description and comments

All the vertebrae were small sized, the centrum length of the largest one do not reached 2 mm (VENCZEL, 1997a). In lateral view the neural arch is depressed, devoid of neural spine; the synapophyses are undivided. In dorsal view the zygospnenal roof is straight, provided laterally with two small tubercles. The prezygapophyses are elongated anteroposteriorly. The prezygapophyseal processes in all the specimens are broken off. In ventral view the centrum lacks haemal keel, and sometimes it is provided with a subcentral foramen. In anterior view the vertebrae lack paracotylar foramina. The cotyle and the condyle are depressed dorsoventrally (Fig. 21).

All the morphological characters described above are not appropriate to identify the fossils below subordinal level (because all these characters are shared by the members of Typhlopidae, Leptotyphlopidae and Anomalepididae too). At the other hand is very improbable that the material represent more than *Typhlops vermicularis*, the sole member of the family Typhlopidae which inhabits presently the south-eastern part of the European continent (SZYNDLAR, 1991a).

The fossil record of Scolecophidia is rather scarce (probable due to small size and fragility of their bones). The oldest known European scolecophidian fossils come from the earliest Eocene (MP 7) of Belgium (RAGE, 1984; RAGE & AUGE, 1993). During Lower/Middle Miocene times this group of snakes was probable widespread in Europe, apparently disappearing from the territory of Central Europe in Middle/Late Miocene times (SZYNDLAR, 1991a). The fossil record, known from the Lower Pleistocene locality of Betfia 9/C, Romania, lies well beyond the group's present range of distribution.

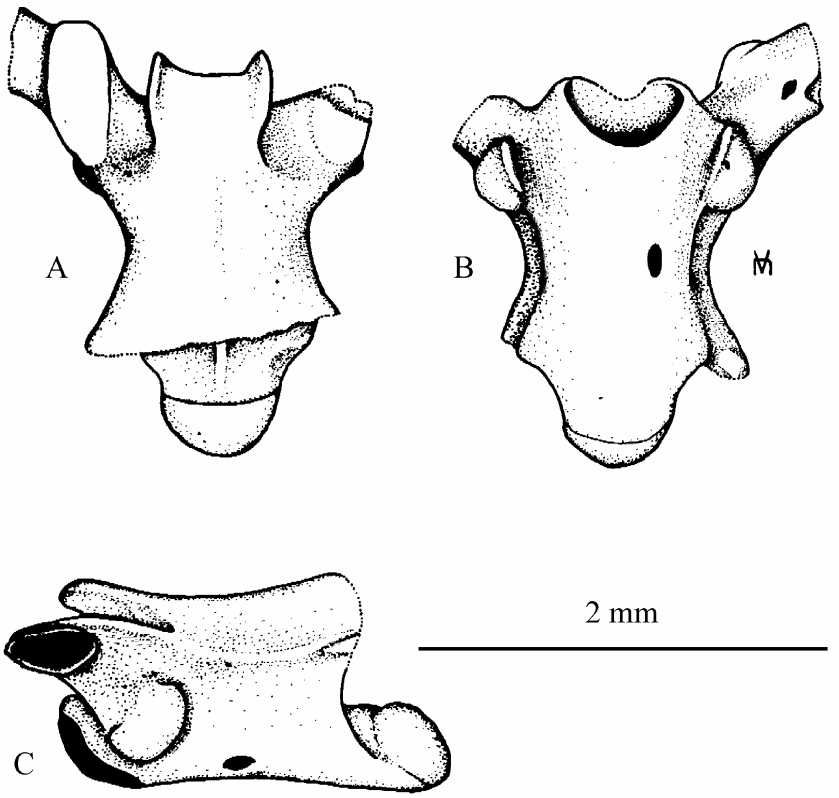


Figure 21. Scolecophidia indet. A-C: trunk vertebra (Betfia 9/C, MTC. No. 21426) in dorsal- (A), ventral- (B) and lateral views (C).

Suborder **Alethinophidia** Nopcsa, 1923

Family **Colubridae** OPPEL, 1811

Due to practical purpose the partition of the family Colubridae in subfamilies "Colubrinae" and "Natricinae" adopted in this paper follows the classification accepted by HOFFSTETTER (1962), RAGE (1974) and SZYNDLAR (1984, 1991a, 1991b). The hypapophyses in the trunk vertebrae of "Colubrinae" are reduced to a haemal keel while in "Natricinae" the vertebrae are provided with hypapophyses in the whole presacral region.

Subfamily **"Colubrinae"**

The anterior vertebrae of the trunk region (= cervical vertebrae) are provided with hypapophyses while in the middle- and posterior trunk vertebrae the hypapophyses are reduced to a haemal keel. However in the posterior trunk vertebrae the haemal keel is usually more prominent.

Genus ***Coluber*** LINNAEUS, 1758

This composite taxon most probably comprising several genera (see SCHÄTTI, 1986) is widely distributed in Europe, North Africa, Asia and North America. There are six species distributed in Europe, inhabiting mainly southern areas (ARNOLD & BURTON, 1978). A complete diagnosis based on osteology is not available yet. However some differentiating characters (mainly valid for the European members of the genus) were pointed out by BAILON (1991).

Coluber viridiflavus **LACÉPÈDE, 1789**

1932 *Zamenis viridiflavus* Lacép. var. *carbonaria* Bonap.: VON SZUNYOGHY, Pp. 9 and 48-49, Fig. 115

1964 *Coluber robertmertensi* MLYNARSKI, Pp. 331-332

1977 *Coluber viridiflavus* LACÉPÈDE: RABEDER, Pp. 86-91; Figs. 9: 6, 11; Pl.1: 1,5,7,8,10; Pl.2: 15, 16, 20, 22, 23.

1984 *Coluber robertmertensi* MLYNARSKI: Rage, P. 45

1984 *Coluber robertmertensi* MLYNARSKI: SZYNDLAR, Pp. 53-62, Figs. 19-21

1987 *Coluber robertmertensi*: REDKOZUBOV, P. 71

1991 *Coluber* cf. *viridiflavus*: VENCZEL, P. 86, Fig. 3
1992 *Coluber viridiflavus*: VENCZEL, Pp. 473-476, Fig. 1:a

Material: Betfia 5: 38 vertebrae (MTC. No. 18720/ 1-38); Betfia 7: 1 frontal (MTC. No. 18616), 2 fragmentary basiparasphenoids (MTC. No. 18617/ 1-2), 1 prootic (MTC. No.18618), 1 maxilla (MTC. No. 18619), 1 ectopterygoid (MTC. No. 18620), 1 quadrate (MTC. No. 18621), 1 compound bone (MTC. No. 18622), 395 vertebrae (MTC. No. 18623 /1-395); Betfia 9: 1 fragmentary exoccipital (MTC. No. 18651), 1 fragmentary basiparasphenoid (MTC. No. 18652), 2 maxillae (MTC. No. 18653/ 1-2), 2 ectopterygoids (MTC. No. 18654/ 1-2), 6 quadrates (MTC. No. 18655/1-6), 3 dentaries (MTC. No. 18656/1-3), 15 compound bones – 4 of them fragmentary (MTC. No. 18657/1-15), 270 (MTC. No. 18658/1-270); Betfia 10: 160 vertebrae (MTC. No. 18682/1-160); Betfia 11: 1 fragmentary basioccipital (MTC. No. 18686), 2 quadrates (MTC. No. 18687/1-2), 100 vertebrae (MTC. No. 18688/1-100); Betfia 12/A: 1 prefrontal (MTC. No. 18707), 2 frontals (MTC. No.18708/1-2), 4 fragmentary parietals (MTC. No. 18709/1-4), 3 basioccipitals (MTC. No. 18710/1-3), 2 supraoccipitals – 1 of them fragmentary (MTC. No. 18711/1-2), 3 fragmentary basiparasphenoids (MTC. No. 18712/1-3), 1 fragmentary maxilla (MTC. No. 18713), 1 ectopterygopid (MTC. No. 18714), 1 supratemporal (MTC. No. 18715), 8 fragmentary quadrates (MTC. No. 18716/1-8), 2 dentaries (MTC. No. 18717/1-2), 15 compound bones – 14 of them fragmentary (MTC. No. 18718/1-15), 6190 vertebrae (MTC. No. 18719- 18730); Betfia 12/B: 1 frontal (MTC. No. 18741), 9 vertebrae (MTC. No. 18742/1-9); Betfia 13: 1 fragmentary compound bone (MTC. No. 18750), 5 vertebrae (MTC. No. 18751/1-5); Betfia pothole/A: 9 vertebrae (MTC. No. 18752/1-9); Betfia pothole/B: 2 fragmentary frontals (MTC. No. 18756/1-2), 1 basioccipital (MTC. No. 18757), 1 exoccipital (MTC. No. 18758), 1 basiparasphenoid (MTC. No. 18759), 3 quadrates (MTC. No. 18760/1-3), 1 dentary (MTC. No. 18761), 1 axis (MTC. No. 18762), 450 vertebrae (MTC. No. 18763/1-450); Subpiatră: 17 vertebrae (MTC. No. 18439/1-17).

Description and comments

Prefrontal (Fig. 22: A, B). In lateral view the anterior margin is convex, while the posterior margin is slightly concave. The lateral surface is provided with four foramina. In posterolateral view the lacrimal foramen is relatively small and circular shaped.

Frontal (Fig. 22: C-G). The posterior part of the bone distinctly becomes narrower. The prefrontal processes are relatively short and distinctly projected anteriorly.

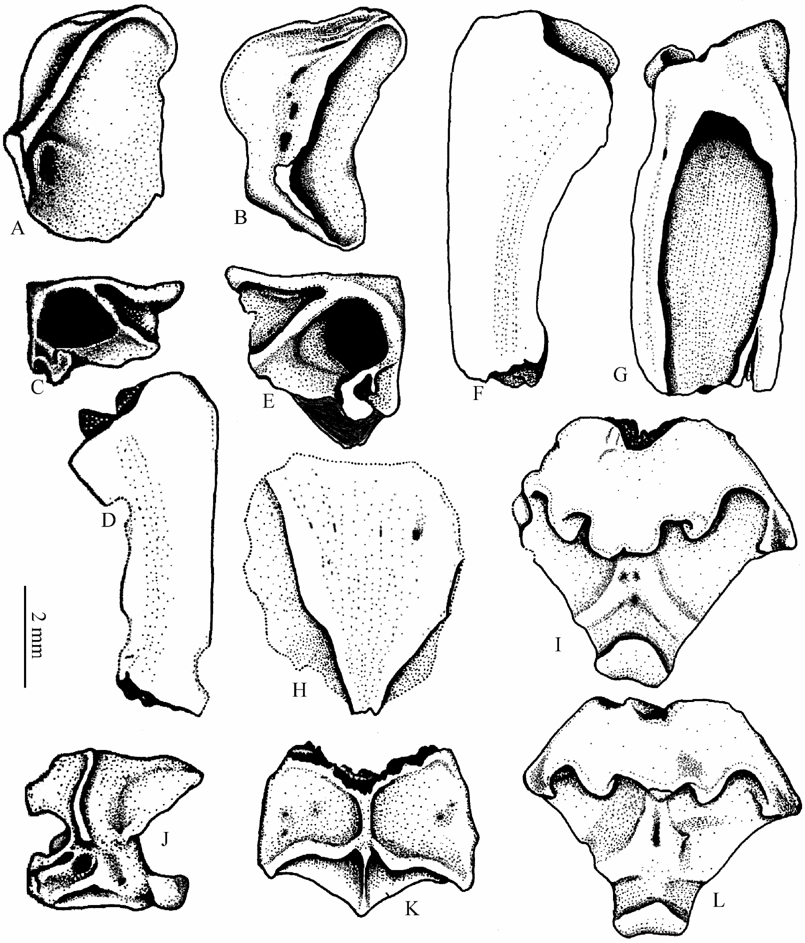


Figure 22. *Coluber viridiflavus*. A, B: left prefrontal (Betfia 12/A, MTC. No. 18707); C, D: left frontal (Betfia 7, MTC. No. 18616); E, F, G: right frontal (Betfia 12/B, MTC. No. 18741); H: fragmentary parietal (Betfia 12/A, MTC. No. 18709); I, L: basioccipital (Betfia 12/A, MTC. No. 18710/1, 2); J: left exoccipital (Betfia pothole/B, MTC. No. 18758); K: supraoccipital (Betfia 12/A, MTC. No.18711). A – posterolateral view; B, J – lateral views, C, E – anterior views, D, F, H, K – dorsal views; G: medial view; I, L – ventral views.

The anterior margin of the specimen No. 18741 is somewhat damaged, including the prefrontal processes and consequently the latter character could not be observed. The internal prefrontal process is usually shorter than the external one. In anterior view the frontal aperture is oval in shape. The nasal process is rather large and projected anteriorly. In medial or lateral views the trabecular crest is prominent, provided with a sharp ventral margin.

Parietal (Fig. 22: H). Only small fragments were available for study (assigned with some doubt to this species), having their parietal crests convergent posteriorly ("V"- shaped).

Basioccipital (Fig. 22:I, L). The bones are somewhat wider than long. In ventral view the basioccipital crest is strongly developed, having three prominent lobes, the medial one being larger than the lateral ones. Laterally the basioccipital crest reaches the well-developed occipital tubercle (= occipital process). The sagittal crest is usually lacking or weakly marked. Posterior to the medial lobe, 1-3 small foramina are present. The anterior margin of the bone is notched medially, receiving the posteromedial protuberance of the basisphenoid. The occipitocondylar tubercle (= basioccipital condyle) is distinct and widely separated from the remaining portion of the basioccipital by a distinct furrow. The basioccipital is relatively easy to distinguish from the other European members of the genus *Coluber* by its size and morphology. In *C. gemonensis* usually the medial lobe is developed only (VON SZUNYOGHY, 1932; RABEDER, 1977), while in *Coluber caspius* the occipital crest is situated more closely to the anterior margin of the bone.

Exoccipital (Fig. 22: J). In lateral view the occipital crest is prominent and slightly inclined posteriorly. The jugular foramen is relatively large serving for the exit of the vagus-hypoglossal nerve. Posterior to the latter there is a small additional foramen. The postoccipital foramen is small and the paroccipital process is well developed. The circumfenestral crest is prominent. The exoccipital part of the occipital condyle is well marked.

Supraoccipital (Fig. 22: K). In dorsal view the occipital crest is well developed and slightly inclined posteriorly. The anterior sagittal crest is distinctly longer and more prominent than the posterior sagittal crest. The posterior supraoccipital area is reduced. In *C. caspius*, having a body-size comparable to *C. viridiflavus*, the anterior sagittal crest of the homologous bone is distinctly shorter.

Basiparasphenoid (Fig. 23: A-D). The parasphenoid process in all the specimens is lacking. In ventral view, the pterygoid crests are prominent, slightly inclined anterolaterally and they usually reach the lateral margin of the bone. The basipterygoid processes are well developed. The posterior foramina of Vidian canal are situated approximately at the half of the distance between the pterygoid crest and the posterior margin.

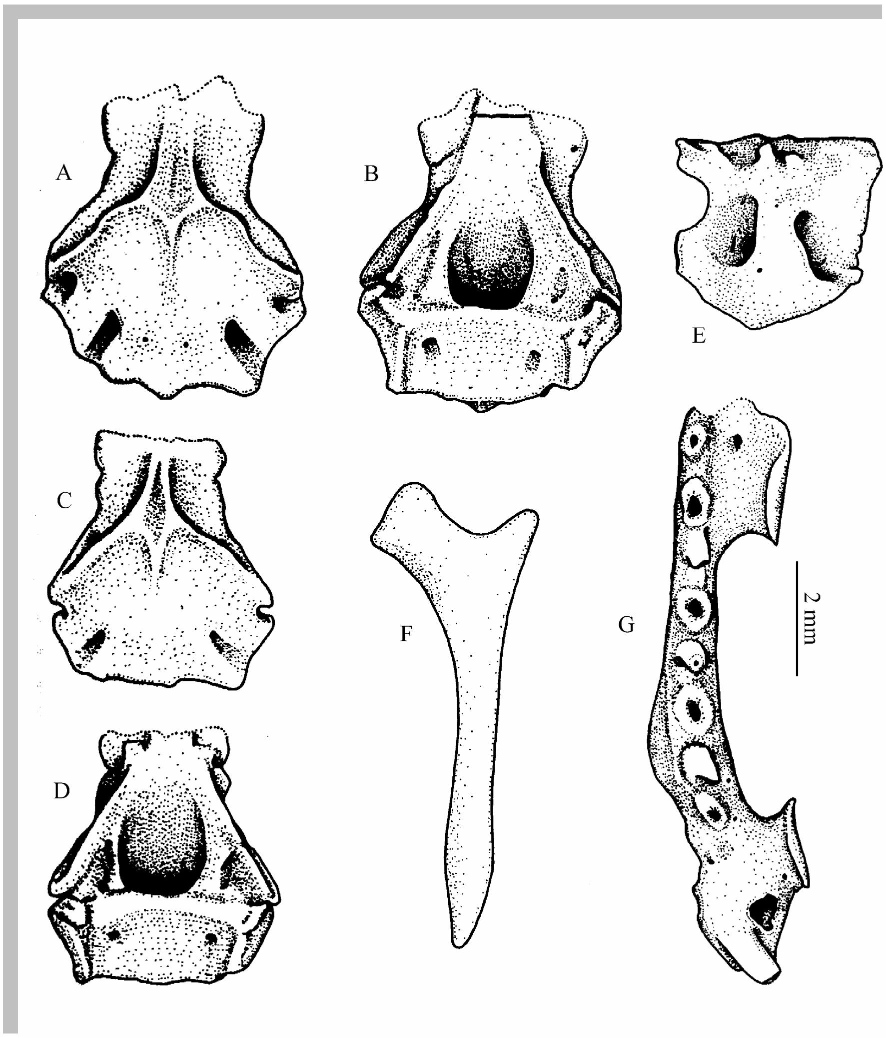


Figure 23. *Coluber viridiflavus*. A - D: basiparasphenoids from Betfia 7 (A, B)(MTC. No. 18617) and Betfia pothole/B (C, D)(MTC. No. 18759); E: right prootic (Betfia 7, MTC. No. 18618); F: left ectopterygoid (Betfia 9/A, MTC. No. 18654/1); G: right maxilla (Betfia 7, MTC. No. 18619). A, D, G – ventral views; B, D, F – dorsal views; E – lateral view.

However regarding this, an accentuated intraspecific variation may be observed. The anterior foramina are entirely or partially covered by pterygoid crests. The sagittal basisphenoid crest is undeveloped, slightly evidenced in the posterior vicinity of the central area. The suborbital flanges are weakly developed. The posterior margin of the bone is distinctly trilobate, but sometimes nearly straight, provided with a medial protuberance. The latter structure covers the anteromedial margin of the basioccipital. Due to this on the anteroventromedial margin of the latter an incisure is observed. In dorsal view, the hypophyseal fossa is deep and of oval shape. The posterior and anterior abducens nerve foramina in both sides are well evidenced. The similar statement holds true for the foramina of palatine nerves (= cid nerves). The distance between the latter and the anterior abducens foramina is seemingly variable, in most cases lying close to each other (but sometimes closer in the right side).

Prootic (Fig. 23: E). The supraoccipital crest is slightly prominent, continuous or interrupted by short grooves running dorsoventrally. In lateral view two large foramina are present, delimited by a bony ridge: the laterosphenoid. The anterior foramen is of oval shape and is for the exit of the maxillary ramus of trigeminal nerve (V2), while the posterior one is for the exit of the mandibular ramus of the trigeminal nerve (V3). Posterior to V3 there is a small foramen for the facial nerve. Sometimes below the V2 foramen there is another foramen, which serves for the exit of the constrictor internus dorsalis ramus of the trigeminal (=cid) nerve. The latter reenters in the neurocranium at the prootic and basiparasphenoid border. The otic incisure is large but relatively shallow.

Maxilla (Fig. 23: G). Only posterior fragments have been found. Each fragment is provided with a diastema and by a dorsal constriction for the maxillary ramus of the ectopterygoid. Posterior to the diastema two posterior tooth positions are observed. The length of the ectopterygoid process equals that of the diastema while its anterior margin is pointed and strongly projects anteromedially. In the specimen No. 18619 has been preserved the prefrontal process too, being distinctly wider than the ectopterygoid process. The distal part of the latter is curved ventrally while the posterior margin is oriented posteriorly.

Ectopterygoid (Fig. 23: F). The bone is “Y” shaped. The stem of the bone (= posterior ramus) is elongated, somewhat dilated before its posterior tip; the latter ended in a point. The two anterior rami are situated in a right angle to each other. The external ramus is distinctly wider than the internal one with its distal part dilated. The internal ramus is slender and somewhat shorter than the external one.

Quadrate (Fig. 24: A, B). The bone is elongated and somewhat triangular shaped, having its proximal end distinctly widened.

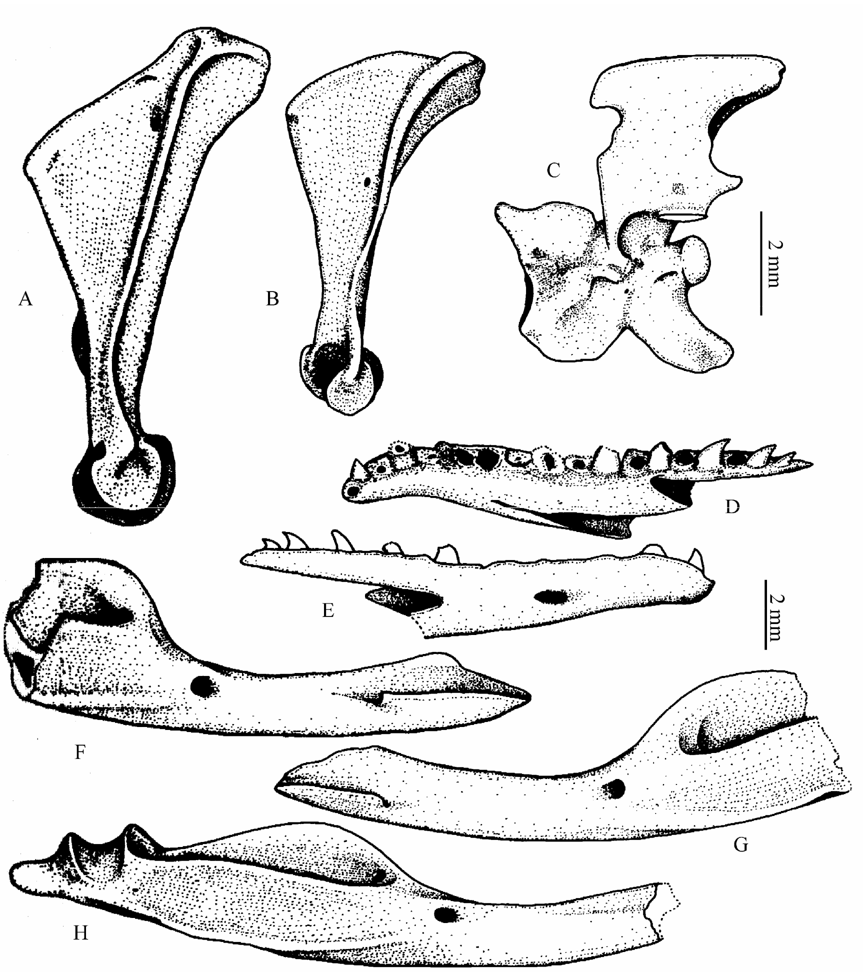


Figure 24. *Coluber viridiflavus*. A, B: right quadrates (Betfia pothole/B, MTC. No. 18760 and Betfia 12/A, MTC. No. 18716); C: axis (Betfia pothole/B, MTC. No. 18762); D, E: right dentary (Betfia 9/A, MTC. No.18656); F, H: right compound bones (Betfia 9/A, MTC. No. 18657/1,2); G: left compound bone (Betfia 9/A, MTC. No. 18657/3). A, B – posterolateral views; C, E, F, G, H – lateral views; D – medial view.

The quadrate crest is prominent, delimiting anterodorsally a small lobe, oriented medially. The stapedial process is oval-shaped and situated on the posterointernal margin of the bone. The trochlea quadrati is rather robust.

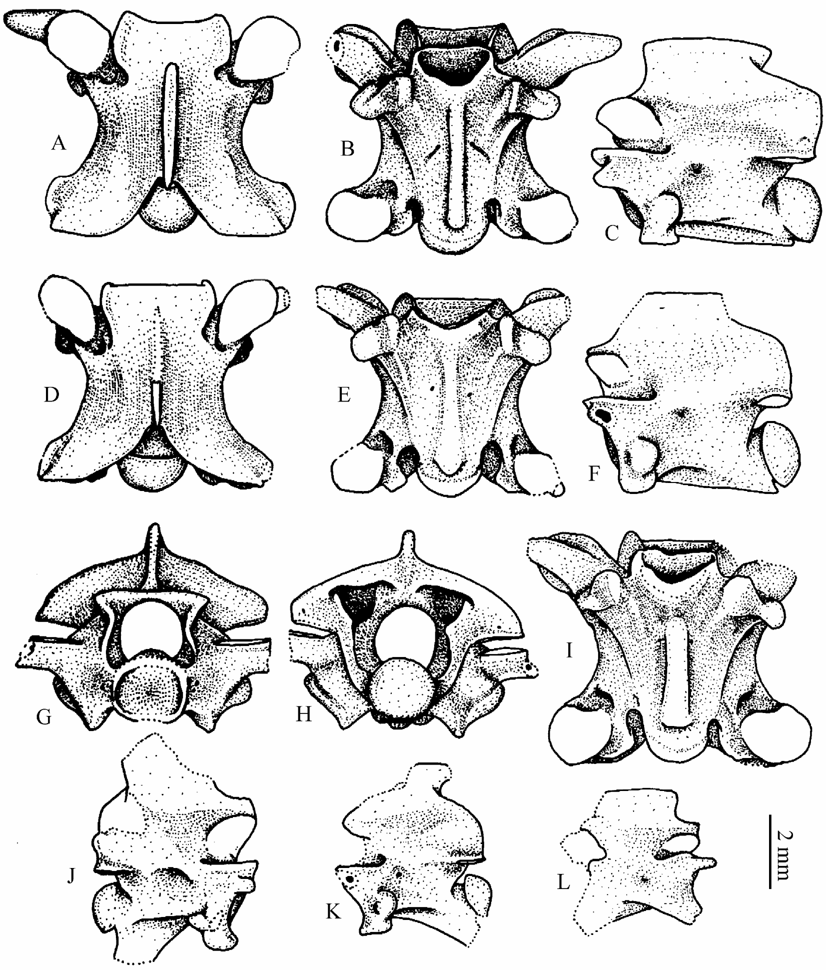
Dentary (Fig. 24: D, E, G). The bone is long, having its anterior tip curved medially. The dentition is of proterodont type, a complete dentary preserving 18 tooth positions. The Meckel's groove closes completely at the level of 8th tooth position, while the compound notch at the level of the 11th tooth. The mental foramen is situated at the level of the 8th tooth position.

Compound bone (Fig. 24: F, H). All the fragments are similar to recent *Coluber viridiflavus*. The mandibular fossa is delimited by two osseous lamina, the medial margin having 1.5 times higher than the lateral margin. The supraangular crest is well developed extending from the sigmoid fossa to the supraangular foramen. The latter is situated anterolaterally to the mandibular fossa. The retroarticular process is oriented ventromedially.

Axis (Fig. 24: C). The neural arch is relatively high and slightly compressed laterally. The spinal process is well developed, strongly overhanging posteriorly and only slightly anteriorly. There is a robust odontoid process. The pleurapophyses are broken off. The hypapophysis is curved posteriorly and it is comparatively shorter than in recent *C. viridiflavus*.

Cervical vertebrae (Fig. 25: J, K). The centrum is short, while the neural arch and spinal process is relatively high. The zygosphene usually is concave. The paradiapophyses are well differentiated: the parapophyses are provided with small processes oriented anteriorly. The hypapophysis is shorter than the vertebral centrum, with the distal part somewhat dilated and laterally compressed.

Trunk vertebrae (Fig. 25: A-I). In ventral view the centrum is short and of triangular shape. The haemal keel is long and flattened, of cuneate shape, but sometimes is spatulate-shaped (e.g. those coming from Subpiatră). The neural spine is as high as long or somewhat longer than high. The zygosphene is straight, provided with two lateral tubercles. The prezygapophyseal articular facets are oval while the postzygapophyseal articular facets are square. The prezygapophyseal processes are long, approximately equal in length those of the prezygapophyseal articular facets; they are oriented laterally (sometimes anterolaterally) and pointed distally. The interzygapophyseal ridges are well developed being parallel with the centrum. The subcentral ridges are better evidenced in the posterior vicinity of the diapophyses. The paradiapophyses are prominent, incompletely differentiated into diapophyseal and parapophyseal portions. The above structures are equal in length. The cotyle is circular. The paracotylar-, lateral-, and subcentral foramina are present. The trunk vertebrae in general are small sized. In twelve trunk vertebrae coming from Betfia 12/A, the centrum length (CL) ranges between 4.38 – 5.47 mm (mean = 5.03) while



Fiugre 25. *Coluber viridiflavus*. A-I: trunk vertebrae (A-C – Betfia pothole/B, MTC. No. 18763; D-H – Betfia 12/A, MTC. No. 18719; I – Betfia 12/A, MTC. No. 18719/2); J, K: cervical vertebrae (Betfia pothole/B, MTC. No. 18763/2,3); L: caudal vertebra (Betfia pothole/B, MTC. No. 18763/4). A, D – dorsal views; B, E, I – ventral views; C, F, J, K, L – lateral views; G – anterior view; H – posterior view.

the centrum width (CW) between 3,61 – 4.72 mm (mean = 4.12). The CL /CW ratio ranges between 1.13 – 1.27 (mean = 1.21). The centrum length in twelve vertebrae from Betfia pothole/B, ranges between 4.7 – 5.54 mm (mean = 4.98), while the centrum width between 3.82 – 4.6 mm (mean = 4.13). The CL/CW ratio ranges between 1.11 – 1.38 (mean = 1.2) (Fig. 26 and Fig. 27).

The haemal keel, as well as the subcentral ridge of the posterior trunk vertebrae is more prominent; the neural arch, as well as the neural spine is of lower height, when compared to those of middle trunk vertebrae.

Caudal vertebrae (Fig. 25: L). The centrum is elongated, having its neural spine long and of low height. The zygosphene is usually crenate. The pleurapophyses are well developed, their distal portion being somewhat dilated. The haemapophyses are oriented ventrolaterally.

Intraspecific variations. In basioccipitals – the shape and size of the basioccipital processes (the medial one being the largest); in basiparasphenoids – the length of the Vidian canal and the position of the common foramina (situated far or somewhat closer to the posterolateral margin), the shape of the grooves for the "cid " nerves; in compound bones – the shape of the anterior margin of the coronoid process (less or more abrupt); in middle trunk vertebrae – the shape of the haemal keel (flattened or prominent), as well as the shape of the zygosphene (in large specimens usually is concave).

Fossil record. The fossil remains of C. *viridiflavus* coming from the Lower Pleistocene of Bihor County are comparable with those coming from the Upper Pliocene (MN16) of Rebielice Królewskie 1A, Poland, described for the first time as belonging to a new large sized extinct species, namely *C. robertmertensi* (MLYNARSKI, 1964). The latter had a considerably larger size compared to recent *C. viridiflavus*, but considering the morphology of the above species, they practically can not be differentiated from each other. Consequently *C. robertmertensi* has been synonymized with *C. viridiflavus* by SZYNDLAR (1991a). The morphology of cranial bones of the above species are closely similar to those coming from Betfia (e.g. basiparasphenoid, basioccipital, quadrate, compound bone, a. o.). In contrary the vertebrae coming from Betfia and those from Subpiatră are distinctly smaller, having their centrum length/centrum width ratio distinctly higher than those known from the Upper Pliocene of Poland, fact which may be connected with the different paleoecological conditions (more optimal in the case of *C. viridiflavus* from the Upper Pliocene of Poland). In fossil state *C. viridiflavus* has been recorded in numerous fossil localities from the Neogene and Quaternary of Europe: Middle

Pliocene (MN15) of Etuliya, Valeny and Musaid, Moldova Republic (REDKOZUBOV, 1987); Upper Pliocene (MN16) of Rebielice Królevskie 1A, Poland (SZYNDLAR, 1984; 1991a); Chismikioy and Bachoy, Moldova Republic (REDKOZUBOV, 1987); Beremend 1, Hungary (VON SZUNYOGHY, 1932), Osztramos 7 (MN 16), Hungary (VENCZEL, 1998a); Lower Pleistocene of Montuosse 5, France (BAILON, 1991); Middle Pleistocene of St. Margarethen, Austria (RABEDER, 1977) and Varbeshnitza, Bulgaria (SZYNDLAR, 1991a); Upper Pleistocene of Abri de la Citoyenne, France (BAILON, 1991). A number of fossil remains have been described as *Coluber* cf. *viridiflavus* from the Middle Pliocene (MN15) of Weze 1, Poland (MLYNARSKI, 1961; SZYNDLAR, 1984, 1991a), Upper Pliocene (MN16) of Rebielice Królewskie 2, Poland (MLYNARSKI, 1977; SZYNDLAR, 1984, 1991a), Bad Deutsch Altenburg 20, Austria (RABEDER, 1974), Pleistocene of Spinagallo, Italy (KOTSAKIS, 1977a); Lower Pleistocene of Subpiatră, Romania (VENCZEL, 1991), Lower Pleistocene of Osztramos 2, Villány 8 and Somsich-hegy 2, Hungary (VENCZEL, 1997b, 1998b) and from the Middle Pleistocene of Bad Deutsch Altenburg, Austria (RABEDER, 1974). It is also known from the Pleistocene of Stránská Skála, Mladeč, and Malá Dohoda, Czech Republic (IVANOV, 1993, 1994, 1995). The fossil occurrences from Rebielice Królewskie 1A and those from Moldova Republic have been described, respectively listed, as C. *robertmertensi*. Based on a compound bone, VON SZUNYOGHY (1932) described *C. caspius (= Zamenis jugularis* var. *caspia* Gmel.) from the Lower Pleistocene locality of Betfia 2. Considering the large intraspecific variation observed in this bone, as well as the absence of vertebrae (rather easy to differentiate from the other members of the genus *Coluber*), we can believe that this bony remain may be assigned to *C. viridiflavus*, rather common in the fossil localities of Betfia. A basioccipital from the Upper Pleistocene (Weichselian) of Râpa has been assigned to *C. viridiflavus* by VENCZEL (1989: Fig. 3a). The specimen had a well-developed basioccipital crest with three prominent basioccipital tubercles of same length. The basioccipital tubercle was undeveloped. When the above specimen was compared with a large number of recent and fossil basioccipitals of *Natrix tesselata* the above author reconsidered the assignment of the mentioned specimen, including it in the synonymy of the latter (VENCZEL, 1995). On the other hand it can be mentioned, that contrary to the observation of FUHN & VANCEA (1961), the fossil locality of Râpa has never yielded vertebrae of the genus *Coluber*. The present range of distribution of C. *viridiflavus* is restricted to Italy and France, Northeastern Spain and to few islands in the Mediterranean Sea (BAILON, 1991).

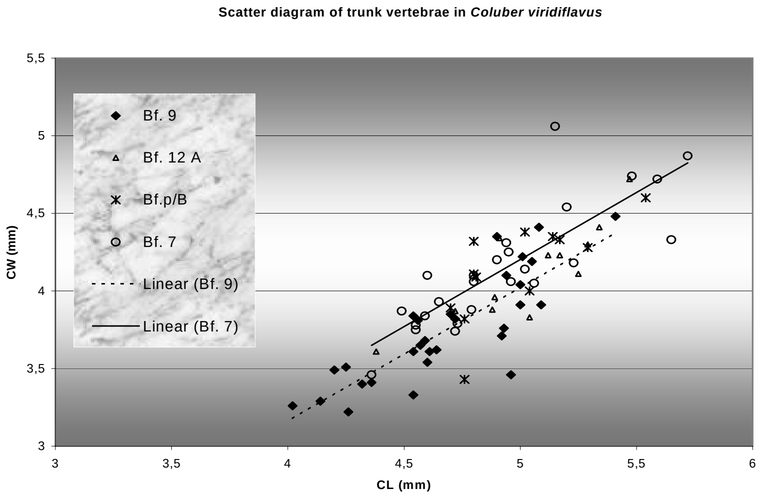


Figure 26. Scatter diagram of CL and CW of trunk vertebrae in *C. viridiflavus*. Abbreviations: Bf. – Betfia, Bf. p/B – Betfia pothole.

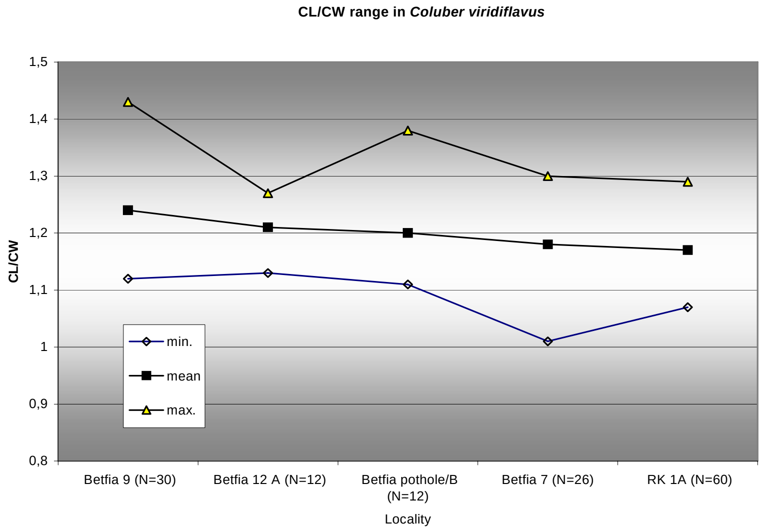


Figure 27. Cl/CW range in *C. viridiflavus.* Abbreviation: RK 1A – Rebielice Królewskie 1A (Poland).

Coluber cf. *C. gemonensis* (LAURENTI, 1768)

1974 *Coluber* cf. *gemonensis* (LAUERENTI): RABEDER, P.148, Fig. 4
1991a cf. *Coluber gemonensis* (LAURENTI, 1768): SZYNDLAR, P. 117, Fig. 14

Material: Betfia 7: one vertebra; Betfia pothole/B: one fragmentary frontal (MTC. No. 18764), one basioccipital (MTC. No. 18765), one prootic (MTC. No. 18766), three quadrates (MTC. No. 18767/1-3), nine vertebrae (MTC. No. 18768/1-9); Betfia 12 A: seven vertebrae (MTC. No.18731/1-7).

Description and comments

Frontal (Fig. 28: A). Only the dorsal part of the bone is preserved. The supraorbital crest is well developed, curved laterally while the medial margin is straight. The posterior portion of the frontal is somewhat widened. The internal and external prefrontal processes are less prominent when compared to those of *C. viridiflavus.*

Basioccipital (Fig. 28: B). The bone is wider than long. The basioccipital crest is well developed, more prominent medially and slightly diminishing laterally. There is only one basioccipital process, contrary to *C. viridiflavus*, the latter always being provided with three well-developed basioccipital processes. The basioccipital tubercle is prominent while the medial crest is lacking. The occipitocondylar tubercle is wide and incompletely separated off from the bone.

Prootic (Fig. 28: E). The supraotical crest is slightly evidenced. The V2 foramen equals in size that of V3 foramen. The laterosphenoid is comparatively thinner that in *C. viridiflavus*. The facial nerve foramen is located posterior to V3 opening.

Quadrate (Fig. 28: C, D). The bone is slightly curved anterodorsally, widening in its proximal tip. The quadrate crest is prominent and thin, its height being somewhat lower between the level of trochlea quadrati and stapedial process. Proximally the quadrate crest delimits a small lobe which is oriented medially. In posterolateral view the bone is of same thickness in its whole length. The stapedial process is of oval shape.

Trunk vertebrae (Fig. 28: F-M). The vertebrae are of small size, the length of centra never reaching 5 mm. In eight measured vertebrae from Betfia pothole/B, the centrum length ranged between 3.33 – 3.87 mm (mean = 3.64), while the centrum width between 2.1 – 3.08 mm (mean = 2.67). The centrum length/centrum width ratio ranged between 1.22 – 1.59 (mean = 1.36).

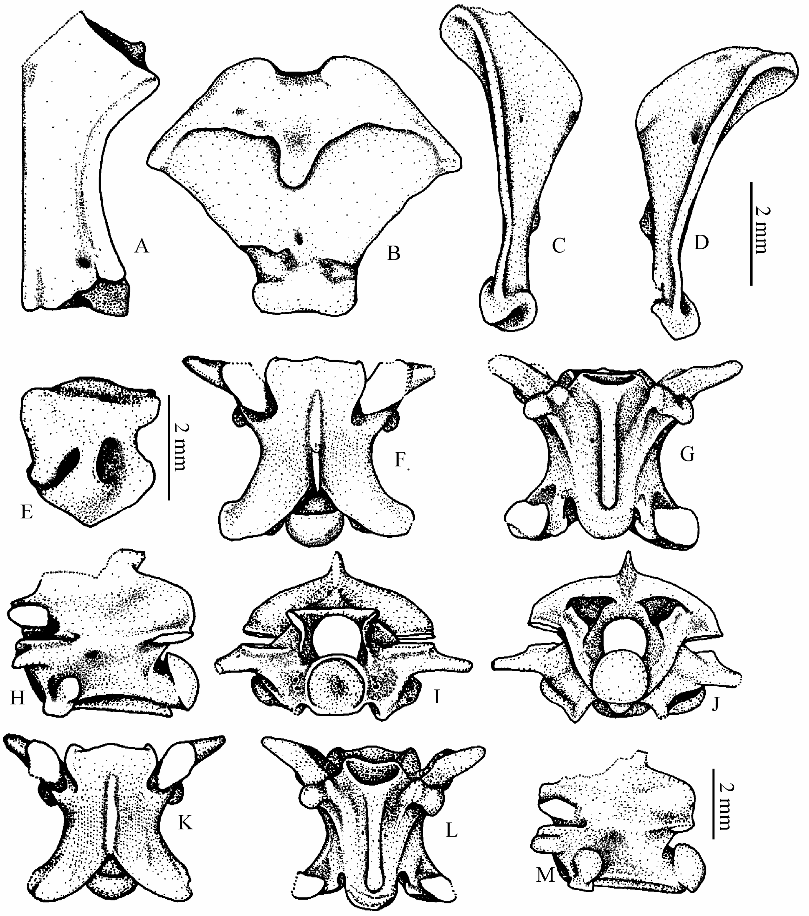


Figure 28. *Coluber* cf. *C. gemonensis*. A: right frontal (Betfia pothole/B, MTC. No. 18764); B: basioccipital (Betfia pothole/B, MTC. No. 18765); C, D: quadrates (Betfia pothole/B, MTC. No. 18767/1, 2); E: left prootic (Betfia pothole/B, MTC. No. 18766); F-M: trunk vertebrae from Betfia 12/A (F-J)(MTC. No. 18731/1) and Betfia 7 (K-M). A, F, K – dorsal views; B, G, L – ventral views; C, D – posterolateral views; E, H, M – lateral views; I – anterior view, J – posterior view.

In five vertebrae from Betfia 12/A, the centrum length ranged between 3.5 – 3.78 mm, while the centrum width between 2.64 – 3.01 mm. The centrum length/centrum width ratio ranged between 1.22 – 1.41 (mean = 1.29) (Fig. 29 and 30). In ventral view the centrum is of subtriangular shape. The haemal keel is prominent and flattened. Between the latter structure and the subcentral crest there is a subcentral fossa, more evident in the case of posterior trunk vertebrae. The neural arch is moderately high. The neural spine is distinctly longer than high. The roof of the zygosphene is convex, its anterior margin being provided with two larger lateral-, and with a smaller medial lobe. The prezygapophyseal articular facets are oval while the postzygapophyseal articular facets are slightly rounded or obovate. The prezygapophyseal processes are shorter, but sometimes equal in length, those of the prezygapophyseal articular facets. The paradiapophyses are prominent but incompletely differentiated into parapo- and diapophyseal portions. The latter structures are equal in length. The cotyle is circular, similarly to the vertebral canal. In each sides of the cotyle there is a paracotylar foramen (sometimes doubled). The lateral and subcentral foramina are well evidenced. The condyle is rounded.

All the above remains are comparable in size and shape to those of recent *C. gemonensis.* Of the remains known from the Middle Pleistocene of St. Margarethen, described by RABEDER (1977), only the basioccipital is comparable with those coming from Betfia. The above author had not considered vertebrae from the mentioned locality. The centrum length/centrum width ratio of vertebrae known from Betfia (1.22 – 1.59) is comparable with those coming from the Middle Pleistocene locality of Varbesnitza and from the Upper Pleistocene locality of Stoilovo, Bulgaria (1.29 – 1.50), reported by SZYNDLAR (1991a).

C. hungaricus, an extinct member of the genus, described by Bolkay (1913) from the Late Miocene (MN13) of Polgárdi 2, Hungary, is morphologically extremely similar to *C. gemonensis.* However the above author in his description was based on a single quadrate only. Due to this SZYNDLAR (1991a, 1991b), questioned the validity of the above taxon. Later VENCZEL (1994b, 1998c) reported numerous cranial bones and vertebrae coming from the newly discovered localities of Polgárdi 4 "Upper", Polgárdi 4 "Lower" and Polgárdi 5 demonstrating the wide intraspecific variability of *C. hungaricus* and the fact that it was the commonest snake of the above mentioned localities.

C. gemonensis in fossil state has been found in the following Neogene and Quaternary localities of Europe: Middle Pliocene (MN15) of Etuliya, Luchesty and Musait, and Upper Pliocene (MN16) of Novye Tanatary, Salchiya and Chismikioy of Moldova Republic (REDKOZUBOV, 1987); Middle Pleistocene of St. Margarethen (Austria) (RABEDER, 1977). A number of records were described under the name cf. *C. gemonensis* coming from the

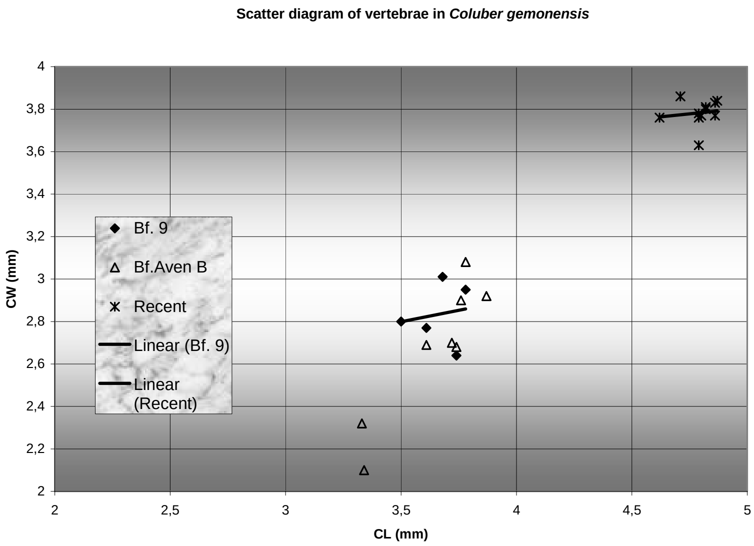


Figure 29. Scatter diagram of CL and CW of trunk vertebrae in *C. gemonensis.* Abbreviation: Bf. aven B – Betfia pothole/B.

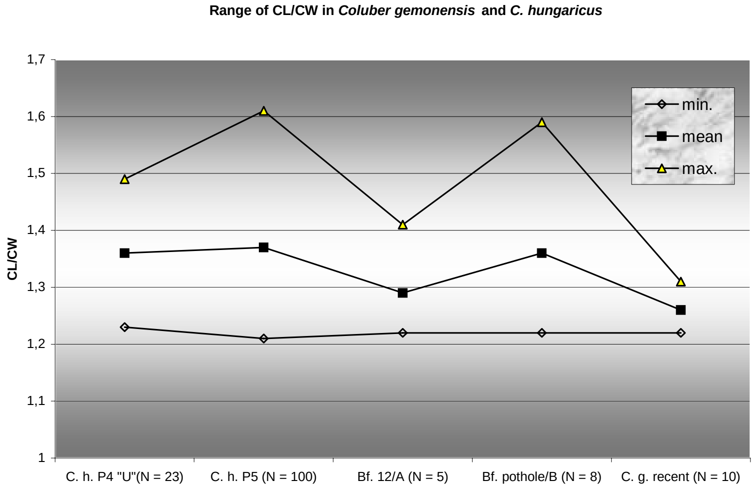


Figure 30. CL/CW range in *C. gemonensis* and *C. hungaricus.* Abbreviations: C. h. – *C. hungaricus*, C. g. – *C. gemonensis*, P4"U" – Polgárdi 4 Upper, P5 – Polgárdi 5 (Hungary).

Upper Pliocene (MN16) of Deutsch Altenburg 20 and from the Middle Pleistocene of Deutsch Altenburg 2, Austria (RABEDER, 1974), from the Pleistocene of Rethymnon, Greece (KOTSAKIS, 1977b), and from the Middle Pleistocene of Varbeshnitsa and from the Upper Pleistocene of Stoilovo, Bulgaria (SZYNDLAR, 1991a).

Genus ***Coronella*** LAURENTI, 1768

In Europe there are two members of the genus *Coronella* (*C. austriaca* and *C. girondica*). The former is distributed widely in our continent, while the distribution of the latter is limited to the Iberian Peninsula, southern France and north-western Africa.

Coronella austriaca **LAURENTI, 1768**

1990 *Coronella* cf. *austriaca*: VENCZEL, p.548

Material: Betfia 5: one vertebra (MTC. No. 18611); Betfia 7: one basiparasphenoid (MTC. No. 18624), 13 vertebrae (MTC. No. 18625/1-13); Betfia 9: six vertebrae (MTC. No. 18659/1-6); Betfia 10: one vertebra (MTC. No. 18683); Subpiatră: eight vertebrae (MTC. No. 19651/1-8); Râpa: two vertebrae (MTC. No. 18798/1-2).

Description and comments

Basiparasphenoid (Fig. 31: A, B). In dorsal or ventral view the parasphenoid process of the basiparasphenoid tapers to a point. There is a longitudinal groove on the ventral surface of the parasphenoid process. The sagittal crest on the basisphenoid portion is slightly developed. The pterygoid crests beginning from the central area reach the lateral margin of the bone. The latter structure is moderately developed. The suborbital flanges are reduced. The Vidian canal is rather long (considered a primitive character, by UNDERWOOD, 1967). The posterior orifices of the Vidian canal are located near the posterior margin while the anterior foramina are covered by the pterygoid crests. In dorsal view the anterior foramina of the abducens nerve are located far from the “cid” nerve foramina. The frontal step is of low height.

Vertebrae (Fig. 31: C-G). Only middle trunk vertebrae were considered. They are of reduced dimension, the centrum length never reaching 3.5 mm. The interzygapophyseal ridge of the trunk vertebrae is strongly reduced, having an “X” shape in dorsal or ventral view. In ventral view the centrum is subtriangular shaped.

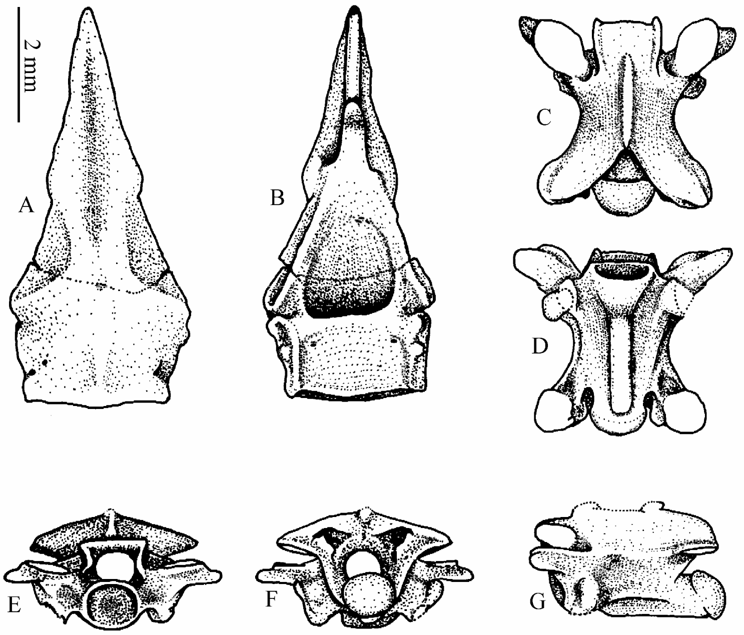


Figure 31. *Coronella austriaca*. A, B: basiparasphenoid (Betfia 7, MTC. No. 18624); C-G: trunk vertebra (Râpa, MTC. No. 18798/1). A, D – ventral views; B, C – dorsal views; E – anterior view; F – posterior view; G – lateral view.

The haemal keel is prominent, wide and usually is not flattened (more or less having a hemicylindrical shape). The neural arch is strongly flattened dorso-ventrally, lacking for epizygapophyseal spine. The neural spine is long and of low height. The roof of the zygosphene is straight, the anterior margin having provided with two lateral- and an indistinct medial lobe. The prezygapophyseal- and postzygapophyseal articular facets are relatively large having ovaloid or circular shape. The prezygapophyseal processes are extremely short (two or three times the length of the prezygapophyseal processes) and obtuse-shaped. The paradiapophyses are incompletely separated off having almost the same length. In anterior view the vertebral canal is of cylindrical shape, the cotyle and the condyle is slightly flattened dorsoventrally. The lateral, subcentral and paracotylar foramina are always present. In six measured vertebrae coming from Subpiatră the centrum length ranged between 2.64 – 2.88 mm (mean = 2.76), while the centrum width between 1.96 – 2.28 mm (mean = 2.12). The centrum length/ centrum width ratio ranged between 1.24 – 1.39 (mean = 1.29) (Fig. 32 and Fig. 33). In two recent specimens of *C. austriaca* (N = 15) we obtained the following measurements:

a.) CL: 3.06 – 3.23 mm (mean = 3.14), CW: 2.22 – 2.40 (mean = 2.32); CL/CW: 1.28 – 1.41 (mean = 1.34).

b.) CL: 3.12 – 3.31 (mean = 3.24), CW: 2.2 – 2.34 (mean = 2.28); CL/CW: 1.36 – 1.48 (mean = 1.41).

The different shape of haemal keel (e.g. prominent, flattened, or nearly absent), observed in specimens of *C. austriaca*, may be interpreted as ontogenetic variations only.

The earliest fossil record of the genus *Coronella* comes from the Late Miocene (MN13) localities of Polgárdi 2, 4 and 5, Hungary (VENCZEL, 1994b, 1998b), while the fossil record of *C. austriaca* is mainly restricted to Quaternary (SZYNDLAR, 1984). The above species is known also from the Upper Pliocene (MN16) of Chismikioy of Moldova Republic (REDKOZUBOV, 1987); from the Lower Pleistocene of Osztramos 2, 8, 14, Hungary (VENCZEL, 1997b) and of Villány 8, Hungary (VENCZEL, 1998b); from the Lower - Middle Pleistocene localities of Zalesiaki B, Kielniki, Zalesiaki A, Kadzielina, Kozi Grzbiet, Poland (SZYNDLAR, 1984; MŁYNARSKI and SZYNDLAR, 1989); from the Upper Pleistocene of Montousse 5, Terra Amata, Grotte de Lazaret, France (BAILON, 1991), from Breitenberghöhle bei Grossweinstein, Germany (BRUNNER, 1957), from Braşov, Romania (BOLKAY, 1913); from the Pleistocene – Holocene localities of Dietfurt, Spitzbubenhöhle, Euerwanger Buhl, Germany (MARKERT, 1975, 1976), Pisede from Malchin, Germany (PETERS, 1977a, 1977b), Niedostepna Cave, Poland (SZYNDLAR, 1984), Combe-Grenal and Baume Claire/Baume Sourde, France (BAILON, 1991). Some occurrences of *Coronella* sp. comes from the Upper Pliocene (MN16) of Chismikioy and Bachoy, Moldova Republic (REDKOZUBOV, 1987), as well as some described as cf. *Coronella* sp. from the Middle Pleistocene of Varbesnitza, Bulgaria, Tourkobounia 2, Greece, Bacho Kiro, Bulgaria, and from the subrecent locality of Pili B, Greece (SZYNDLAR, 1991a).

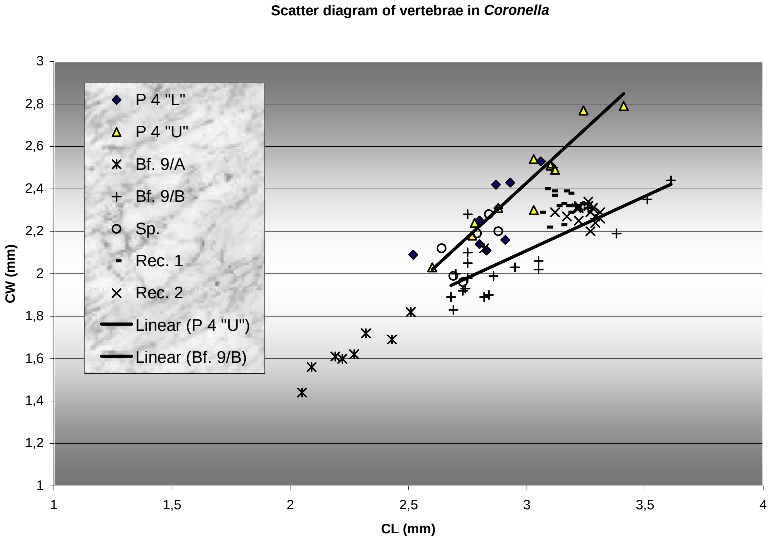


Figure 32. Scatter diagram of CL and CW in trunk vertebrae in *Coronella.* Abbreviations: Bf. – Betfia, P4"L" and "U" – Polgárdi 4 Lower and Upper, Sp. – Subpiatră, Rec. – *C. austriaca*, recent specimen.

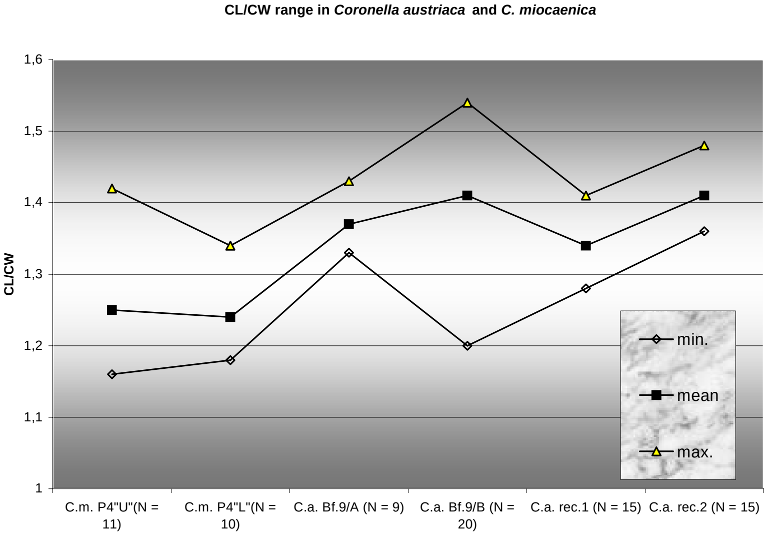


Figure 33. CL/CW range in *C. miocaenica* (C. m.) and *C. austriaca* (C. a.).

Genus ***Elaphe*** FITZINGER, 1833

The members of the genus *Elaphe* are widely distributed in Eurasia and North America. The European territory presently is inhabited by six species (*E. dione*, *E. hohenackeri*, *E. longissima*, *E. quatuorlineata*, *E. situla* and *E. scalaris*). A number of fossil species were described from the American and European Neogene and Quaternary (AUGÉ & RAGE, 2000). The oldest remains assigned to this genus are known from North America (HOLMAN, 1979), but most of them were described from the European Neogene. Based on skeleton, few differentiating morphological characters for European members of the genus *Elaphe* were mentioned by BAILON (1991).

Elaphe paralongissima **SZYNDLAR, 1984**

1984 *Elaphe paralongissima* SZYNDLAR: SZYNDLAR In: MLYNARSKI et.al., P. 222, fig. 7: 1,2
1991a *Elaphe paralongissima* SZYNDLAR: P.120, fig. 17
1992 *Elaphe paralongissima* : VENCZEL, Pp. 473-477, fig. 1

Material: Betfia pothole/A: 12 vertebrae (MTC. No. 18753/1-12); Betfia pothole/B: one fragmentary prootic (MTC. No. 18769); 90 vertebrae (MTC. No. 18770); Betfia 5: 113 vertebrae (MTC. No. 18612/1-113); one basiparasphenoid (MTC. No. 18626); one prootic (MTC. No. 18627); one fragmentary parietal (MTC. No. 18628); 373 vertebrae (MTC. No. 18629/1-373); Betfia 9: 170 vertebrae (MTC. No. 18660/1-170); Betfia 12/A: one fragmentary neurocranium (MTC. No. 18732), 18 vertebrae (MTC. No. 18733/1-18).

Description and comments

Fragmentary neurocranium (Fig. 34). From the neurocranium the basioccipital, the two exoccipitals, the supraoccipital and the right prootic are preserved. The specimen belonged to an adult snake having some pathological signs on the surface of the basioccipital and on the left exoccipital. The basioccipital is distinctly wider than long. The basioccipital crest is prominent, its shape being unique in the genus *Elaphe*. The basioccipital tubercles are well developed while the medial crest is lacking. A keel of pathologic nature traverses the left part of the basioccipital. The basioccipital condyle is of irregular shape. There are two foramina between the basioccipital crest and the basioccipital condyle. The exoccipital is relatively high; the occipital crest is prominent, ended in the vicinity of the vagus-hypoglossal nerve foramina.

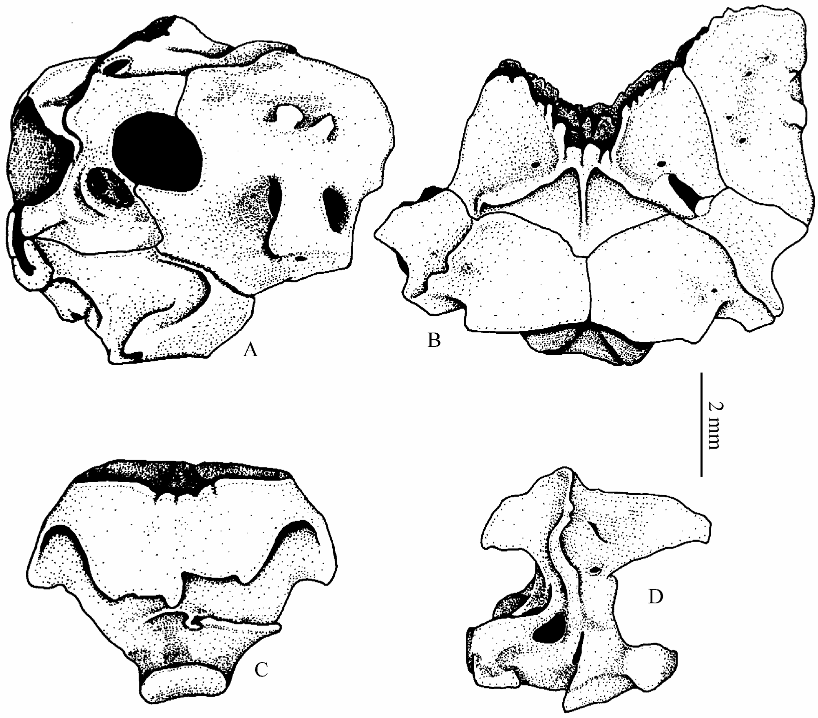


Figure 34. *Elaphe paralongissima*. A, B: fragmentary neurocranium (Betfia 12/A, MTC. No. 18732). C: basioccipital; D: left exoccipital. A, D – lateral views; B – dorsal view; C – ventral view.

The parotic process is elongated while the supraotic process is somewhat smaller, delimiting dorsally the recessus scalae tympani. The circumfenestral crest is well evidenced. Some pathologic signs are observed in the ventral margin of the left exoccipital too. The occcipital crests of the supraoccipital are prominent. The anterior sagittal crest is lacking, while the height of the posterior sagittal crest is diminished gradually (it does not reach the posterior margin of the bone). The supraoccipital crest of the prootic is reduced to two tubercles, situated dorsally to laterosphenoid. The V2 foramen (for the maxillary branch of

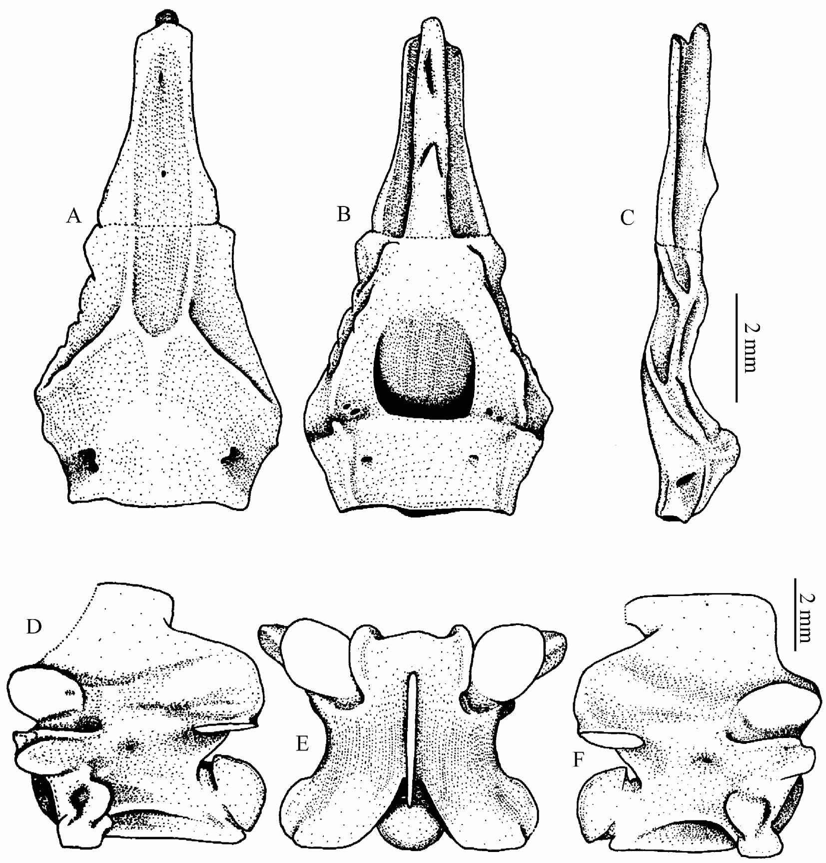


Figure 35. *Elaphe paralongissima*. A-C: basiparasphenoid (Betfia 7, MTC. No. 18626); D-F: posterior trunk vertebrae (Betfia 7, MTC. No. 18629/1, 2). A – ventral view; B, E – dorsal views; C, D, F – lateral views.

the trigeminal nerve) is of ovaloid shape while the V3 foramen (for the mandibular branch of the trigeminal nerve) is covered partially by a posterior overhang of the laterosphenoid. The ventral part of the latter structure is provided with a small foramen, corresponding to the exit of the V4 (constrictor internus dorsalis = "cid" nerve). The otic incisure is relatively deep.

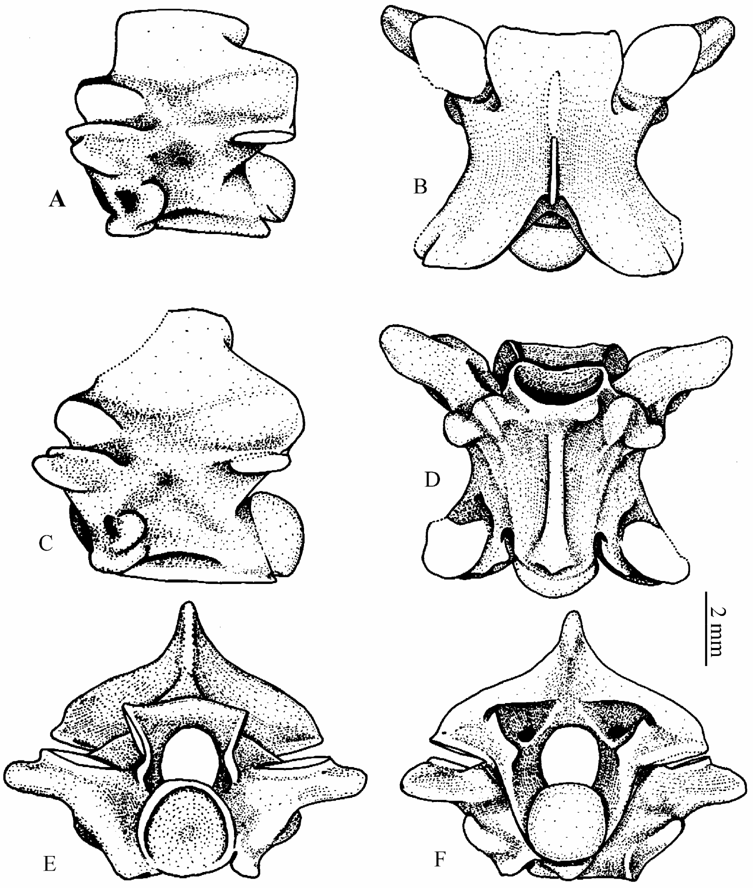


Figure 36. *Elaphe paralongissima*. A-F: trunk vertebrae (Betfia 7, MTC. No. 18629/3, 4). A, C – lateral views; B – dorsal view; D – ventral view; E – anterior view; F – posterior view.

Basiparasphenoid (Fig. 35: A-C). The specimen from Betfia 7 is completely preserved. In ventral view the basisphenoid crest is slightly evidenced. The basipterygoid processes are only moderately prominent. The pterygoid crests are oriented anterolaterally, reaching the lateral margin of the bone. A deep groove, beginning from the central area, is observed on the parasphenoid part of the bone. The suborbital flange is reduced. The Vidian canal is relatively long, the posterior foramina being situated at some distance from the posterolateral margin, while the anterior ones are covered by the pterygoid crests. In dorsal view the posterior foramina of the paired abducens nerve are situated posterolaterally to the hypophyseal fossa, while the anterior ones are situated in the vicinity of the cid nerve foramina. The frontal step is of low height, while the trabecular grooves are relatively shallow. In recent specimens of *E. longissima* the suborbital flange is distinctly larger, the posterior foramina of the Vidian canal are situated near the posterolateral margin of the bone (similarly as in *E. quatuorlineata*), while the groove on the ventral side of the parasphenoid is distinctly shallower and shorter (never reaching the junction of the pterygoid crests) than in *E. paralongissima*.

Parietal. The pars descendens of the specimen No. 18628 is lacking. The dorsal surface is flat; the parietal foramina are situated in the posterior part of the bone. The parietal crests are confluent in front of the posterior margin. The postfrontals are relatively small. In *E. longissima* the postfrontals are somewhat larger, while the parietal crests are confluent well in front of the posterior margin.

Vertebrae (Fig. 36). The vertebral centrum is relatively short, in ventral view having triangular shape. The neural arch is relatively high. The haemal keel is prominent, cuneate shaped and flattened. In the close vicinity of the paradiapophyses two small subcotylar tubercles are always present. The interzygapophyseal- and the subcentral crests are well developed. The height of the neural spine usually equals its length. The dorsal margin of the latter is thickened and overhangs posteriorly and slightly anteriorly (sometimes only the posterior overhang is present). The roof of the zygosphene in dorsal or anterior views is straight, while the anterior margin is concave, provided with two lateral lobes only. The pre- and postzygapophyseal articular facets are square shaped. The prezygapophyseal processes are shorter than the prezygapophyseal articular facets, flattened dorsoventrally and obtused distally. The paradiapophyses are distinctly differentiated into diapo- and parapophyseal portion, the latter structure being twice longer than the former. The paracotylar-, lateral- and subcentral foramina are always present. The cotyle and the condyle are rounded, the latter being slightly dorsally inclined.

In 30 measured middle trunk vertebrae, coming from Betfia 7, we obtained the following results:

Measurements	Min. – Max. (mm.)	Mean	SD
PR - PO	5.71 – 7.57		
CL	4.64 – 6.12		
PO - PO	6.91 – 9.11		
CW	3.76 – 6.03		
ZW	3.30 – 4.30		
CTH	1.59 – 2.48		
CTW	1.77 – 2.58		
PR - PR	7.00 – 9.48		
CL/CW	0.98 – 1.29	1.08	± 0.10
PO - PO/CW	1.45 – 1.86	1.62	± 0.12
CTW/CTH	1.04 – 1.27	1.10	± 0.04
ZW/CW	0.69 – 0.93	0.78	± 0.05
PR – PR/PR - PO	1.00 – 1.29	1.18	± 0.17
CL/ZW	1.29 – 1.51	1.37	± 0.04
PR - PR/CW	1.54 – 1.92	1.67	± 0.12

Table 2. Measurements of trunk vertebrae in *Elaphe paralongissima* (Betfia 7, N = 30).

In some specimens the vertebral centrum is wider than long, character rarely seen in other colubrids (Fig. 37 and Fig. 38). The haemal keel of the posterior trunk vertebrae is prominent (Fig. 35: D-F) and the subcentral grooves relatively deep (delimited laterally by prominent subcentral keels). Usually the zygosphene of these vertebrae is distinctly crenate. The cervical and caudal vertebrae of *E. paralongissima* are hardly distinguishable from those of recent *E. longissima*.

E. paralongissima was described for the first time exclusively on the basis of vertebrae, from the Upper Pliocene (MN 16) locality of Weze II, Poland. The holotype of the above species is a middle trunk vertebra (SZYNDLAR, 1984). The middle trunk vertebrae of *E. paralongissima* can be easily differentiated from those of its closest relative, *E. longissima*, by having a prominent, cuneate-shaped end flattened haemal keel provided anteriorly by two subcotylar tubercles (rarely seen in other Colubridae and more frequent in Natricinae), by strong interzygapophyseal ridges, by concave zygosphene and having their parapophyses twice longer than diapophyses. The presence of typical vertebrae from Betfia pothole/A, Betfia 5, Betfia 7, Betfia 9 and Betfia 12/A, allowed us to assign some cranial bones, differing from those of *E. longissima* and other members of *Elaphe* and *Coluber*, to this form, too. Remains of *E. paralongissima* have been reported from the Lower Pleistocene locality of Villány 8 (layers 9-12), Hungary, too (VENCZEL, 1998b).

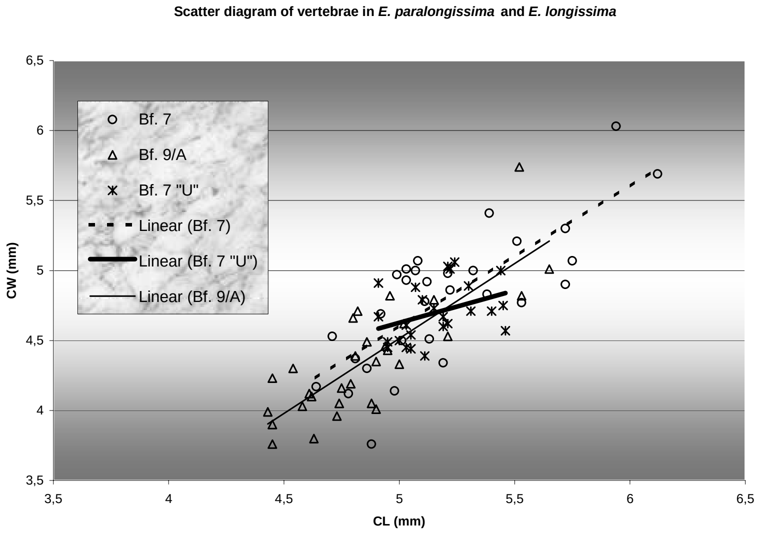


Figure 37. Scatter diagram of CL and CW of trunk vertebrae in *E. paralongissima* (Betfia 7 and 9/A) and *E. longissima*. (Betfia 7 "Upper" layers).

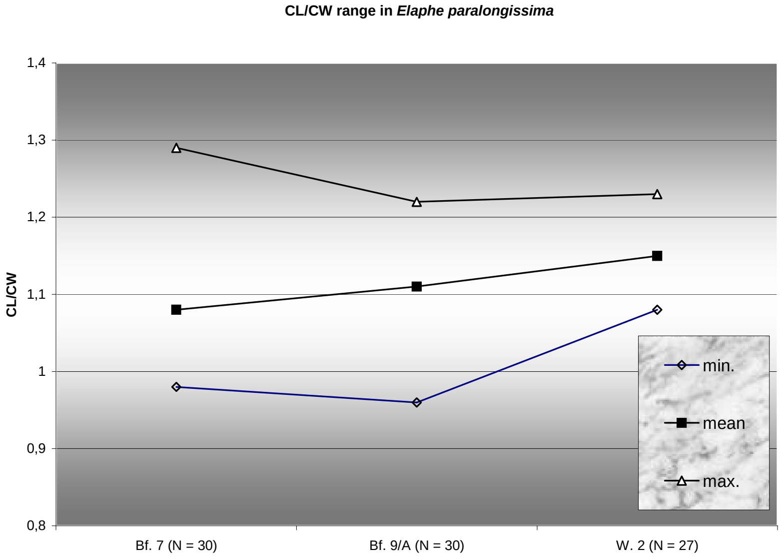


Figure 38. CL/CW range in *E. paralongissima*. Abbreviations: Bf. – Betfia, W2 – Weze II (Poland).

Elaphe quatuorlineata (LACÉPÈDE, 1789)

1974 *Elaphe* cf. *quatuorlineata* (LACÉPÈDE): RABEDER, P.148, fig. 3.

1991 *Elaphe quatuorlineata* LACÉPÈDE, 1789: VENCZEL, P. 475-476.

Material: Betfia pothole/A: three vertebrae (MTC. No. 18754/1-3). Betfia pothole/B: one fragmentary basiparasphenoid (MTC. No. 18771), three frontals (MTC. No. 18772/1-3), two compound bones (MTC. No. 18773/1-2), one quadrate (MTC. No. 18774), one prefrontal (MTC. No. 18775), one exoccipital (MTC. No. 18776), one nasal (MTC. No. 18777), one ectopterygoid (MTC. No. 18778), one axis (MTC. No. 18779), 130 vertebrae (MTC. No. 18780/1-130). Betfia 5: 123 vertebrae (MTC. No. 18613/1-123). Betfia 7: one frontal (MTC. No. 18630), two quadrates (MTC. No. 18631/1-2), one fragmentary parietal (MTC. No. 18632), two fragmentary basiparasphenoids (MTC. No. 18633/1-2), one exoccipital (MTC. No. 18534), one ectopterygoid (MTC. No. 18635), one prefrontal (MTC. No. 18636), 275 vertebrae (MTC. No. 18637/1-275). Betfia 9: two basioccipitals (MTC. No. 18661/1-2), two ectopterygoids (MTC. No. 18662/1-2), one supraoccipital (MTC. No. 18663), two frontals (MTC. No. 18664/1-2), one compound bone (MTC. No. 18665), 80 vertebrae (MTC. No. 18666/1-80). Betfia 11: one prootic, 11 vertebrae (MTC. No. 18689/1-11).

Description and comments

Prefrontal (Fig.39: C, D). The size and shape of the specimen approaches those of recent *E. quatuorlineata*. In lateral view the bone is “Z” shaped, the anterior margin is convex while the posterior margin is slightly concave. The lateral surface is flat, provided with small foramina, the dorsal and ventral margins are convex. In posterolateral view the lacrimal foramen is of moderate size.

Frontal (Fig. 39: E, F). A well preserved specimen from Betfia 7 (No. 18630), and further fragmentary frontals resemble those of recent *E. quatuorlineata*. The internal and external prefrontal processes are slightly prominent. In the posterolateral area of the dorsal surface is a shallow groove, provided with two large foramina. In anterior view the septomaxillary process (= nasal process) is relatively large, square shaped and oriented slightly anterolaterally. The frontal aperture is ovaloid.

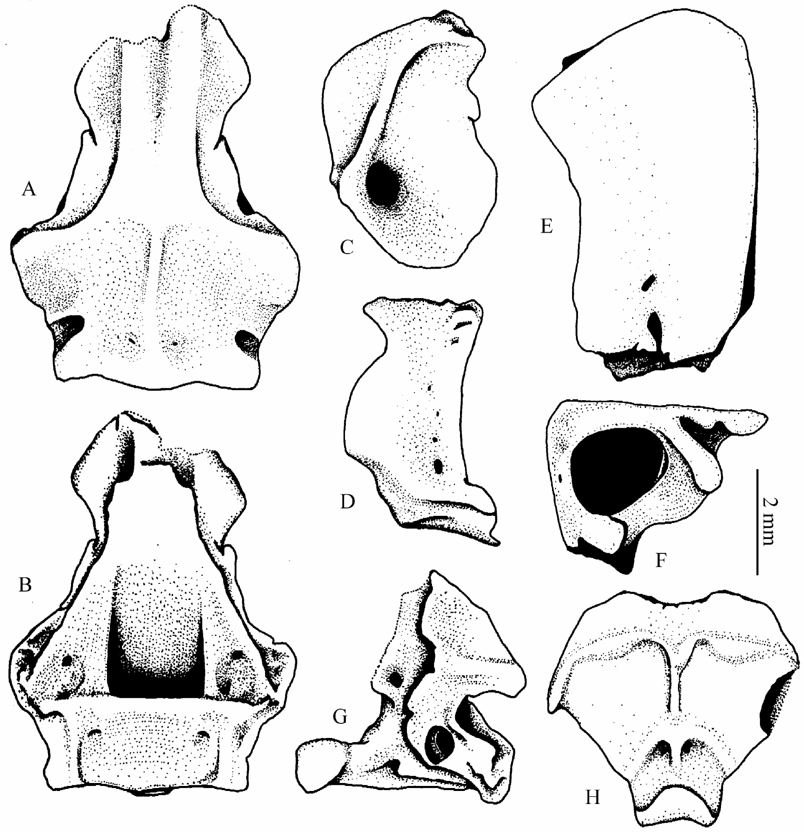


Figure 39. *Elaphe quatuorlineata*. A, B: fragmentary basiparasphenoid (Betfia pothole/B, MTC. No. 18771); C, D: left prefrontal (Betfia pothole/B, MTC. No.18775); E, F: left frontal (Betfia 7, MTC. No. 18630); G: right exoccipital (Betfia pothole/B, MTC. No. 18776); H: basioccipital (Betfia 9/A, MTC. No. 18661/1). A, H – ventral views; B, E – dorsal views; C – posterolateral view; D, G – lateral views; F – anterior view.

Basioccipital (Fig. 39: H). Some well-preserved specimens have been assigned to this species. The basioccipital crest and the basioccipital tubercles are moderately developed. The lateral lobes of the basioccipital processes are better marked while the medial one is practically confounded with the medial crest. The latter structure is widely separated off from the occipitocondylar tubercle by a deep groove. On the anteroventral part of this groove one or two foramina are present.

Exoccipital (Fig. 39: G). The occipital crest is prominent. The descendent part runs ventrally, delimiting posteriorly the vagus-hypoglossal nerve foramina. There are two foramina in a concavity. Posteroventrally to the latter is a small additional foramen, covered partially by an osseous lamina. The postoccipital foramen is relatively large. The paroccipital process is large and lacks the foramina. In recent *E. quatuorlineata* on the latter structure usually one or two small foramina can be observed. The circumfenestral crest, delimiting the relatively deep recessus scalae tympani, is well developed.

Basiparasphenoid (Fig. 39: A, B). A fragmentary specimen from Betfia pothole/B (lacking its parasphenoid process), closely resembles in shape and size that of recent *E. quatuorlineata*. In ventral view the central area is relatively wide. The pterygoid crests running from the central area to the lateral margins are of low height. The basipterygoid processes are very large and prominent (characteristic for *E. quatuorlineata)*. The sagittal basisphenoid crest is poorly evidenced. The posterior margin is nearly straight, having a small medial process (visible only in dorsal view). The posterolateral margins are concave. The relatively large posterior foramina of the Vidian canal are situated near to the posterolateral margins. The anterior foramina are situated well before the pterygoid crests, near to the lateral margins of the bone. The suborbital flanges are small, their margin being convex and curved ventrally. In dorsal view the pituitary fossa is somewhat square-shaped, being delimited posteriorly by the crista sellaris, the latter being penetrated by the paired abducens nerves. The anterior foramina of the latter are situated laterally to the posterior corner of pituitary fossa in a common recess with the foramina of “cid” nerves. A specimen with similar characters, coming from the Lower Pliocene of Deutsch Altenburg, Austria, was described by RABEDER (1974).

Prootic (Fig. 40: B). In lateral view the supraoccipital crest is slightly evidenced in the posterior half of the bone. The V2 foramen is relatively small and doubled ventrally by a small foramen which serves for the exit of “cid” nerves. The V3 foramen is somewhat larger, when compared with V2 foramen. The laterosphenoid is relatively wide, its ventral part being penetrated by the laterosphenoid foramen. In recent *E. quatuorlineata* the posterior margin of the laterosphenoid is strongly convex.

Ectopterygoid (Fig. 40: A). In dorsal view the stem of the bone is elongated and slightly curved laterally. The external ramus is wide and the dorsal surface slightly convex. The internal ramus is relatively short, its tip being pointed distally.

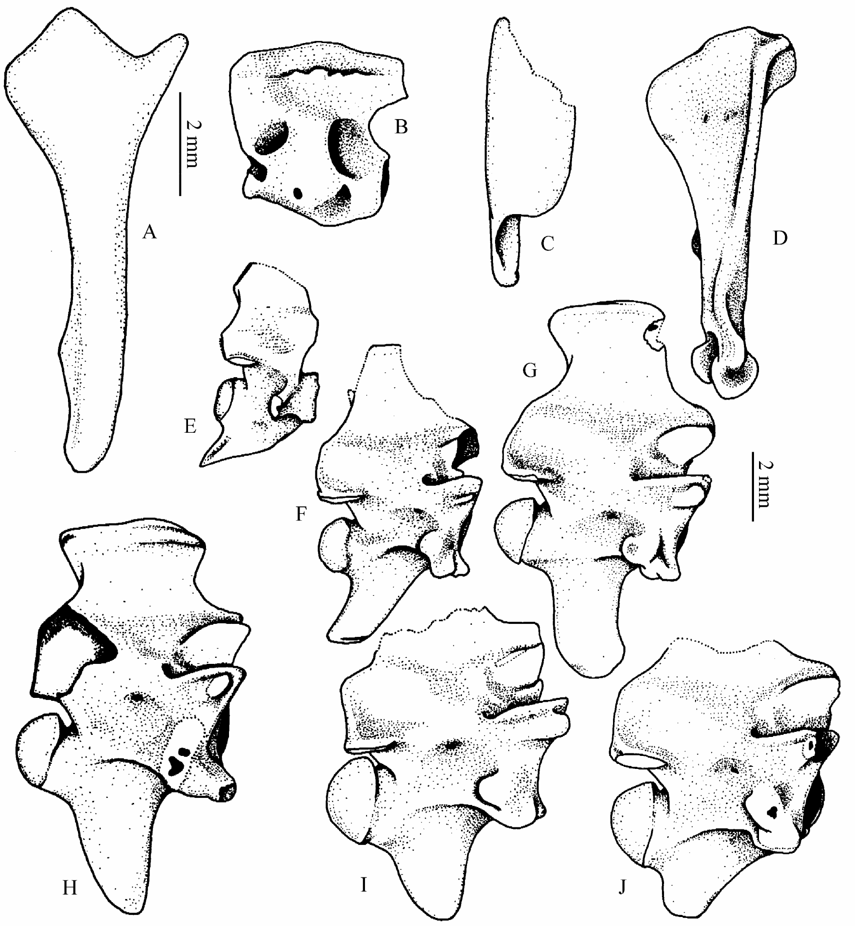


Figure 40. *Elaphe quatuorlineata*. A: left ectopterygoid (Betfia 7, MTC. No. 18635); B: left prootic (Betfia 11); C: left nasal (Betfia pothole/B, MTC. No. 18777); D: right quadrate (Betfia pothole/B, MTC. No. 18774); E: axis (Betfia pothole/B, MTC. No. 18779); F-J: cervical vertebrae (Betfia pothole/B, MTC. No. 18780/1-5). A, C – dorsal views; B, E-J – lateral views; D – posterolateral view.

Quadrate (Fig. 40: D). In dorsal view the bone is long having its proximal end moderately widened. In posterolateral view the anterior margin is straight while the posterior one is slightly concave. The quadrate crest is prominent, its height diminishing below the level of the stapedial process. The lobe delimited by the quadrate crest in the anterodorsal part of the bone is relatively small.

Compound bone (Fig. 41: E). The mandibular fossa is elongated, but relatively narrow. The medial flange (= coronoid process) is about twice higher than the lateral flange. The height of the anterior margin of the coronoid process is diminished gradually. The lateral surface is smooth, devoid of supraangular crest. The supraangular foramen is situated well in front of the mandibular fossa. The retroarticular process is slightly curved posteromedially.

Nasal (Fig. 40: C). A large sized specimen, comparable in morphology with recent *E. quatuorlineata*, was assigned to this form too.

Axis (Fig. 40: E). A relatively well-preserved specimen comes from Betfia pothole/B. The tip of the neural spine and the pleurapophyses are broken off. The hypapohysis is relatively thick, being shorter than the centrum, and oriented posteroventrally. Its tip is widened (slightly bicuspid). The neural arch is short and high. The anterior margin of the zygosphene is straight, while the neural spine is prominent.

Cervical vertebrae (Fig. 40: F-J). *E. quatuorlineata* is the only European colubrid snake in which the cervical vertebrae are oriented anteroventrally and may be regarded as an adaptation to oophagous mode of life. In recent specimens the hypapophyses of the first cervical vertebrae (third – 8th) are oriented posteroventrally, in the 9th – 11th vertebrae the hypapophyses are oriented ventrally while in 12th – 38th vertebrae antero-ventrally (pers. obs.). Almost all types of cervical vertebrae have been recovered from the fossil deposits of Betfia. The centrum of the anterior cervical vertebrae is relatively short and the neural arch is vaulted. The prezygapophyses are short, while the height of the neural spine equals its length. The dorsal margin of the neural spine is thickened.

Middle trunk vertebrae (Fig. 41: A-D). The vertebrae are strongly built and of large size, the centrum length usually exceeding 7 mm. In ventral view the centrum is short, the haemal keel is flattened and the subcentral keel is slightly evidenced. In lateral view the neural arch is moderately vaulted, the posterior margin of the neural lamina is straight, the neural spine is lower than long, overhanging posteriorly and slightly anteriorly. The dorsal margin of the latter structure is strongly thickened. The paradiapophyses are distinctly differentiated into diapophyseal and parapophyseal portions, the latter being slightly longer. The roof of the zygosphene, in anterior or dorsal view is convex while its anterior margin is always concave. The prezygapophyseal articular facets are oval while the postzygapophyseal articular facets are rounded. The prezygapophyseal process are always shorter than the prezygapophyseal articular facets, their tips being pointed distally.

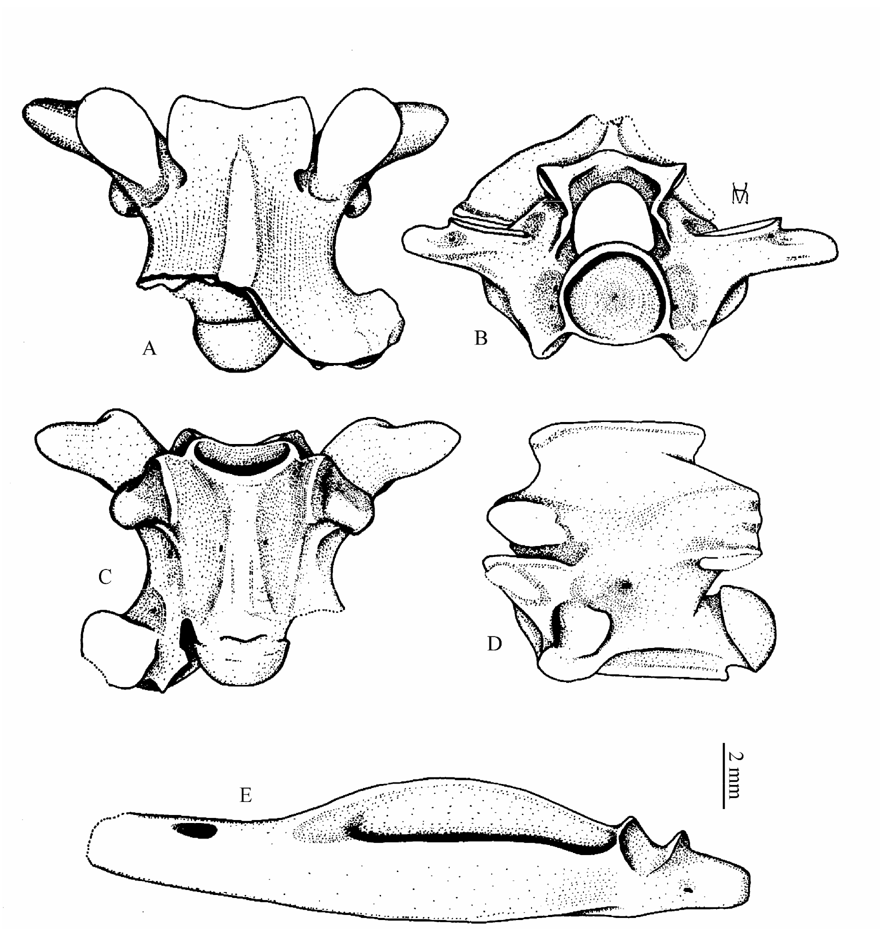


Figure 41. *Elaphe quatuorlineata*. A-D: trunk vertebrae (Betfia 5, MTC. No. 18613/1, 2); E: left compound bone (Betfia 9/A, MTC. No. 18665). A – dorsal view; B – anterior view; C – ventral view; D, E – lateral views.

The cotyle and the condyle are slightly appressed dorsoventrally. All the foramina are well evidenced, but the paracotylar foramina are sometimes doubled. In fifteen measured middle trunk vertebrae, coming from Betfia pothole/B, the centrum length ranges between 5.6 – 6.49 mm (mean = 5.97 mm), while the centrum width between 4.97 – 5.89 mm (mean = 5.3 mm).

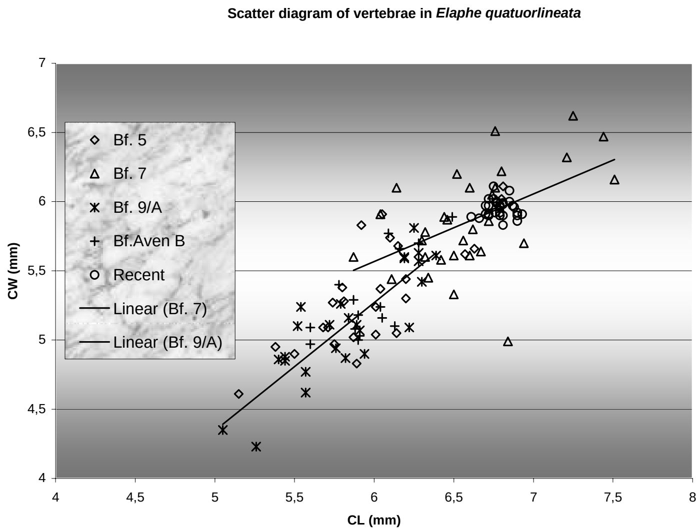


Figure 42. Scatter diagram of CL and CW of trunk vertebrae in *E. quatuorlineata*. Abbreviations: Bf. aven B – Betfia pothole/B.

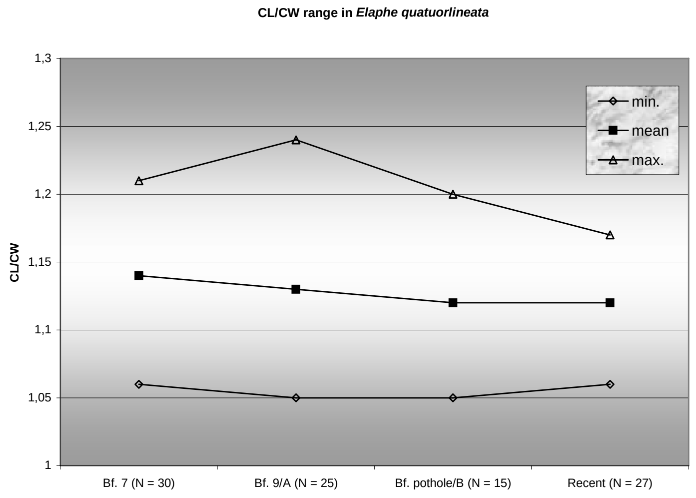


Figure 43. CL/CW range in *E. quatuorlineata*.

The centrum length/centrum width ratio ranges between 1.05 – 1.2 (mean = 1.12). The measurements made in middle trunk vertebrae (between the 70th – 96th vertebrae) of a recent specimen of *E. quatuorlineata* gave the following results: the centrum length ranges between 6.6 – 6.93 mm, the centrum width ranges between 5.88 – 6.3 mm, while the centrum length/centrum width ratio between 1.06 – 1.17 (mean = 1.12) (Fig. 42 and Fig. 43).

The cloacal and caudal vertebrae are less numerous in the material, and usually are very damaged, with the lymphapophyses, haemapophyses and respectively the pleurapophyses broken off. The neural spine is relatively of low height, the dorsal margin being thickened. The anterior margin of the zygosphene is usually concave, but sometimes is crenate.

The fossil remains of *E. quatuorlineata* in our hand do not differ significantly from those of recent comparative materials. Some bony remains belonging to large sized specimens suggest optimal habitat conditions and that the mentioned individuals reached an appreciable age.

The fossil record of *E. quatuorlineata* comes from the Upper Pliocene (MN16) of Deutsch Altenburg 20, Austria (RABEDER, 1974), from the Lower Pleistocene of Csarnóta 4, Hungary (SZYNDLAR, 1991a), from the Lower Pleistocene of Osztramos 2 and 14, Hungary (VENCZEL, 1997b), from the Middle Pleistocene of Deutsch Altenburg 2, Austria (RABEDER, 1977), from the Middle Pleistocene of Varbeshnitza, Bulgaria, Tourkobounia 2 and Tourkobounia 5, Greece, as well as from the Upper Peistocene of Stoilovo, Bulgaria (SZYNDLAR, 1991a). A trunk vertebra from the Upper Pliocene (MN17) of Villány 3, Hungary, was identified as cf. *E. quatuorlineata*, by SZYNDLAR (1991a).

***Elaphe longissima* (LAURENTI, 1768)**

1932 *Elaphe longissima* (LAURENTI): VON SZUNYOGHY, Pp. 10, 49-50.
1977 *Elaphe longissima* (LAURENTI): RABEDER, P. 92, Fig. 11:4, Pl. 1: 11.
1984 *Elaphe longissima* (LAURENTI): SZYNDLAR, Pp. 86-97, Figs. 34-37.
1987 *Elaphe longissima* LAURENTI: VENCZEL , Pp. 580-581, Fig. 2
1989 *Elaphe longissima* (LAURENTI), 1768: VENCZEL, Pp. 765-768, Figs. 2: j, 3:b, 4: a – k, 5: a – c.
1992 *Elaphe longissima*: VENCZEL, P. 475
1995 *Elaphe longissima* (LAURENTI, 1768): VENCZEL, Pp. 78-90, Fig. 23-26
2000 *Elaphe longissima*: VENCZEL & DAMM, Pp. 148-149

Material: Betfia 10: one left prootic (MTC. No. 18684); Subpiatră: one left prootic (MTC. No. 16948), one premaxilla (MTC. No. 16949), 80 vertebrae (MTC. No. 16950/1-80); Chişcău 3: one quadrate and 13 vertebrae; Râpa: 10 prefrontals (one of them fragmentary)(MTC. No. 18799/1-11), 17 frontals (two of them fragmentary) (MTC. No. 13665/1-17), 5 parietals (two of them fragmentary)(MTC. No. 13666/1-5), four basioccipitals (MTC. No. 13667/1-4), 13 exoccipitals (three of them fragmentary)(MTC. No. 18800/1-13), four supraoccipitals (one of them fragmentary)(MTC. No. 18801/1-4), 5 basiparasphenoids (three of them fragmentary)(MTC. No. 13669/1-5), 15 prootics (MTC. No. 13668/1-15), 12 maxillae (five of them fragmentary)(MTC. No. 13670/1-12), three pterygoids (two of them fragmentary)(MTC. No. 13671/1-3), five ectopterygoids (MTC. No. 13672/1-5), nine palatines (MTC. No. 13673/1-9), three supratemporals (one of them fragmentary)(MTC. No. 18802/1-3), 12 quadrates (one of them fragmentary)(MTC. No. 13674/1-12), 25 dentaries (five of them fragmentary)(MTC. No. 13676/1-25), 20 compound bones (four of them fragmentary)(MTC. No. 13675/1-20), three intranasals (one of them fragmentary)(MTC. No. 18803/1-3), one premaxilla (MTC. No. 13677), eight vomers (four of them fragmentary)(MTC. No. 18804/1-8), one atlas (MTC. No. 18805), seven axises (MTC. No. 18806/1-7), 3300 vertebrae (MTC. No. 13765); Vadu Crişului: two middle trunk vertebrae (MTC. No. 18817/1-2); Valea Morii: 5 middle trunk vertebrae (MTC. No. 20743), 1 parietal (MTC. No. 20748), 1 quadrate, 1 palatine, 1 pterygoid, 32 vertebrae (MTC. No. 20755).

Description and comments

Prefrontal (Fig. 44: A, B). The anterior margin is strongly convex, while the posterior margin is slightly concave. The lateral surface is provided with a large foramen and with several small foramina. In posterolateral view there is a relatively large lacrimal foramen.

Frontal (Fig. 44: D-F). The frontal aperture is of circular shape; the septomaxillary process is small, in lateral view having rectangle shape. The prefrontal processes are triangle shaped; the external prefrontal process is wider than the internal one. In ventral view the trabecular grooves are well evidenced.

Parietal (Fig. 44: C). The dorsal surface is flat, provided with two parietal foramina, situated close to each other in the posterior half of the bone. The parietal crests are prominent especially in the posterior part of the bone and converge before reaching the posterior margin. The descending part is strongly convex.

Basioccipital (Fig. 44: G). The basioccipital crest is present, with the lateral lobes better marked then the medial one.

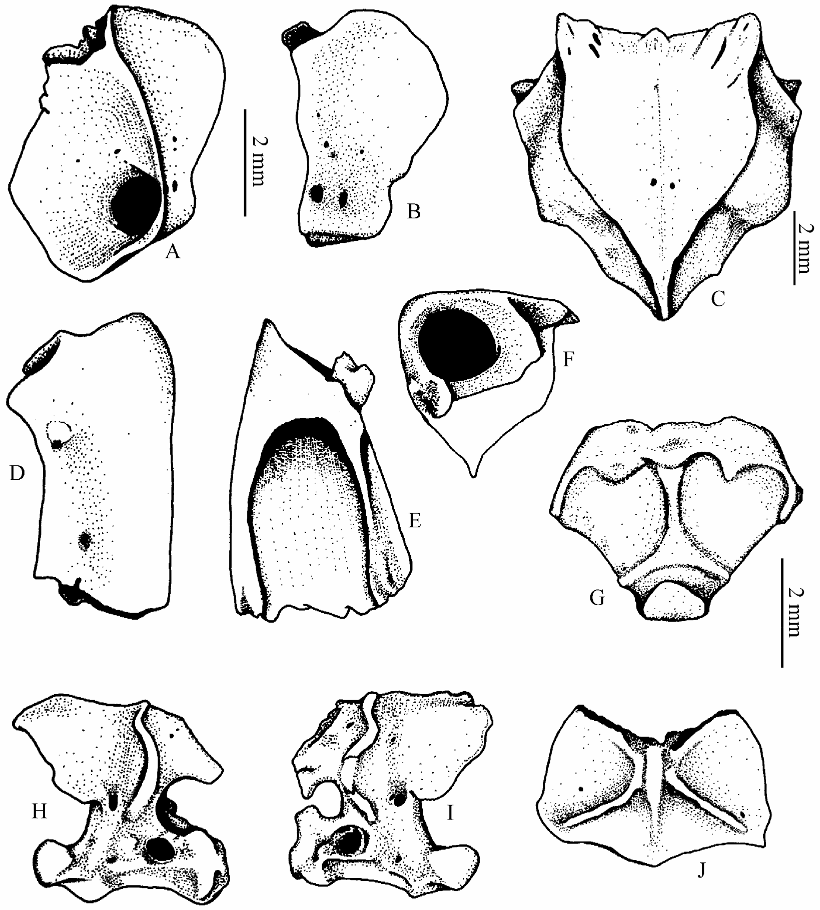


Figure 44. Fossil remains of *Elaphe longissima* from Râpa. A, B: right prefrontal (MTC. No. 18799/1); C: parietal (MTC. No. 13666/1); D-F: left frontal (MTC. No. 13665/1); G: basioccipital (MTC. No. 13667/1); H, I: exoccipitals (MTC. No. 18800/1,2); J: supraoccipital (MTC. No. 18801/1). A – posterolateral view; B, H, I – lateral views; C, D, J – dorsal views; E – medial view; F – anterior view.

The medial crest is divergent posteriorly and distinctly separated from the occipitocondylar tubercle by a deep furrow. In the smaller specimens (e.g. those coming from Râpa) the crests on the basioccipital are more reduced.

Exoccipital (Fig. 44: H, I). The occipital crest is prominent, running laterally above the vagus-hypoglossal nerve foramina. The latters are situated in a concavity comprising one larger and two smaller foramina. The postoccipital foramen is relatively large. The circumfenestral crest surrounds the otic incisure. The size of the former shows a wide range of intraspecific variation. In a specimen the recessus scalae tympani is almost entirely closed in the exoccipital (Fig. 44: I). The paroccipital process is relatively large.

Supraoccipital (Fig. 44: J). The anterior and the posterior sagittal crests are relatively short. The height of the latter is abruptly diminished posteriorly and does not reaches the posterior margin of the bone. The occipital crests are prominent and slightly inclined posteromedially, and similarly as in the case of the posterior sagittal crests, they do not reach the posterior margin of the supraoccipital.

Basiparasphenoid (Fig. 45: E, F). The pterygoid crests are slightly inclined anterolaterally. In ventral view, beginning just anteriorly to the junction of the pterygoid crests, a deep furrow runs through the parasphenoid process. The common foramen is situated close to the posterolateral border of the basisphenoid. The pterygoid crests hide the anterior opening of the Vidian canal. The suborbital flanges are relatively small and are slightly bent ventrally. In dorsal view the pituitary fossa is deep and nearly circular shaped. Laterally and posteriorly to the latter, all the cranial foramina are well evidenced. The anterior foramina of the abducens nerves are situated close (but not in a common concavity) to those of the “cid” nerves.

Prootic (Fig. 45: A-C). The supraoccipital crest is lacking or is slightly evidenced. The V2 foramen is usually circular, but sometimes is of oval shape, or provided with a groove running to the anteroventral margin. The V3 foramen is partially covered by the posterior margin of the laterosphenoid. Posteriorly to the V3 foramen is observed a smaller foramen, the exit for the facial nerve. The laterosphenoid bar is widened ventrally, its posterior wall being strongly convex. Near its base a laterosphenoid foramen is usually present.

Maxilla (Fig. 46: A). In a complete bone the number of teeth range between 18 – 20. The dentition is of isodont type, with the tips strongly curved posteriorly. The prefrontal process, having its tip pointed and oriented posteroventrally, is situated at the level of 8th – 9th teeth (in a specimen coming from Râpa at the level of 8th – 10th teeth). The ectopterygoid process is situated at the level of 15th –17th teeth.

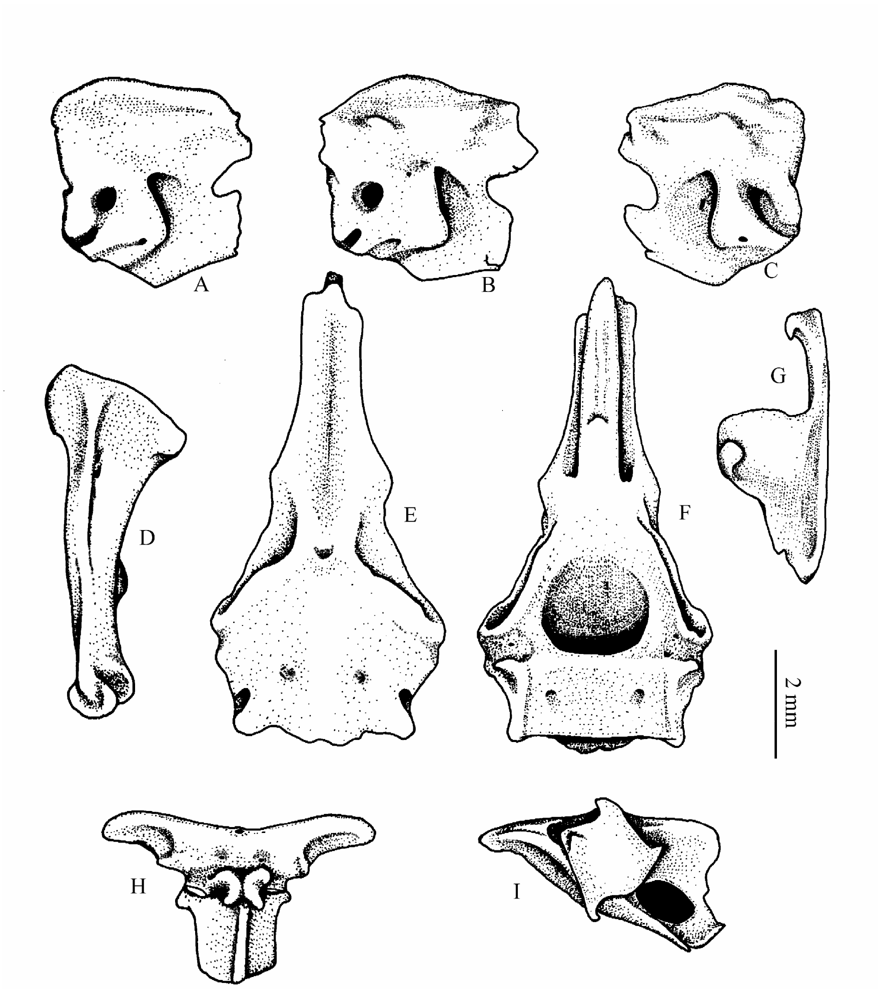


Figure 45. Fossil remains of *Elaphe longissima* from Râpa. A-C: prootics (MTC. No. 13668/1-3); D: left quadrate (MTC. No. 13674/1); E, F: basiparasphenoid (MTC. No. 13669/1); G: left intranasal (MTC. No. 18803/1); H: premaxilla (MTC. No. 13677); I: left vomer (MTC. No. 18804/1). A-C, I – lateral views; D – posterolateral view; E – ventral view; F, G – dorsal views; H – posteroventral view.

Pterygoid (Fig. 46: E). The bone in ventral or dorsal view is slightly curved. The ectopterygoid process is slightly evidenced, the pterygoid crest is lacking. The anteromedial part is slightly convex, while the lateral margin is bent upward forming a dorsal crest. Between the former structures is observed an elongated groove. The pterygoid teeth are of isodont type. The number of teeth in the observed specimens is 11. The length of the tooth row is approximately twice shorter than the whole length of the bone.

Ectopterygoid (Fig. 46: F). The stem of the bone is elongated and is slightly curved laterally, having its distal part more slender. The ectopterygoid rami meet in a right angle with each other. The external ramus is broad, while the internal one is relatively slender, with its tip tapering.

Palatine (Fig. 46: B). The number of teeth is 11 (except for a specimen, provided with 12 teeth); the dentition is of isodont type, the tips of the teeth being strongly curved posteriorly. The maxillary process is long and relatively slender and projected posteriorly. At the base of the latter structure is observed the maxillary nerve foramen, continued in an anteriorly directed groove. The vomeral process is situated at the level of the 5th – 9th teeth, being oriented anteriorly. The choanal process (if conserved) is well developed.

Supratemporal (Fig. 46: G). The bone, lacking any taxonomic characters, is elongated, strongly flattened dorsoventrally and slightly curved laterally.

Quadrate (Fig. 45: D). In posterolateral view the posterior margin is concave, while the anterior one is convex. The proximal portion is slightly dilated, provided with a small projection in its posteromedial side. The quadrate crest is better evidenced above the trochlea quadrati as well as above the level of the stapedial process. The latter is prominent in posterolateral view.

Dentary (Fig. 46: C). In twelve specimens coming from the Upper Pleistocene of Râpa the number of teeth is ranged between 21 – 25. The dentition is of proterodont type. The Meckel's groove closes completely at the level of the 6th or 5th tooth, more rarely at the level of the 4th tooth. The mental foramen is slightly elongated, or oval and situated at the level of the 9th – 11th teeth, but sometimes at the level of the 8th – 10th, 8th – 11th, 9th – 10th and respectively at the level of the 9th – 12th teeth. The compound notch is situated at the level of the 14th tooth or sometimes at the level of the 13th, 12th, or at the level of the 15th tooth.

Compound bone (Fig. 46: D). The medial flange (= coronoid process) is twice higher than the lateral flange, the latter being slightly concave in its posterolateral portion. The supraangular crest is lacking. The supraangular foramen is situated anteriorly and relatively close to the mandibular fossa. The retroarticular process is thick and slightly curved ventromedially.

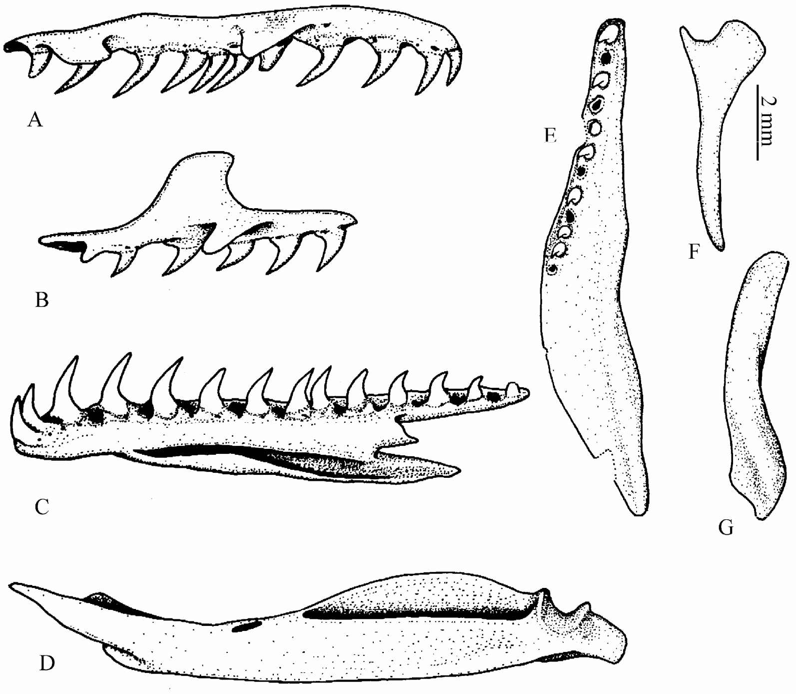


Figure 46. Fossil remains of *Elaphe longissima* from Râpa. A: left maxilla (MTC. No. 13670/1); B: right palatine (MTC. No. 13673/1); C: right dentary (MTC. No. 13676/1); D: left compound bone (MTC. No. 13675/1); E: left pterygoid (MTC. No. 13671/1); F: right ectopterygoid (MTC. No. 13672/1); G: left supratemporal (MTC. No. 18802/1). A-C – medial views; D – lateral view; E – ventral view; F, G – dorsal views.

Intranasal (= septomaxilla) (Fig. 45: G). The bone is closely similar to that of recent *E. longissima.* The frontal process is relatively long and slender. The medial and posterior margins are slightly convex while the anterior margin is concave. The ascendant nasal process is prominent and rounded while the dorsal fossa is relatively shallow.

Vomer (Fig. 45: I). A well preserved specimen coming from Râpa differs in some details from those of recent *E. longissima*: the vomeral foramen in the fossil specimen is distinctly larger than in recent ones, while the posterior margin of the former has a different shape, characters which probably may be attributed to intraspecific variations.

Premaxilla (Fig. 45: H). The lateral arms are relatively long. The vomeral process is relatively short being situated at right angle with the nasal processes. The ventral foramina of the premaxillary canals are situated close to each other.

Atlas (Fig. 47: A). The bone is of ring-like shape, lacking the neural spine and the hypapophysis. The pleurapophyses are projected posteroventrally.

Axis (Fig. 47: B). The neural spine is prominent, its distal portion projected posteriorly and pointed. Above the postzygapophyses are observed the well-developed epizygapophyseal spines. The first hypapophysis is relatively long, curved posteroventrally. The latter structure in *E. quatuorlineata* is distinctly shorter. The pleurapophyses are long and projected posteriorly.

Cervical vertebrae (Fig. 47: C, D). The centrum is short and the neural arch is vaulted. The neural spine is higher than long, provided with anterior and posterior projections. The hypophysis is long and projected posteroventrally. The paradiapophyses are indistinctly separated into parapo- and diapophyseal portions. The parapophyses are provided with small processes, projected anteriorly.

Middle trunk vertebrae (Fig. 47: E-G). In ventral view the centrum is relatively short and triangular shaped. The haemal keel is prominent, the ventral surface being rounded or flattened; in smaller specimens (e.g. those coming from Chişcău 3) usually it is sharp. Posteriorly the haemal keel becomes slightly widened and flattened, ended in an acute point. The subcentral ridges are better developed in the posterior vicinity of the parapophyses. The neural arch is moderately vaulted, while the neural canal is usually rounded. The neural spine is relatively high, its dorsal margin usually being thickened, overhanging posteriorly and in a lesser degree anteriorly. The anterior margin of the zygosphene usually is crenate, provided with two lateral and a smaller medial lobe. The specimens provided with concave or straight zygosphene are more rare. The prezygapophyseal articular facets are oval, while the postzygapophyseal articular facets are rounded, obovate or of irregular shape. The prezygapophyseal processes are long, slightly curved anteriorly, flattened dorsoventrally and obtuse distally. Their length usually equals the diameter of the prezygapophyseal articular facets. The cotyle and the condyle are rounded. The paracotylar, subcentral and lateral foramina are always well evidenced. The posterior trunk vertebrae slightly differ from those of middle trunk vertebrae, by having their neural spine of lower height and the haemal keel as well as the subcentral ridges being more prominent.

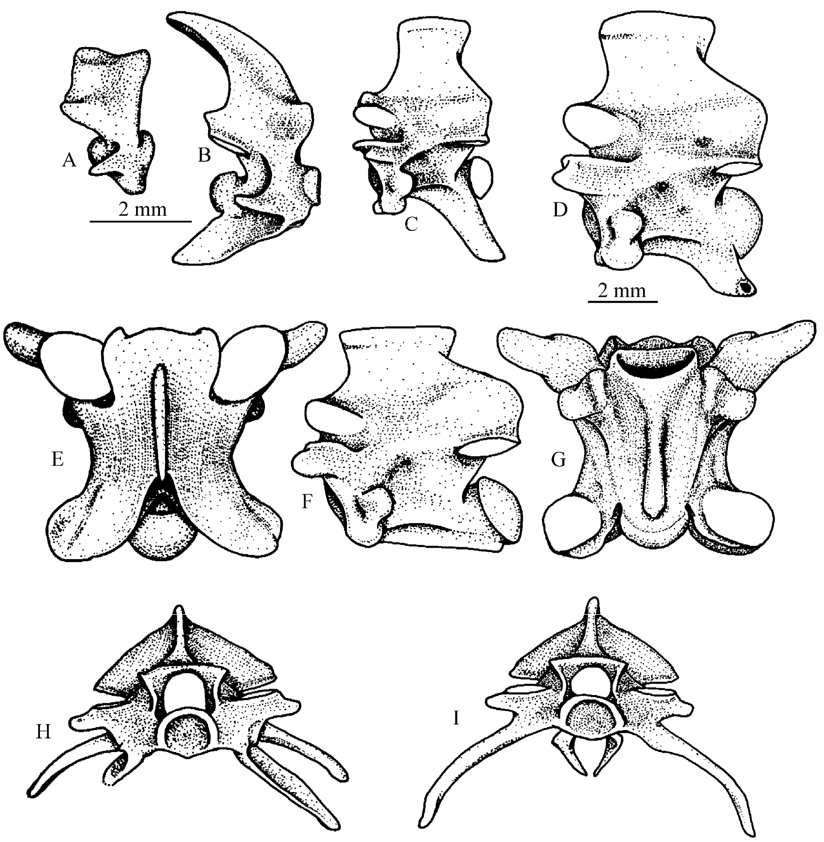


Figure 47. Fossil remains of *Elaphe longissima* from Râpa. A: atlas (MTC. No. 18805); B: axis (MTC. No. 18806/1); C, D: cervical vertebrae (MTC. No. 13765/1, 2); E-G: trunk vertebra (MTC. No. 13765/3); H: sacral vertebra: (MTC. No. 13765/4); I caudal vertebra (MTC. No. 13765/5). A-D, F – lateral views; E – dorsal view; G – ventral view; H, I – anterior views.

In 30 measured vertebrae coming from the Upper Pleistocene of Râpa, we obtained the following results:

Measurements	Min. – Max. (mm)	Mean	SD.
PR-PO	6.12 – 7.29		
CL	4.78 – 5.57		
PO-PO	6.84 – 8.68		
CW	3.90 – 5.00		
ZW	3.21 – 3.93		
CTH	2.18 – 2.94		
CTW	2.32 – 2.91		
PR-PR	7.00 – 8.78		
CL/CW	1.11 – 1.22	1.15	±0.01
PO-PO/CW	1.62 – 1.84	1.72	±0.04
CTW/CTH	0.92 – 1.08	1.00	±0.03
ZW/CW	0.75 – 0.88	0.81	±0.02
PR-PR/PR-PO	1.06 – 1.24	1.18	±0.02
CL/ZW	1.33 – 1.54	1.40	±0.05
PR-PR/CW	1.56 – 1.82	1.74	±0.05

Table 3. Measurements of trunk vertebrae in *Elaphe longissima* (N = 30).

Cloacal vertebrae (Fig. 47: H). The neural spine is short and of relatively low height, without anterior and posterior overhangs. The dorsal rami of the lymphapophyses are shorter than the ventral ones. The haemapophyses are relatively short.

Caudal vertebrae (Fig. 47: I). The neural spine is of variable shape, usually provided with an anterior prominence. The pleurapophyses are relatively long and slender, oriented anteroventrally. The haemapophyses are relatively short, widened distally and sometimes are in contact medially.

The oldest fossil record of *Elaphe longissima* is known from the Upper Pliocene (MN16) locality of Beremend, Hungary (VON SZUNYOGHY, 1932). The remaining records come from the Quaternary of Europe. SZYNDLAR (1984, 1991a) cited 15 localities comprising *E. longissima* from Poland (of Lower/Middle Pleistocene to Holocene age). Remains of the latter are known also from the Middle Pleistocene of St. Margarethen, Austria (RABEDER, 1977); from the Pleistocene of Stránská Skála, Mladeč, Malá Dohoda, Czech Republic (IVANOV, 1993, 1994, 1995); from the Pleistocene of Braşov, Romania (VON SZUNYOGHY, 1932); Varbeshnitza, Bulgaria and Tourkobounia, Greece (SZYNDLAR, 1991a). From Germany only Upper Pleistocene and Holocene remains are known, reported by BRUNNER (1942 – 1943), MARKERT (1975, 1976), MLYNARSKI and ULRICH (1975, 1977), and PETERS (1977a, 1977b). From the territory of France it is known from the Middle Pleistocene of Terra Amata only (BAILON, 1991).

Elaphe cf. *E. longissima* (LAURENTI, 1768)

Material: Betfia 11: three fragmentary basiparasphenoids (MTC. No. 18690/1-3), one basioccipital (MTC. No. 18691), three fragmentary quadrates (MTC. No. 18692/1-3), one supratemporal (MTC. No. 18693), 60 vertebrae (MTC. No. 18694); Betfia 12/B: one fragmentary basiparasphenoid (MTC. No. 18743), five vertebrae (MTC. No. 18744).

Description and comments

Despite of fragmentary state of the overwhelming part of the material, they do not differ significantly from those described as *E. longissima.* Due to this in the following description mainly the differences will be mentioned only.

Basioccipital (Fig. 48: F). The bone is provided with a more prominent medial crest, contrary to those observed in specimens coming from the Upper Pleistocene of Râpa or in recent species.

Basiparasphenoid (Fig. 48: A-C). Only the basisphenoid portion is preserved. The common foramen is situated close to the posterolateral margin. In a specimen the latter structure is situated somewhat farther from the posterolateral margin, condition observed in *E. paralongissima* (see above). The fragmentary basiparasphenoid coming from Betfia 12/B belonged to a relatively large individual. The pituitary fossa is extremely deep, and laterally to the latter, the anterior foramina of the abducens nerves, as well as those of the "cid" nerves in a common concavity are situated. The quadrate and supratemporal fragments do not differ from those of recent *E. longissima.*

Vertebrae. The trunk vertebrae coming from Betfia 11 are very fragmentary and having signs of erosion (in all the specimens the neural spine is broken off). The zygosphene is variable in shape, the anterior margin being crenate, straight or concave. The prezygapophyseal processes in few specimens have been preserved only. They are shorter than the diameter of the prezygapophyseal articular facets, flattened dorsoventrally and obtused distally. The paradiapophyses if present are incompletely divided into parapo- and diapophyseal portions. The latter equals in length the former. Sometimes the parapophyses show a sharp ventral prominence. In few large specimens coming from Betfia 12/B (Fig. 48: D, E, G-I) the neural arch is vaulted, the neural spine is high with the upper margin thickened, the centrum is short and the interzygapophyseal ridge is extremely well-developed. The haemal keel is prominent, thick and rounded without subcotylar tubercles. The parapophyses are slightly longer than the diapophyses. The anterior margin of the zygosphene is concave.

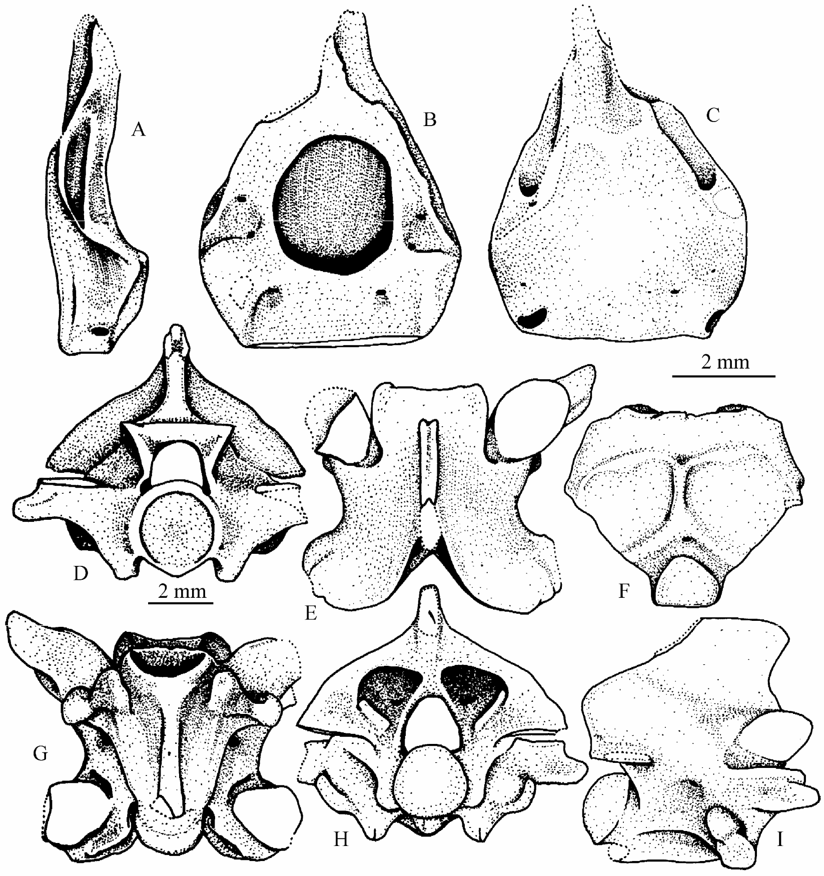


Figure 48. *Elaphe* cf. *E. longissima*. A-C: fragmentary basiparasphenoid (Betfia 12/B, MTC. No. 18743); D, E, G-I: trunk vertebra (Betfia 12/B, MTC. No. 18744); F: basioccipital (Betfia 11, MTC. No. 18691). A, I – lateral views; B, E – dorsal views; C, F, G – ventral views; D – anterior view; H – posterior view.

Fossil remains described as *Elaphe* cf. *E. longissima* are known from the Middle Pliocene (MN 15) of Valeny and Dermendzhi, Moldova Republic (REDKOZUBOV, 1987); from the Upper Pliocene (MN 16) of Novye Tanatary, Chismikioy and Bachoy, Moldova Republic (REDKOZUBOV, 1987), Balaruc II, France (BAILON, 1989, 1991); from the Lower Pleistocene of Osztramos 2 and 8, Hungary (VENCZEL, 1997b); from the Middle Pleistocene of Deutsch Altenburg 2, Austria (RABEDER, 1974), Tourkobounia 2, Greece (SZYNDLAR, 1991a), Grotte de Lazaret, France (BAILON, 1991); from the Upper Pleistocene of Gerani 2, Greece (SZYNDLAR, 1991a), Grotte du Bois du Cautet, France (BAILON, 1991); and from the Holocene of Pili B, Greece (SZYNDLAR, 1991a), and Baume Claire/Baume Sourde (BAILON, 1991).

Subfamily **"Natricinae"**

The vertebrae in natricine snakes are provided with hypapophyses in the whole presacral region. There is a well defined subcentral groove, bordered laterally by a subcentral ridge; the parapophyses are provided with well-developed parapophyseal processes; small and paired tubercles are evidenced below the cotyle lip (AUGÉ & RAGE, 2000). Several fossil taxa (e.g. members of the genera *Palaeonatrix* and *Neonatrix*) are known exclusively on the basis of vertebrae only (BAILON, 1991).

Genus ***Natrix*** LAURENTI, 1768

In Europe the genus is represented by four species (*Natrix maura*, *N. megalocephala*, *N. natrix* and *N. tesselata*). The fossil members of the genus are known exclusively from the territory of Europe (SZYNDLAR, 1984; RAGE, 1988; AUGÉ & RAGE, 2000).

***Natrix natrix* (LINNAEUS, 1758)**

1913 *Tropidonotus natrix* L.: BOLKAY, P. 223

1956 *Natrix natrix* (LINNÉ): KRETZOI, P.259

1977 *Natrix natrix* L.: RABEDER, Pp. 83-86, Fig. 9: 5, Pl.1: 3, 4, 6, 9, 13, Pl.2: 14, 18, 19, 24

1984 *Natrix natrix* (LINNAEUS): SZYNDLAR, Pp. 106-122, and Fig.44-49

Material: Betfia pothole/B: one fragmentary parietal (MTC. No. 18781), two prootics (MTC. No. 18782/1-2), two exoccipitals (MTC. No. 18783/1-2), one compound bone (MTC. No. 18784), 30 vertebrae (MTC. No. 18785); Betfia 7: one basiparasphenoid (MTC. No. 18638), one ectopterygoid (MTC. No. 18639), one compound bone (MTC. No. 18640), 50 vertebrae (MTC. No. 18641); Betfia 11: one fragmentary basiparasphenoid (MTC. No. 18695), one supraoccipital (MTC. No. 18696), three prootics (MTC. No. 18697/1-3), 30 vertebrae (MTC. No. 18698); Betfia 12/A: one basioccipital (MTC. No. 18734), one fragmentary basiparasphenoid (MTC. No. 18735), 23 vertebrae (MTC. No. 18736); Subpiatră: two fragmentary parietals (MTC. No. 16952/1-2), three basioccipitals (MTC. No. 16954/1-3), four supraoccipitals (MTC. No. 16956/1-4), one basiparasphenoid (Inv.No. 16955), four prootics (MTC. No. 16953/1-4), 140 vertebrae (MTC. No. 16957).

Description and comments

Parietal (Fig. 49: A). All the available specimens are fragmentary. The dorsal surface is provided with a longitudinal groove, which is better defined posteriorly. The parietal crista do not converge before the posterior margin of the bone.

Basioccipital (Fig. 49: B, C). The bone is slightly wider than long. The basioccipital crest is well developed, with prominent basioccipital processes which are projected posteroventrally. The basioccipital tubercles are well evidenced. The medial crest is lacking or only slightly defined in the posterior vicinity of medial lobe. The occipitocondylar tubercle usually is strongly built and evidently separated off by a deep groove.

Exoccipital (Fig. 49: D). The bone is similar to recent *N. natrix*. The occipital crest is well developed; it runs laterally, ending in a posteriorly projected prominence above the vagus-hypoglossal nerve foramina. Similarly, the circumfenestral crest is well developed. The paroccipital process is large. The vagus-hypoglossal nerve foramina are relatively large, joined posteriorly by a small additional foramen.

Supraoccipital (Fig. 49: E, F). The bone is considerably wider than long. The anterior sagittal crest is lacking, while the posterior sagittal crest is well defined, extending to the posterior margin of the bone. The occipital crista are prominent and inclined posteromedially. The supraoccipital foramina are present.

Basiparasphenoid (Fig. 50: A, B). The morphology of the bone shows large intraspecific variations. The suborbital flange is reduced. In ventral view the pterygoid crests are extremely prominent, inclined posteromedially, but do not cover the posterior openings of the Vidian canal.

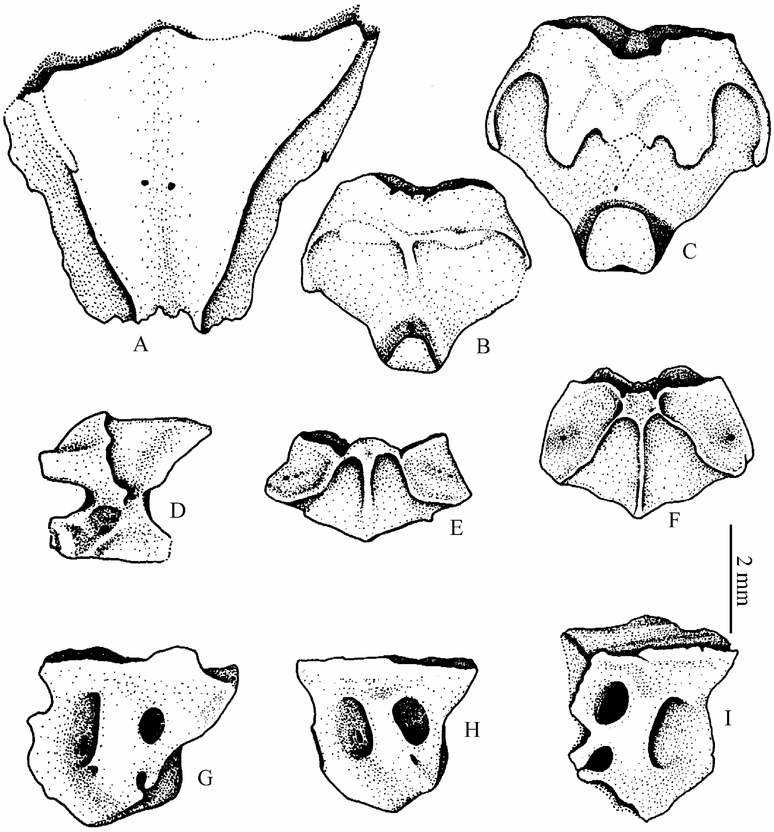


Figure 49. *Natrix natrix*. A: fragmentary parietal (Subpiatră, MTC. No. 16952/1); B,C: basioccipitals from Betfia 12/A (B)(MTC. No. 18734) and Subpiatră (C)(MTC. No. 16954/1); D: fragmentary left exoccipital (Betfia pothole/B, MTC. No. 18783/1); E, F: supraoccipitals from Betfia 11 (E) (MTC. No. 18696) and Subpiatră (F)(MTC. No.16956/1); G, H: right prootics (Betfia 11, MTC. No. 18697/1, 2); I: left prootic (Subpiatră, MTC. No. 16953/1). A, E, F – dorsal views; B, C – ventral views; D, G-I – lateral views.

The pterygoid processes are well developed, situated close to the posterolateral margin of the basisphenoid. The Vidian canal is extremely short, anteriorly giving birth to two foramina: the medial one is the anterior foramen of the

Vidian canal, while the lateral one serves as the exit of the constrictor internus dorsalis ramus of the trigeminal nerve. The basisphenoid crest usually is prominent, running from the central area posteriorly without reaching the posterior margin of the bone. In dorsal view the pituitary fossa is relatively deep, and of ovaloid shape. The anterior foramina of the abducens nerve are situated close to those of the “cid” nerve, but they are not included in a common concavity.

Prootic (Fig. 49: G, H). The supraoccipital crest is prominent. The foramen for the maxillary ramus of the trigeminal nerve (V2) is of oval shape, and usually is joined anteroventrally by the foramen for the exit of the constrictor internus dorsalis nerve (V4). The foramen for the mandibular ramus of the trigeminal nerve (V3) is situated posteriorly and is always larger than the V2 foramen. On the lateral wall of the prootic, posterior to the V3 opening is observed a small foramen, serving as the exit to the facial nerve.

Ectopterygoid (Fig. 50: D). The shape of the bone is very characteristic, its stem (= posterior ramus) being elongated, and the ectopterygoid rami, meeting in a right angle, are incompletely separated off from each other. Dorsally, in the proximal portion a convexity is observed.

Compound bone (Fig. 50: E). The bone is elongated with the medial flange moderately higher than the lateral flange. The anterior margin of the coronoid process diminishes its height very slowly. The supraangular foramen is situated relatively far from the anterior margin of the mandibular fossa. The latter structure is relatively wide and shallow. The retroarticular process is strongly curved ventromedially.

Axis (Fig. 56: G). The centrum is short. In a specimen coming from Subpiatră the neural spine, the zygosphene and the distal part of the pleurapophyses are broken off. The first hypapopysis is short and slightly curved posteroventrally.

Cervical vertebrae are extremely difficult to be differentiated from those of trunk vertebrae. Generally the former ones are provided with longer hypapophyses and with higher neural spines than the latter ones.

Trunk vertebrae (Fig. 56: H, I). The vertebral centrum is long, provided with sigmoid shaped hypapophyses having rounded tips. The subcentral ridges are prominent extending from the posterior margin of the parapophyses to the base of the condyle. The neural arch is relatively vaulted without epizygapophyseal spines. The neural spine is longer than high, the dorsal margin usually being thickened and provided with a prominent anterior and posterior overhangs.

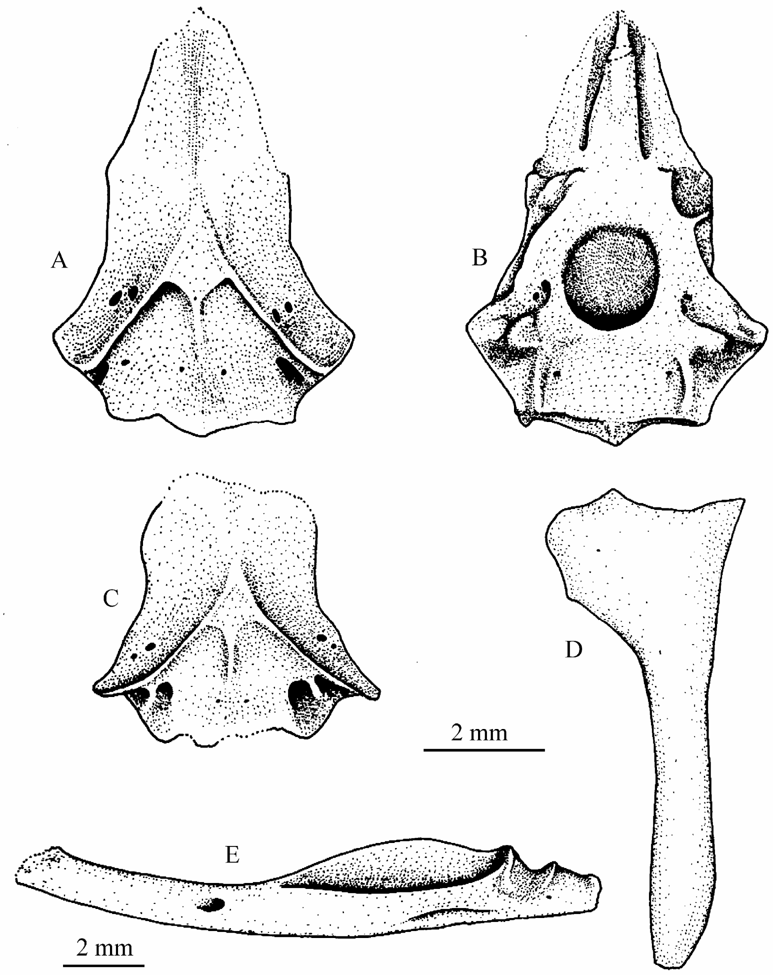


Figure 50. *Natrix natrix*. A, B: fragmentary basiparasphenoid (Betfia 11, MTC. No. 18695); C: fragmentary basiparasphenoid (Betfia 7, MTC. No. 18638); D: left ectopterygoid (Betfia 7, MTC. No. 18639); E: left compound bone (Betfia 7, MTC. No. 18640). A, C – ventral views; B, D – dorsal views; E – lateral view.

The anterior margin of the zygosphene is crenate. The pre- and postzygapophyseal articular facets usually are of oval shape. The prezygapophyseal processes are long, flattened dorsoventrally and obtuse distally. The paracotylar-, lateral- and subcentral foramina are well evidenced. Variation of CL and CW, as well as the CL/CW ratio of presacral vertebrae, coming from the middle trunk region of *Natrix* are given in Fig. 51 and Fig. 52.

The fossil record of *N. natrix* is extremely numerous coming from the western as well as from the eastern part of the European territory (BRUNNER, 1942-1943, 1958; MARKERT, 1976; MLYNARSKI & ULRICH, 1975, 1977; PETERS, 1977a, 1977b; MLYNARSKI et al., 1978; BLOOS et al., 1991; BAILON, 1991; VENCZEL, 1998b). The oldest record is known from the Upper Pliocene of Hungary and Moldova Republic (VON SZUNYOGHY, 1932; REDKOZUBOV, 1987). *N. longivertebrata*, a form closely related to *N. natrix*, has been described from the Upper Pliocene (MN 16) locality of Rebielice Królewskie 1, Poland by SZYNDLAR (1984). Later a number of occurrence of the former have been reported from the Middle Miocene (MN 7) of La Grive St. Albain, France (RAGE & SZYNDLAR, 1986), Upper Miocene (MN 11) of Kohfidisch, Austria (BACHMAYER & SZYNDLAR, 1985, 1987) and from the Late Miocene (MN 13) of Hungary (VENCZEL, 1994b). A number of morphological characters observed in the basiparasphenoid and prootic of the above species suggest that *N. longivertebrata* is the most probable direct ancestor of *N. natrix* (SZYNDLAR, 1991c).

Natrix tesselata (LAURENTI, 1768)

1932 *Tropidonotus tesselatus* Laur. : BOLKAY, P. 23
1956 *Natrix tesselata* Laurenti: KRETZOI, P. 259
1997b *Natrix tesselata*: VENCZEL, P. 84, fig.4
1998b *Natrix tesselata*: VENCZEL, Pp. 153-154, figs. 33-39

Material: Betfia pothole/B: two fragmentary parietals (MTC. No. 18786), two frontals (MTC. No. 18787/1-2), three basioccipitals (MTC. No. 18788/1-3), one exoccipital (MTC. No. 18789), two prootics (MTC. No. 18790/1-2), six quadrates (MTC. No. 18791/1-6), one fragmentary basiparasphenoid (MTC. No. 18792), six compound bones (MTC. No. 18793/1-6), one fragmentary ectopterygoid (MTC. No. 18794), two palatines (MTC. No. 18795/1-2), one axis (MTC. No. 18796); Betfia 5: 24 vertebrae (MTC. No. 18614); Betfia 7: one basioccipital (MTC. No. 18642), four fragmentary basiparasphenoids (MTC. No. 18643/1-4), three prootics (MTC. No. 18644/1-3), one ectopterygoid (MTC. No. 18645), five compound bones (MTC. No. 18646/1-5), two quadrates (MTC. No. 18647/1-2), 40 vertebrae (MTC. No. 18648);

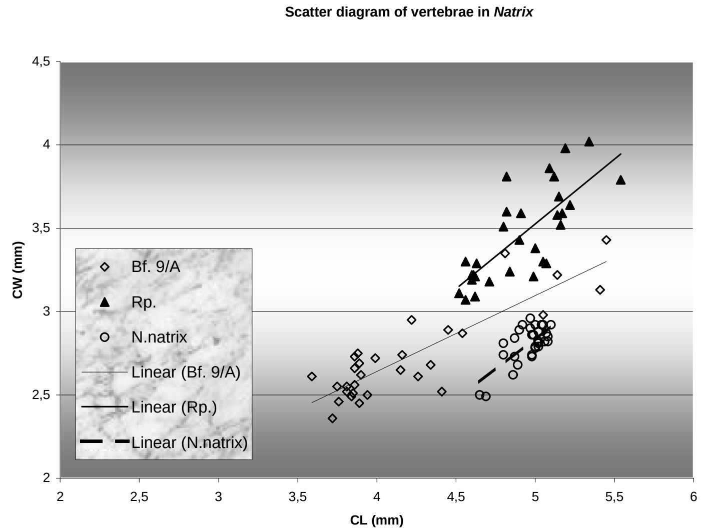


Figure 51. Scatter diagram of CL and CW of presacral vertebrae in recent *N. natrix* and *N. tesselata* (Betia 9/A and Râpa). Abbreviations: Bf. – Betfia, Rp. – Râpa.

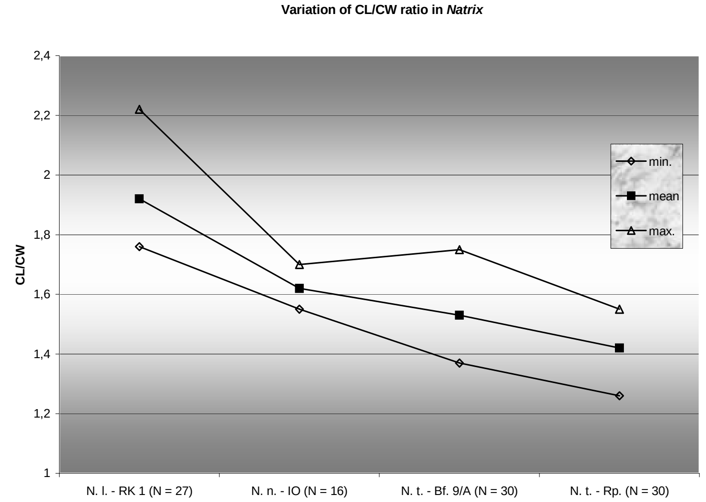


Figure 52. CL/CW range in *Natrix.* Abbreviations: N. l. – *N. longivertebrata*, N. n. – *N. natrix*, N. t. – *N. tesselata*, Bf. – Betfia, Rp. – Râpa, IO – Iózefów (Poland), RK 1 – Rebielice Królewskie I (Poland).

Betfia 9: two frontals (MTC. No. 18667/1-2), one fragmentary parietal (MTC. No. 18668), two basioccipitals (MTC. No. 18669), two exoccipitals (MTC. No. 18670), one fragmentary maxilla (MTC. No. 18671), one ectopterygoid (MTC. No. 18672), seven quadrates (MTC. No. 18673), two fragmentary dentaries (MTC. No. 18674), 24 compound bones (MTC. No. 18675), 220 vertebrae (MTC. No. 18676); Betfia 10: 75 vertebrae (MTC. No. 18685); Betfia 11: one frontal (MTC. No. 18699), three fragmentary parietals (MTC. No. 18700), four basioccipitals (MTC. No. 18701), one supraoccipital (MTC. No. 18702), two prootics (MTC. No. 18703), four basiparasphenoids (MTC. No. 18704), one quadrate (MTC. No. 18705), two compound bones (MTC. No. 18706); Betfia 12/A: one fragmentary basioccipital (MTC. No. 18737), one quadrate (MTC. No. 18738), 13 vertebrae (MTC. No. 18739); Subpiatră: one parietal (MTC. No. 16958), one basioccipital (MTC. No. 16959), 30 vertebrae (MTC. No. 16960); Chişcău 3: one compound bone, one exoccipital, 20 vertebrae; Râpa: 15 prefrontals (MTC. No. 18807), 31 frontals, one of them fragmentary (MTC. No. 18808), two parietals (MTC. No. 13692), ten basioccipitals (MTC. No. 13693/1-9, 13770), 18 exoccipitals (MTC. No. 18809), three supraoccipitals (MTC. No. 18810/1-3), four basiparasphenoids (MTC. No. 13694/1-4), 17 prootics, two of them fragmentary (MTC. No. 18811/1-17), six maxillae, two of them fragmentary (MTC. No. 18812/1-6), eight pterygoids, two of them fragmentary (MTC. No. 13697/1-2), eight ectopterygoids (MTC. No. 13698/1-8), five palatines, three of them fragmentary (MTC. No. 18813/1-5), 7 supratemporals (MTC. No. 13700/1-7), four quadrates (MTC. No. 13699/1-4), 12 dentaries, six of them fragmentary (MTC. No. 13695/1-12), 22 compound bones, six of them fragmentary (MTC. No. 13696/1-22), five vomers, one of them fragmentary (MTC. No. 18814/1-5), one premaxilla (MTC. No. 18815), five axes (MTC. No. 18816), 3500 vertebrae (MTC. No. 3550).

Description and comments

Prefrontal (Fig. 53: A, B). The lateral surface is of irregular shape, its anterior margin being slightly convex, while the posterior one more or less straight, and devoid of foramina, or sometimes with a small foramen (in a specimen the latter structure is incompletely closed by the posterior margin). The ventral part of the posterior margin is provided with an extension. In posterolateral view the lacrimal foramen is relatively small and of circular shape.

Frontal (Fig. 53: C-E). The medial margin is straight, while the lateral one, due to unequal extension of the supraorbital ridge, is concave. The dorsal surface is straight, with a shallow groove, extending parallel with the lateral

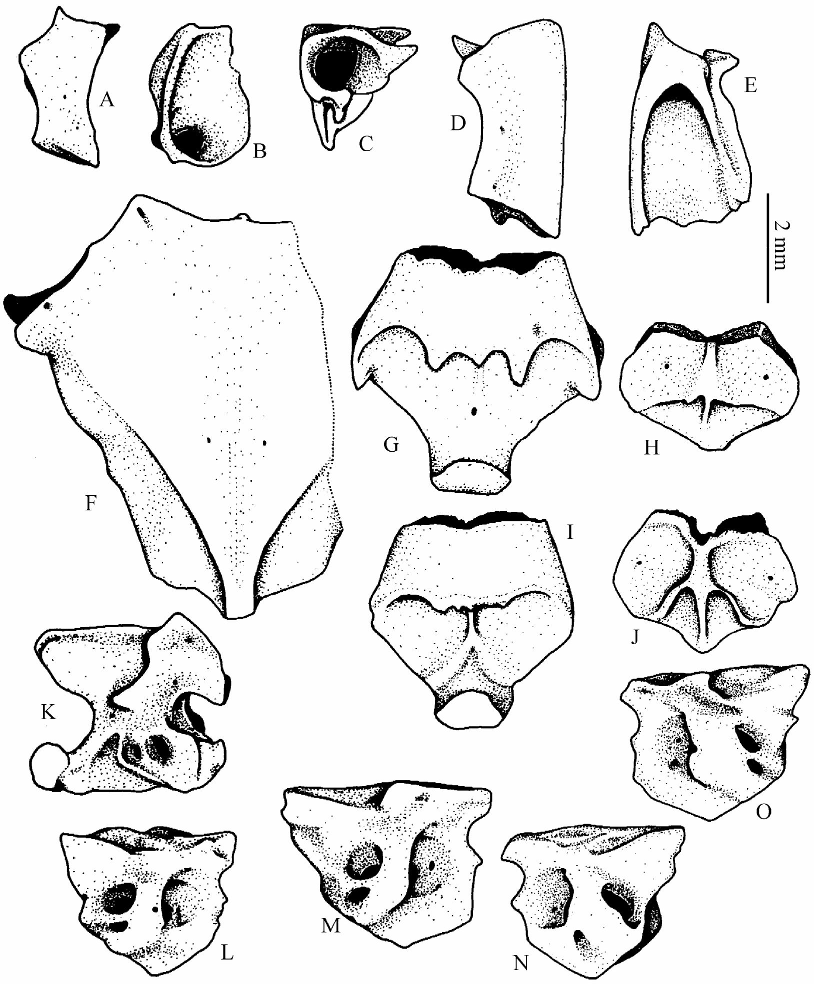


Figure 53. *Natrix tesselata*. A, B: left prefrontal (Râpa, MTC. No. 18807/1); C-E: left frontal (Râpa, MTC. No. 18808/1); F: fragmentary parietal (Betfia 9/A, MTC. No. 18668); G, I: basioccipitals from Betfia 9/A (G)(MTC. No. 18669) and Betfia 11 (I)(MTC. No. 18701); H, J: supraoccipitals from Betfia 9/A (H) and Betfia 11 (J)(MTC. No. 18702); K: right exoccipital (Râpa, MTC. No. 18809/1); L-O: prootics (Râpa, MTC. No. 18811/1-4). A, K-O – lateral views; B – posterolateral view; C – anterior view; D, F, H, J – dorsal views; E – medial view; G, I – ventral views.

margin. The prefrontal processes are well defined, the internal prefrontal process being considerable larger than the external one. The former is projected anterolaterally having pointed tip. In lateral view the nasal process is square shaped, the distal part being slightly dilated and projected anterolaterally. The frontal aperture is of oval shape.

Parietal (Fig. 53: F). The dorsal surface is straight, with a shallow depression in the posteromedial part of the bone. The descending part is convex, while the parietal crests converge well before the posterior margin (contrary to that observed in *N. natrix*).

Basioccipital (Fig. 53: G, H). The basioccipital crest is always well evidenced, sometimes extremely prominent, provided with three well-developed basioccipital processes. The medial process (if conserved) is of similar length with the lateral ones. The basioccipital tubercles are reduced, while the medial crest is always lacking. The occipitocondylar tubercle is uneven, and it is not separated evidently from the basioccipital.

Exoccipital (Fig. 53: K). The occipital crest is prominent, it runs down on the lateral surface, ending well above the jugular foramen. In few specimens the lateral portion of the occipital crest is extremely well-developed, which is ended in a prominent and posteriorly projected process. The jugular foramen is large and of circular shape, joined posteriorly by a small additional foramen. The otic incisure is relatively large and surrounded by a well-developed circumfenestral crest.

Supraoocipital (Fig. 53: I, J). The anterior sagittal crest is of low height, sometimes with a tendency of bifurcation. The posterior sagittal crest is of same height as the anterior one, in few specimens reaching the posterior margin of the bone. The latter is provided with a medial process. The occipital crests run obliquely, dividing the dorsal surface in larger anterior and a more reduced posterior area. The supraoccipital foramina are well defined.

Basiparasphenoid (Fig. 54: A-D). The bone has an elongated triangle shape. In ventral view the central area is prominent. Posterior to the latter there are three crista, two of them running posterolaterally (the pterygoid crests) and a medial one extending posteriorly (the basisphenoid crest). The latter structure is sometimes undeveloped. The suborbital flanges are reduced. The Vidian canal is extremely short, the posterior foramen being joined by a small foramen situated posteromedially to the former. The anterior foramina of the Vidian canal open well before the pterygoid crests. In dorsal view, the anterior foramina of the abducens nerve and the "cid" nerve foramina are situated laterally to the pituitary fossa in a deep concavity. The "cid" nerve reenters the skull above the basipterygoid process, at the border of the prootic and basiparasphenoid. The posterior foramina of the abducens nerves are situated posterior to the crista sellaris.

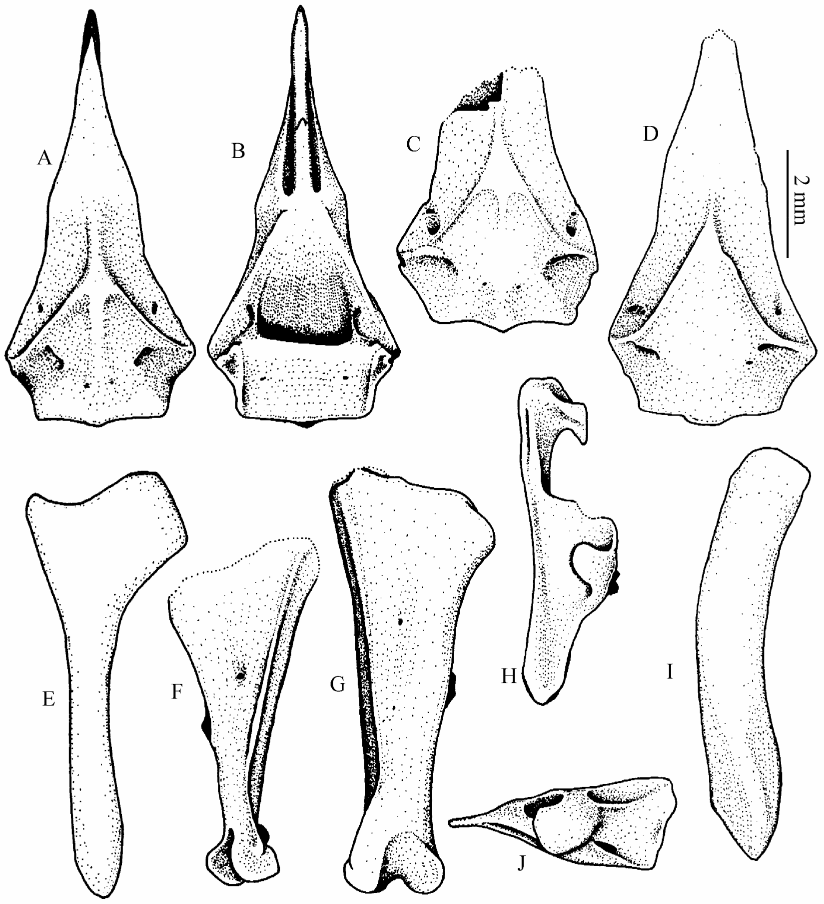


Figure 54. *Natrix tesselata*. A-D: basiparasphenoids from Râpa (A, B)(MTC. No. 13694/1), Betfia 11 (C)(MTC. No. 18704/1) and Betfia 7 (D)(MTC. No. 18643/1); E: right ectopterygoid (Betfia 7, MTC. No. 18645); F, G: quadrates from Betfia 11 (F)(MTC. No. 18705) and Betfia 12/A (G)(MTC. No. 18738); H: right intranasal (Râpa); I: left supratemporal (Râpa, MTC. No. 13700); J: left vomer (Râpa, MTC. No. 18814/1). A, C, D – ventral views; B, E, H, I – dorsal views; F, G – posterolateral views; J – lateral view.

Prootic (Fig. 53: L-O). The supraoccipital crest becomes more prominent in the posterior part of the bone. The foramen for the maxillary ramus of the trigeminal nerve (V2) is of oval shape. Ventrally to this foramen there is a smaller foramen, serving as the exit from the cranial wall of the “cid” nerve (V4). The foramen for the mandibular ramus of the trigeminal nerve (V3) is somewhat larger than the V2 foramen, and laterally is partially closed by the posterior border of the laterosphenoid bar. Posterior to this foramen, the facial nerve foramen can be observed. The laterosphenoid bar is variable in shape, usually its posterior margin being convex. In some specimen there is a common foramen for the V2 and V4 openings.

Maxilla (Fig. 55: A, B). The bone is elongated, having its anterior part curved medially. The prefrontal process is relatively large, situated at the level of the 9th – 13th teeth (or at the level of the 10th – 14th teeth). The ectopterygoidal process is situated at the level of the 23 – 25th or at the level of the 22– 24th teeth. The tooth number in few complete fossil specimens coming from the Upper Pleistocene of Râpa range between 26-27 while in recent specimens between 25-26.

Pterygoid (Fig. 55: F). The bone is elongated, its posterior portion being curved laterally. The tooth row occupies about two third of the whole length of the bone. The tooth number in a complete pterygoid ranges between 22 – 24 (in recent specimens between 20 – 22).

Ectopterygoid (Fig. 54: E). The dorsal part of the bone is convex. The two ectopterygoid rami are only slightly divided: the external ramus is wide, while the internal one is slender and short having pointed tip. The stem of the bone is curved dorsally, slightly widened distally with pointed tip.

Palatine (Fig. 55: C). The number of teeth in a complete bone ranges between 12 – 13, while in few observed recent specimens is 12. The vomeral process is prominent, with its distal part (= choanal process) curved ventrally. The latter structure is situated at the level of the 7th – 9th or 7th – 8th teeth.

Supratemporal (Fig. 54: I). Few well-preserved specimens are flattened dorsoventrally and slightly curved laterally.

Quadrate (Fig. 54: F, G). The proximal portion is slightly widened. The quadrate crest is weakly defined and is practically merged into the anterior margin. The stapedial process is of elongated shape, situated at the posterior margin. In posterolateral view the quadrate is curved medially.

Dentary (Fig. 55: D). The anterior part is curved medially. The tooth number observed in six specimens coming from Râpa ranged between 27 – 29 (in recent specimens the tooth number in the complete dentary is 27). The mental foramen is small and situated at the level of the 11th tooth, or at the level of the 10th – 11th or 11th – 12th teeth. The Meckel’s groove closes completely at

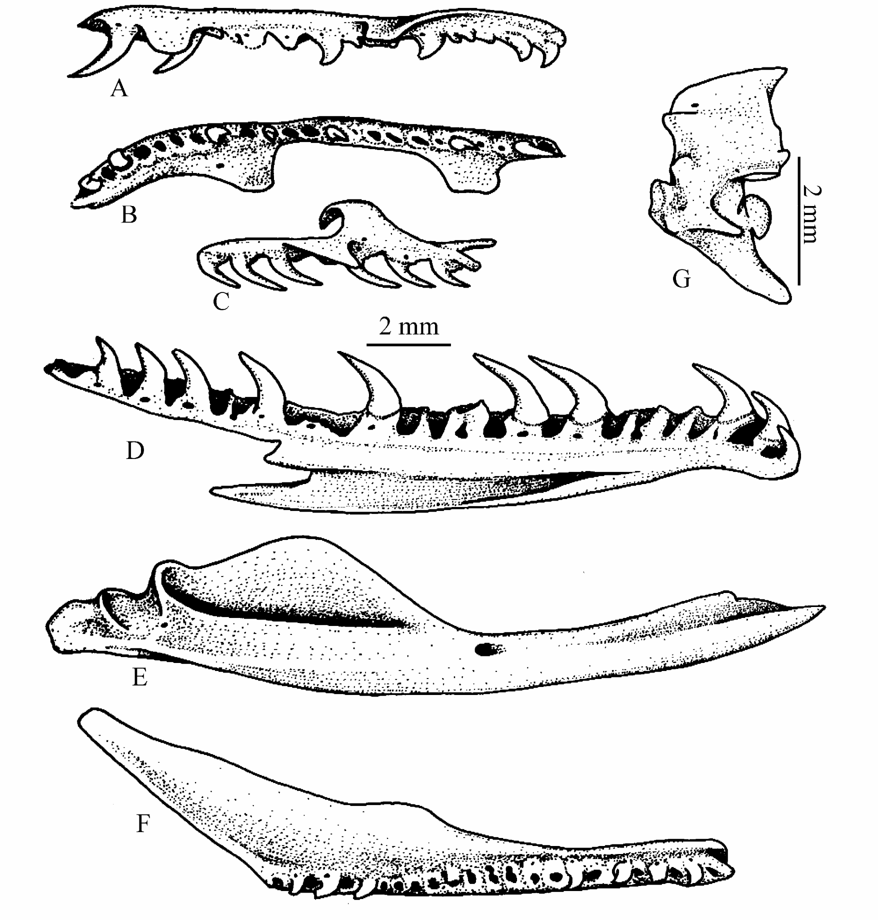


Figure 55. *Natrix tesselata* from Râpa. A, B: left maxilla (MTC. No. 18812); C: right palatine (MTC. No. 18813/1); D: left dentary (MTC. No. 13695/1); E: right compound bone (MTC. No. 13696/1); F: right pterygoid (MTC. No. 13697/1); G: axis (MTC. No. 18816/1). A, C, D – medial views; B, F – ventral views; E, G – lateral views.

the level of the 8th tooth, but sometimes at the level of the 7th tooth (in a specimen at the level of the 5th tooth). The compound notch is situated at the level of the 15th or 16th tooth.

Compound bone (Fig. 55: E). The medial flange is 1.5 – 2 times higher than the lateral flange. The anterior margin of the coronoid process is prominent, contrary to that observed in *N. natrix*, in which is extremely low. The supraangular crest is well defined beginning from the ventral border of the sigmoid fossa into the supraangular foramen. The retroarticular process is curved medially.

Intranasal (Fig. 54: H). The dorsal fossa is shallow. The dorsal ascendant process is extremely prominent. The frontal process is slender with its distal part somewhat dilated and uncinate in shape.

Vomer (Fig. 54: J). The posterior margin is slightly convex or with a small medial protuberance. The premaxillary process is slender and pointed distally. The vomeral foramen is small having an elongated or oval shape. In recent specimens this foramen is considerably larger.

Axis (Fig. 55: G). The neural spine is of low height with an accentuated posterior apophysis. The pleurapophyses are projected posteriorly. The first hypapophysis is shorter than the centrum and it is projected posteroventrally.

Cervical vertebrae (Fig. 56: A). They may be differentiated from the trunk vertebrae by having higher neural spines and more vaulted neural arch. Their hypapophyses are relatively longer.

Trunk vertebrae (Fig. 56: B-D). The centrum is relatively long and somewhat triangular shaped. The subcentral crest is well developed. The neural arch is vaulted. The neural spine is longer than high with its dorsal margin thickened, provided with a smaller anterior and a larger posterior overhang. The anterior margin of the zygosphene is straight or concave with two lateral lobes. In lateral view the hypapophysis is sigmoid shaped and having pointed tip, sometimes with a tendency of bifurcation. The pre- and postzygapophyseal articular facets are of oval shape. The prezygapophyseal processes are flattened dorsoventrally and obtuse distally. Their length usually do not exceed the length of the prezygapophyseal articular facets. The paradiapophyses are distinctly separated into parapo- and diapophyseal portions. The parapopyseal processes are long, projected anteriorly, provided with pointed tips. The cotyle and the condyle are circular in shape. All the foramina are well evidenced.

The measurements in 30 trunk vertebrae coming from the Upper Pleistocene of Râpa are given in Table 4.

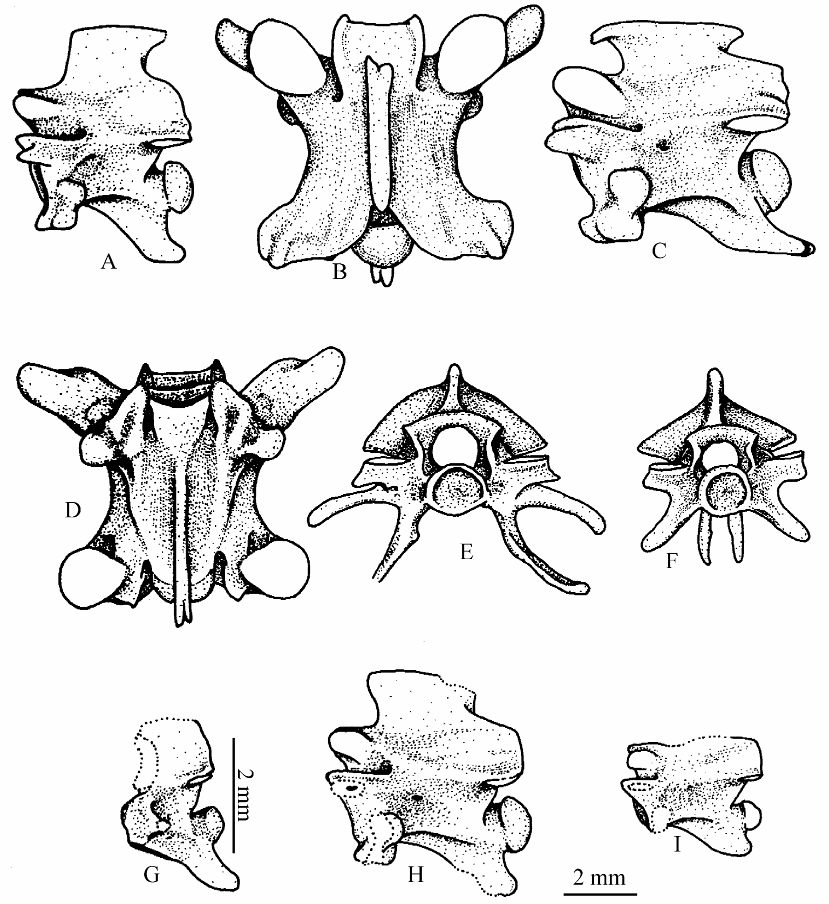


Figure 56. *Natrix tesselata* (A-F) and *N. natrix* (G-I). A: cervical vertebra (Râpa, MTC. No. 13701/1); B-D: trunk vertebra (Râpa, MTC. No. 13701/2); E: sacral vertebra (Râpa, MTC. No. 13701/3); F: caudal vertebra (Râpa, MTC. No. 13701/4); G: axis (Subpiatră, MTC. No. 16960/1); H, I: presacral vertebrae (Subpiatră, MTC. No. 16960/2, 3). A, C, G, H, I – lateral views; B – dorsal view; D – ventral view; E, F – anterior views.

Measurement	Min.- max. (mm)	Mean	SD
PR – PO	5.41 – 6.83		
CL	4.52 – 5.54		
PO – PO	5.67 – 6.99		
CW	3.07 – 4.02		
ZW	2.43 – 3.09		
CTH	1.70 – 2.04		
CTW	1.74 – 2.11		
PR – PR	5.87 – 7.38		
CL/CW	1.26 – 1.55	1.42	±0.01
PO – PO/CW	1.61 – 2.10	1.84	±0.12
CTW/CTH	0.99 – 1.18	1.06	±0.12
ZW/CW	0.63 – 0.93	0.80	±0.12
PR – PR/PR – PO	0.99 – 1.22	1.08	±0.03
CL/ZW	1.54 – 2.05	1.77	±0.64
PR – PR/CW	1.74 – 2.01	1.86	±0.08

Table 4. Measurements of trunk vertebrae in *Natrix tesselata* (N=30) from Râpa.

Based on trunk vertebrae, *N. tesselata* may be differentiated from *N. natrix* by the shape of parapophyseal processes and hypapophyses. However in scarcely preserved vertebrae (or due to overlapping intraspecific variations), the identification of the above species based exclusively on vertebrae can not by fully demonstrated.

Cloacal vertebrae (Fig. 56: E). The neural spine is of low height. The lymphapophyses are long and slender.

Caudal vertebrae (Fig. 56: F). The pleurapohyses are long and projected ventrolaterally, the haemapophyses are parallel with each other having their distal part widened.

The fossil record of *N. tesselata* is known from the Upper Pliocene (MN17) of Villány 3 and Villány 6, Hungary and from the Lower Pleistocene of Nagyharsányhegy and Beremend 4, Hungary (VON SZUNYOGHY, 1932; KRETZOI, 1956); from the Lower Pleistocene of Osztramos 2, 4 and 14 as well as from Villány 8 (VENCZEL, 1997b, 1998b); from the Pleistocene of Stránská Skála, Czech Republic (IVANOV, 1995); from the Middle Pleistocene of Braşov, Romania (BOLKAY, 1913) and from the Upper Pleistocene of Euerwanger Bühl and Spitzbubenhöhle, Germany (MARKERT, 1975, 1976).

VON SZUNYOGHY (1932) assigned two basiparasphenoids and two compound bones, coming from the Upper Miocene (MN13) of Polgárdi, Hungary to the above species. Later studies do not confirm the presence of N. *tesselata* in the mentioned locality (VENCZEL, 1994b).

***Natrix* sp.**

Material: Betfia 5: 13 vertebrae; Betfia 7: 840 vertebrae; Betfia 9: 640 vertebrae; Betfia pothole/A: 22 vertebrae; Betfia pothole/B: 1000 vertebrae; Betfia 12/A: 70 vertebrae; Subpiatră: 150 vertebrae.

Description and comments

The material is very fragmentary and consequently more closer assignment of the remains can not be fully demonstrated. Despite of their fragmentary state the vertebrae differ from those of other Colubridae and Viperidae, having sigmoid shaped hypapophyses, long and distally obtused prezygapophyseal processes, and relatively long parapophyseal processes.

Genus ***Telescopus*** Wagler, 1830

Telescopus* cf. *T. fallax

Material. One fragmentary basiparasphenoid (MTC. No. 20290), 3 fragmentary vertebrae (MTC. No. 20291).

Description and comments

The fragmentary basiparasphenoid belonged to a relatively small specimen (Fig. 57: A, B). The bone is tapering anteriorly. The parasphenoid process is broken off, while the right side of the basipterygoid process is damaged. The ventral surface of the bone lacks sagittal basisphenoid crest and pterygoid crests. The central area is slightly convex ventrally. In the posterior portion of the parasphenoid process a relatively wide and shallow groove is preserved. The suborbital flanges are undeveloped, while the pterygoid processes (preserved on the left side only) are well-projected posterolaterally. The posterior margin is slightly trilobate. On the left side of the bone, the cerebral foramen and the posterior orifice of Vidian canal (= posterior carotid foramen) are distinctly separated, the former being situated posteromedially to the latter. The anterior orifice of the Vidian canal opens well inside the parasphenoid border. There is a wide and shallow groove between the cerebral and carotid foramina and posterolateral border of the basisphenoid. On the right side of the bone, the relatively short Vidian canal is not closed in a bony wall. In dorsal view there is a large pituitary fossa. The abducens nerves penetrate the crista sellaris of its posterolateral margin.

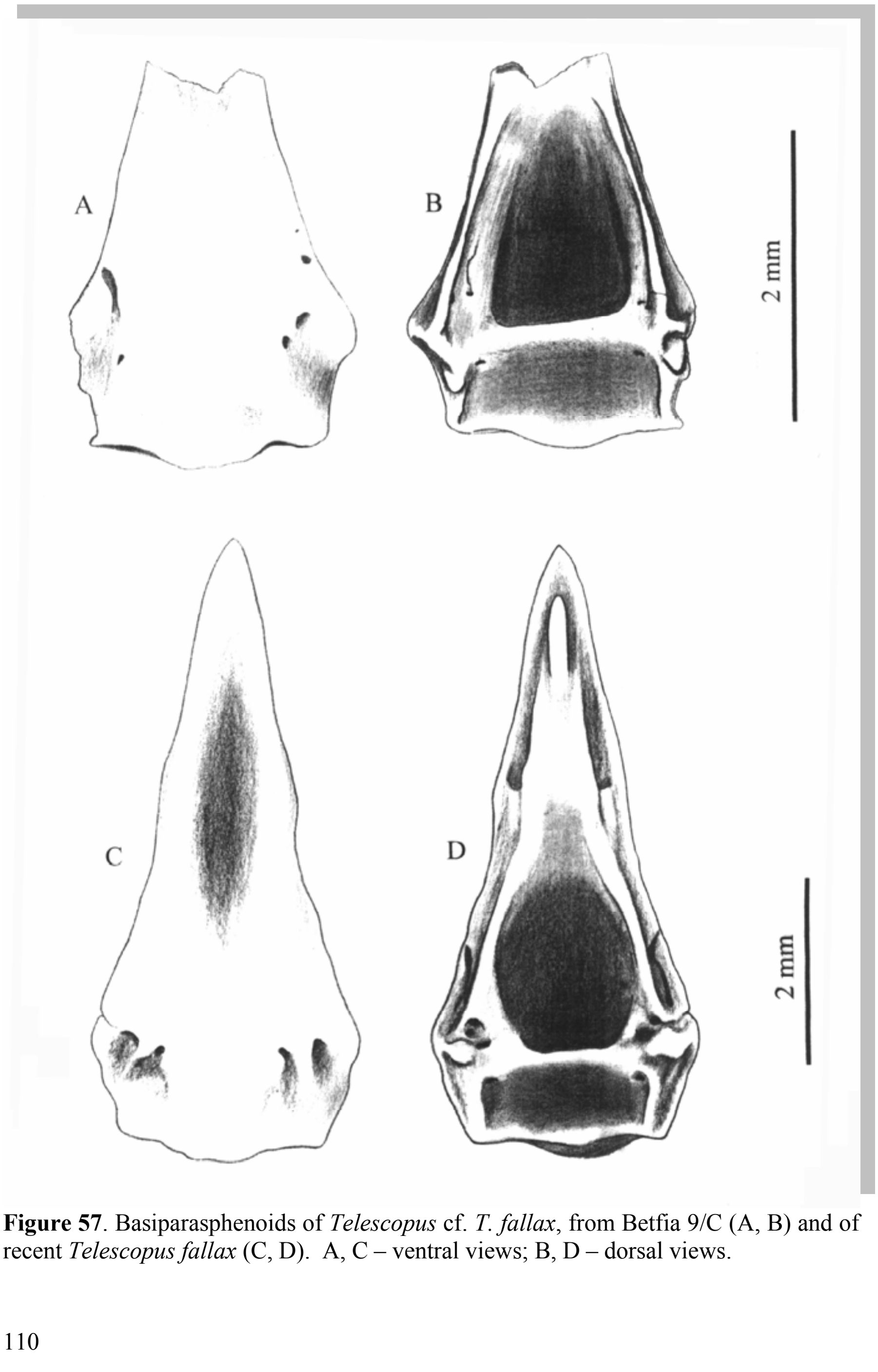


Figure 57. Basiparasphenoids of *Telescopus* cf. *T. fallax*, from Betfia 9/C (A, B) and of recent *Telescopus fallax* (C, D). A, C – ventral views; B, D – dorsal views.

The anterior foramina of the latter are situated close to the “cid” nerve foramina. The parasphenoid process bearing a frontal steppe is broken off.

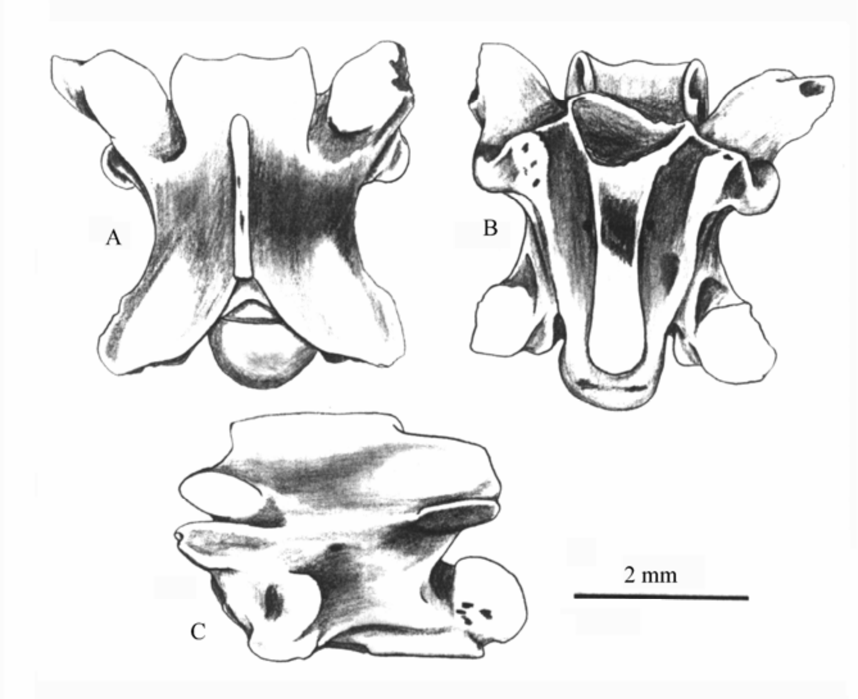


Figure 58. Trunk vertebrae of *Telescopus* cf. *fallax* from Betfia 9/C, in dorsal- (A), ventral- (B), and lateral views (C).

The vertebrae are of small size (Fig. 58). The neural arch is depressed and provided with a long neural spine of low height. The dorsal margin of the neural spine is thickened. The vertebral centrum is moderately elongated. The centrum length of the best-preserved vertebra is 3.4 mm while its width is 2.56 mm. The centrum is 1.32 times longer than its width. The hypapophysis is prominent, flattened and wide. The parapophyses are distinctly longer than the diapophyses. The zygosphene is moderately wide and trilobate; the central lobe is distinctly smaller than the lateral ones. The prezygapophyseal processes (if preserved) are short and flattened dorsoventrally.

The above-described remains closely resemble in skeletal morphology those of recent *Telescopus fallax*. The main difference observed in the morphology of the basiparasphenoid, when compared with recent comparative materials, consist in the different position of the cerebral foramina and the course of Vidian canal. In the specimen from Betfia 9/C the cerebral foramen is situated posteriorly to the Vidian orifice while in recent specimens both orifices are situated at the same level. The anterior orifice of the Vidian canal (present only in the left side) opens near the lateral border of the parasphenoid. In recent *T. fallax* the anterior orifice of the Vidian canal opens on the lateral border of the parasphenoid, and is covered from below by the ventral margin of the parasphenoid (Fig. 57: C, D). The vertebrae display all the diagnostic characters of *T. fallax* (SZYNDLAR, 1991a). On the other hand it should be noticed that, some vertebral characters (mentioned as having diagnostic value) show considerable intraspecific variation (e.g. in a recent specimen of *T. fallax* from Andikithira, Greece, the parapophyses equals the length of the diapophyses, the zygosphene is strongly crenate with large central lobe and the prezygapophyseal processes are not flattened dorsoventrally, cf. Fig. 16: D-F).

The oldest fossil record of the genus *Telescopus* comes from the Latest Miocene (MN 13) of Polgárdi, Hungary (VENCZEL, 1998c). The fossil record from the Quaternary of Europe is restricted to two fossil localities only: Betfia 9/C, Romania, of Lower Pleistocene age (described above), and Varbeshnitsa, Bulgaria, of Middle Pleistocene age. The latter locality is situated at the northern limit of the present range of distribution of this snake (SZYNDLAR, 1991a).

Family **Viperidae** OPPEL, 1811

The family comprise about 20 genera assigned in more than 200 species (GOLAY et. al., 1993). The maxilla is much shortened, its dentition being reduced to a pair of solenoglyphe fangs at its rear just behind its ectopterygoid articulation (MCDOWELL, 1987). Other osteological characters among others includ: the quadrate and ectopterygoid are elongated; the vertebrae of the presacral region bear hypappophyses; the neural arch is depressed dorsoventrally (BAILON, 1991; AUGÉ & RAGE, 2000).

Genus ***Vipera*** LAURENTI, 1768

The members of the genus *Vipera* (s. l.) presently inhabit Eurasia and North Africa. Based on morphological and biochemical data in the late twenty years there were several attempts for partition of this genus (e. g. GROOMBRIDGE, 1980, 1986; OBST, 1983; NILSON & ANDRÉN, 1986;

ASHE & MARX, 1988; HERRMANN et al., 1992; ZEROVA, 1992; a. o.). According to SZYNDLAR & RAGE (1999) the new subdivisions do not necessarily reflect osteological differences. The latter authors adopted the traditional subdivision of the genus *Vipera* (s. l.) into three informal complexes: 1. '*Vipera berus*' complex (*V. berus*, *V. ursinii*, and *V. seoanei*); 2. '*Vipera aspis*' complex (*V. ammodytes*, *V. aspis*, and *V. latastei*); 3. *Vipera* – 'Oriental vipers' (*V. deserti*, *V. lebetina*, *V. mauritanica*, *V. palaestinae*, *V. schweizeri*, *V. xanthina*); and 4. *Daboia* (*D. russelii*). The isolated trunk vertebrae of different complexes may be distinguished by their shape and size. The vertebrae of the '*Vipera berus'* complex are small, elongate and provided with low neural spine and hypapophyses; the vertebrae of 'Oriental vipers' are large, relatively short and provided with high neural spines and long hypapophyses; the vertebrae of '*Vipera aspis*' complex display an intermediate condition between the two former groups (SZYNDLAR & RAGE, supra. cit.). The oldest members of the '*Vipera aspis*' complex in Europe are known since the beginning of the Miocene (MN 1), while those of 'Oriental vipers' since the Lower Miocene (MN 3) (SZYNDLAR & BÖHME, 1993; SZYNDLAR & RAGE, 1999). The oldest fossils referable to the '*Vipera berus*' complex are known from the Lower Pliocene of Hungary (VENCZEL, in press.)

***Vipera ammodytes* (LINNAEUS, 1758)**

1984 *Vipera ammodytes* (LINNAEUS): SZYNDLAR, P. 82-84, Figs. 31-32 .

Material: Betfia pothole/B: three fragmentary vertebrae (MTC. No. 18797/1-3); Betfia 7: ten vertebrae (MTC. No. 18649); Betfia 9: one vertebra (MTC. No. 18677); Betfia 12/B: one maxilla (MTC. No. 18745), one fragmentary ectopterygoid (MTC. No. 18746), one fragmentary compound bone (MTC. No. 18747), one fragmentary parietal (MTC. No. 18748), ten vertebrae (MTC. No. 18749).

Description and comments

The fragmentary parietal belonged to a relatively big specimen, but it is without detailed morphological characters.

Maxilla (Fig. 59: A, B). The bone belonged to a large individual with the venom fangs broken off. The ascendant process is relatively thick and high. In posterior view the fossa for the ectopterygoid articulation is relatively deep, delimited dorsally by a transversal crest. The dental canal foramina are situated on the medial side of the bone (two foramina in a common deep fossa), at the base of the ascendant process. On the lateral side of the ascendant process near its apex a small foramen is situated. The specimen is similar in size and shape to recent *V. ammodytes*.

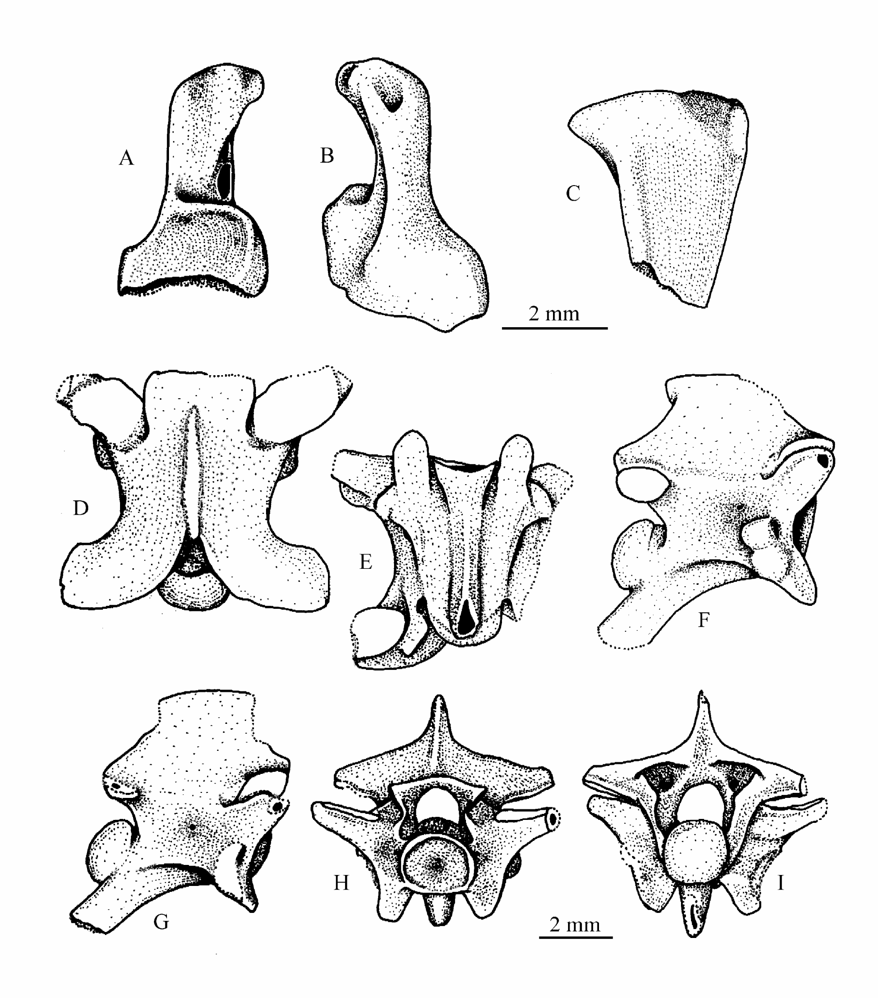


Figure 59. *Vipera ammodytes* from Betfia 12/B. A, B: left maxilla (MTC. No. 18745); C: fragmentary right ectopterygoid (MTC. No. 18746); D-I: presacral vertebrae (MTC. No. 18749/1-3). A – posterolateral view; B – anteromedial view; C, E – ventral views; D – dorsal view; F, G – lateral views; H – anterior view; I – posterior view.

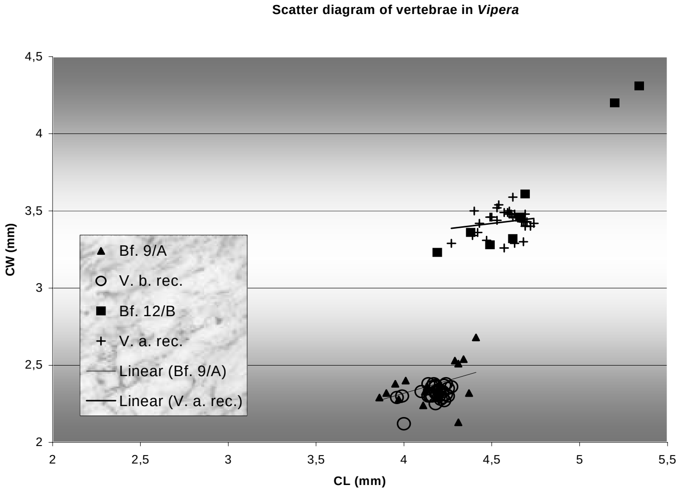


Figure 60. Scatter diagram of CL and CW of presacral vertebrae in *Vipera ammodytes* (V. a.) and *V. berus* (V. b.). Abbreviations: Bf. – Betfia, rec. – recent specimen.

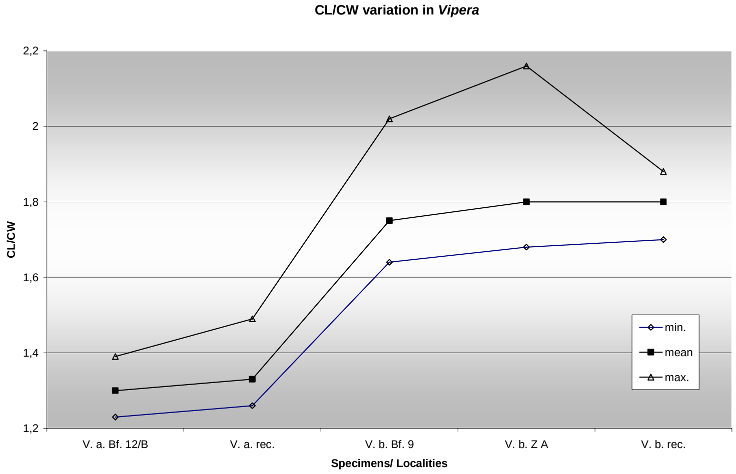


Figure 61. CL/CW variation in *V. ammodytes* (V. a.) and *V. berus* (V. b.). Abbreviations: Bf. – Betfia, Z A – Zalesiaki A (Poland).

Ectopterygoid (Fig. 59: C). The stem of the bone is broken off. The ectopterygoid rami are incompletely separated. The lateral margin of the external ramus is bent ventrally while the anterior margin of the internal ramus is straight.

The medial flange of the compound bone is approximately three times higher than the lateral flange. The mandibular fossa is relatively deep while the supraangular foramen is situated far from the anterior margin of the former. The retroarticular process is strongly curved medially.

Presacral vertebrae (Fig. 59: D-I). The overwhelming part of the vertebrae is very fragmentary. Despite this, they bear some differentiating morphologic characters for *V. ammodytes*. The neural arch is depressed. The neural spine is prominent and is approximately as high as long. The hypapophysis is straight and projected posteroventrally. The anterior margin of the zygosphene is crenate. The prezygapophyseal articular facets are elongated while the postzygapopyseal articular facets are rounded or obovate shaped. The prezygapophyseal processes are extremely short with pointed tips. The paradiapophyses are differentiated into diapo- and parapophyseal portions: the diapophyses are projected laterally, while the parapophyseal processes are projected anteroventrally. The latter are flattened dorsoventrally and obtuse distally. The cotyle is slightly depressed dorsoventrally. The subcentral-, lateral- and paracotylar foramina are well evidenced. The centrum length in eight measured trunk vertebrae, coming from Betfia 12/B ranges between 4.19 – 5.34 mm, while the centrum length/width ratio between 1.23 – 1.39 (mean = 1.30). In *V. berus* this ratio is considerably higher (SZYNDLAR, 1984) (Fig. 60).

The oldest record of vipers closely related to *V. ammodytes* (described as *Vipera* cf. *V. ammodytes*) come from the Lower Pliocene (MN 14) of Osztramos 1, Hungary (VENCZEL, in press) as well as from the Middle Pliocene (MN15) of Weze 1, Poland. The remaining records are known from the Upper Pliocene (MN16) of Rebielice Królewskie 1A and 2, Poland, from the Middle Pleistocene of Varbesnitza, Bulgaria, and Tourkobounia, Greece, and from the Upper Pleistocene of Stoilovo, Bulgaria (SZYNDLAR, 1991b). It is also known from the Upper Biharian of Stránská Skála, Czech Republic (IVANOV, 1995).

Vipera berus (LINNAEUS, 1758)

1913 *Vipera berus* L. : BOLKAY, P. 226, Fig. 5
1932 *Vipera berus* L. : VON SZUNYOGHY , P.10, 50
1977 *Vipera berus* L. : RABEDER, Pp. 92-93, Pl. 1: 3, Pl.2: 21

1984 *Vipera berus* (LINNAEUS) : SZYNDLAR, Pp. 122-131, Figs. 52-55

Material: Betfia 9: one maxilla (MTC. No. 18678), one fragmentary ectopterygoid (MTC. No. 18679, two fragmentary compound bones (MTC. No. 18680/1-2), 90 vertebrae (MTC. No. 18681); Subpiatră: one maxilla (MTC. No. 16961), three fragmentary maxillae (MTC. No. 18444/1-3), one premaxilla (MTC. No. 16962), 20 vertebrae (MTC. No. 16963); Chişcău 3: two fragmentary basiparasphenoids, 26 vertebrae (uncatologued).

Description and comments

Basiparasphenoid. The better preserved specimen from Chişcău 3 closely resembles recent *Vipera berus*. It lacks parasphenoid process. The pterygoid processes are reduced; the opening for cerebral foramina and the Vidian canal are not covered by a crest. The basisphenoid crest is bifurcated anteriorly at the level of central area. The posterior margin is provided with a bifurcated medial process.

Maxilla (Fig. 61: A, B). The specimens are well preserved differing between them by the shape of the ascendant process. The latter structure in the specimen coming from Betfia 9 is relatively slender with its distal portion dilated, provided with a process projected medially. The ascendant process in the specimen coming from Subpiatră is relatively thick. The venom fang is present only in the Betfia 9 specimen: it is curved posteriorly and with the dental canal well evidenced.

Ectopterygoid (Fig. 61: C). The proximal fragment is similar to recent *V. berus*. The ectopterygoid rami are not divided. The anterior margin is provided with a small protuberance.

Compund bone (Fig. 61: D, E). The medial flange is approximately three times higher than the lateral flange. The latter incompletely delimits the mandibular fossa. The retroarticular process is strongly curved ventromedially.

Premaxilla. In lateral view the nasal process is extremely widened. The lateral processes are relatively long and slender. The vomeral process is broken off.

Presacral vertebrae (Fig. 61: F-H). The cervical vertebrae (= anterior presacral vertebrae) is difficult to be differentiated from those of middle trunk region. Generally the hypapophysis of the vertebrae from the cervical region is straight and projected posteroventrally while the height of the neural spine equals its length overhanging anteriorly and posteriorly. The centrum of the middle trunk vertebrae is elongated and of cylindrical shape. The hypapophysis is relatively short and hooked backward while the anterior keel is widened in

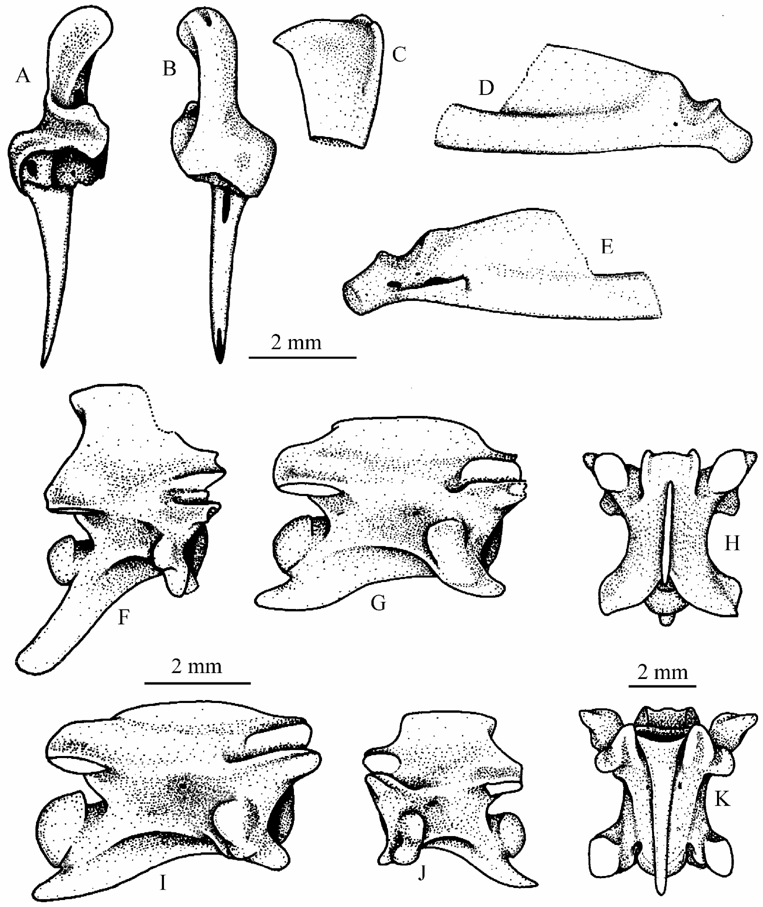


Figure 61. *Vipera berus* (A-G, I) and *Vipera* sp. (H, J, K). A, B: left maxilla (Betfia 9/A, MTC. No. 18678); C: fragmentary right ectopterygoid (Betfia 9/A, MTC. No. 18679); D, E: fragmentary left compound bone (Betfia 9/A, MTC. No. 18680/1); F: anterior presacral vertebra (Betfia 9/A, MTC. No. 18681/1); G, I: presacral vertebrae (Betfia 9/A, MTC. No. 18681/2, 3); H, J, K: presacral vertebra (Râpa, MTC. No. 13720/1). A – posterolateral view; B – anteromedial view; C, K – ventral views; D, F, G, I, J – lateral views; E – medial view; H – dorsal view.

the close vicinity of the cotyle. The neural arch is depressed, provided with a neural spine of low height overhanging only posteriorly. The anterior margin of the zygosphene is strongly crenate. The prezygapophyseal articular facets are oval or of obovate shape while the postzygapophyseal articular facets are circular. The prezygapophyseal processes are short and pointed distally. The paradiapophyses are incompletely divided into parapo- and diapophyseal portions. The parapophyseal processes are robust, projected anteroventrally and obtuse distally. All the foramina are visible, the cotyle and the condyle are slightly depressed dorsoventrally.

The measurements made in 16 vertebrae coming from Betfia 9 are given below:

Measurement	Min. – Max. (mm)	Mean	SD
PR – PO	4.41 – 5.32		
CL	3.86 – 4.37		
PO – PO	4.54 – 5.40		
CW	2.13 – 2.68		
ZW	2.00 – 2.22		
CTH	1.27 – 1.55		
CTW	1.49 – 1.80		
PR – PR	4.62 – 5.58		
CL/CW	1.64 – 2.02	1.75	±0.09
PO – PO/CW	1.97 – 2.27	2.11	±0.04
CTW/CTH	1.07 – 1.36	1.19	±0.07
ZW/CW	0.82 – 0.94	0.89	±0.01
PR – PR/PR – PO	0.90 – 1.09	1.04	±0.01
CL/ZW	1.85 – 2.15	1.94	±0.03
PR – PR/CW	1.96 – 2.30	2.17	±0.07

Table 5. Measurements of presacral vertebrae in *V. berus* (N=16) from Betfia 9.

The oldest fossil record of a form closely related to *Vipera berus* is known from the Lower Pliocene (MN 14) of Osztramos 1, Hungary (VENCZEL, in press). The remaining fossil record of *Vipera berus* are restricted to Quaternary and are known from the Pleistocene of Poland (SZYNDLAR, 1984, 1991b), from the Lower Pleistocene of Osztramos 8 and 14, Hungary (VENCZEL, 1997b); from the Middle Pleistocene of St. Margarethen, Austria (RABEDER, 1977) and Braşov, Romania (BOLKAY, 1913) and from the Upper Pleistocene of Germany (BRUNNER, 1954, 1957; MARKERT, 1975, 1976; PETERS, 1977a, 1977b; BLOOS et. al., 1991).

Vipera sp.

Material: Betfia pothole/A: one vertebra (MTC. No. 18755); Betfia 5: one vertebra (MTC. No. 18615); Betfia 7: 19 vertebrae (MTC. No. 18650); Betfia 12/A: two vertebrae (MTC. No. 18740); Râpa: ten vertebrae (MTC. No. 13720); Galoşpetreu: five vertebrae (MTC. No. 18818).

Description and comments

In all of the above localities only vertebrae have been discovered. The trunk vertebrae are characteristic for the genus *Vipera* (Fig. 61: I-K), and they bear the diagnostic features of the '*Vipera berus*'complex of European vipers. However, the assignment of the remains below the generic level is not actually possible because *V. berus* and *V. ursinii* based exclusively on presacral vertebrae are practically undistinguishable (SZYNDLAR, 1984, 1991b).

4. DISCUSSION

4.1. Fossil record and paleobiogeographic events

The Quaternary fossil localities of Bihor County yielded at least 13 different snake taxa: Scolecophidia indet., *Coluber viridiflavus*, *C.* cf. *C. gemonensis*, *Coronella austriaca*, *Elaphe longissima*, *E.* cf. *E. longissima*, *E. paralongissima*, *E. quatuorlineata, Natrix natrix*, *N. tesselata*, *Natrix* sp., *Vipera ammodytes*, *V. berus*, *Vipera* sp., and *Telescopus* cf. *T. fallax*. Except for *E. paralongissima* most probably all the other forms belonged to extant taxa. Of the remaining taxa, only *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *N. tesselata* and *V. berus* are distributed presently in the territory of Bihor County while the other ones are distributed far from the studied area. According to SZYNDLAR (1984) the recent European snake fauna, except 5 widely distributed species may be divided into two distinct groups: West European species, distributed mainly in the Western part of our continent (9 species) and East European species, distributed mostly in the Eastern part of our continent (at least 11 species). Comparing the above described fossil remains with the list published by SZYNDLAR (supra. cit.) it may be concluded that during Quaternary times only one West European species penetrated into the Carpathian Basin: *Coluber viridiflavus* (VENCZEL, 1998a), the remaining ones belonging either to East European species, or having a wider distribution in Europe (*Coronella austriaca*, *Elaphe longissima*, *Natrix natrix* and *Vipera berus*). Fossil remains of Scolecophidia have never been reported from the Quaternary of Central Europe. The latter group, represented in Europe solely by *Typhlops*, had a distinctly wider distribution during Neogene times (SZYNDLAR, 1991a; SZYNDLAR & ZEROVA, 1992; AUGÉ & RAGE, 1993) and retreated from the territory of Central Europe in Late Miocene times. Two doubtful records of the genus *Coluber* are known from the locality Betfia 2 and Râpa. From the former locality VON SZUNYOGHY (1932) listed a compund bone of *Coluber caspius* (= *Zamenis jugularis* L. var. *caspia*). The mentioned bone at present is not available for study (being lost ?). Judging on the base of relatively wide intraspecific variability of this element in *Coluber* (e.g. shape of the anterior margin of coronoid process and shape of the lateral flange) and lack of trunk vertebrae (also characteristic for *C. caspius*: see the key characters on Fig. 17) from the locality of Betfia 2 as well as from the other sites of Betfia, we can presume that the presence of this species in Betfia is highly improbable. FUHN & VANCEA (1961: p. 99) reported remains of *Coluber* from the "Pliocene" deposits of Râpa. It may be noticed that the latter locality is of Upper Pleistocene age (JURCSÁK et al., 1982, 1984) while the abundant colubrine remains originated from this locality belonged exclusively to *Elaphe longissima*. However, VENCZEL (1989: Fig. 3a) based on a single basioccipital which belonged to a relatively large specimen, provided with a peculiar basioccipital crest (with three well developed and prominent basioccipital processes), reported *Coluber viridiflavus* from the locality of Râpa. More detailed study of the mentioned specimen revealed that it does not represent more than *Natrix tesselata* (VENCZEL, 1995).

Most paleoherpetologists agree that the modern snake fauna of Europe is of Asiatic origine (RAGE, 1984; 1987; SZYNDLAR, 1984, 1985, 1991b; SZYNDLAR & RAGE, 1999; BAILON, 1991; VENCZEL, 1999; a. o.). The modernization of the European snake fauna took place in Neogene times, resulted from several westardly directed faunal waves, which used few migrating routes. The main events during Late Neogene and Quaternary were outlined by SZYNDLAR (1984). The herpetofauna of Quaternary times, being consisted of extant genera and species only is an impoverished one, if compared to those of Neogene times. During Lower Pleistocene few Tertiary survivors retreated in southern or southeastern areas (e. g. Scolecophidia, ericine boids and large vipers of the 'Oriental vipers' group) or died out (e. g. *Elaphe paralongissima*). However in interglacial periods few species migrated into north or northeastern areas (as was the case of *Coluber viridiflavus, C. gemonensis, Elaphe quatuorlineata, Telescopus fallax* and *Vipera ammodytes*). An important migration route into northern areas during Lower Pleistocene could be a corridor extending across the eastern margin of the Pannonian Basin. The presence of recent *Coluber viridiflavus* in the Carpathian Basin was reported by some authors (e.g. BIELZ, 1856; FRIVALDSKY, 1877; MOJSISOVICH, 1889; WERNER, 1897; SCHREIBER, 1912). Despite of the fact that FUHN & VANCEA (1961) considered all these data ambiguous, we can presume that the disappearance of the latter species from the Carpathian Basin may have taken place rather recently. Another interesting case is the presence of *Vipera ammodytes* in the fossil deposits of Betfia. This species in fossil state was for the first time reported from the Upper Pliocene of Poland (SZYNDLAR, 1984, 1991b), while recently VENCZEL (in press) described it from the Lower Pliocene of Osztramos, North Hungary. During Lower Pleistocene times (considering the interglacials only) its distribution in Romania reached the northern part of Pădurea Craiului Mountains (including Betfia), while in present time its northern limit of distribution is in Trascăului and Metaliferi Mountains (about 100 km south to the locality of Betfia). However the drift epochs were survived probably by few eurithermic forms only (STUGREN, 1957, 1986)

4.2. Faunal succesions

Due to climatic oscillations during Quaternary times, with the decreasing tendency of the mean annual temperature, in the composition of snake faunas in the studied area (but it probably holds good for the whole Carpathian Basin) at least three major phases could be delimited, mainly corresponding to the general subdivision of the Quaternary: Lower Pleistocene (Biharian) snake faunal phase, Upper Pleistocene (Toringian) snake faunal phase, and Holocene snake faunal phase.

The Biharian snake faunas roughly were contemporaneous with the Biharian land mammal age, or with the *Microtus-Mimomys* rodent superzone of FEIFAR et al. (1998). All the snake faunas known from Betfia and Subpiatră are included here. Betfia 13 could be an exception, because this is of Villafranchian age (TERZEA, 1973, 1991, 1994, 1995). Moreover only one species is known from this locality (most probable due to inadequate collecting techniques). The composition of the Biharian snake faunas in the studied localities were rather diversified, but a general trend of pauperization is observed in the younger localities (Fig. 63-68, and 71, 72). In this respect all the above localities yielded 5 – 8 different taxa, with at least 1-2 Mediterranean snakes. A considerable proportion of the remains belonged to natricine snakes. Considering the above remarks the snake faunas of these localities lived in mild climatic conditions, with abundant water source in the area, while the paleoenvironment was rather diversified. However the climatic oscillations were probably rather frequent, and they can be noticed even in the composition of the herpetofauna (e. g. compare the list of the herpetofauna of Betfia 9/B and Betfia 9/C published by HIR & VENCZEL, 1997). The richest of all fossil Biharian sites was the locality complex of Betfia 9, with an unexpectedly abundant and well diversified ophidian fauna: Scolecophidia indet., *Coluber viridiflavus*, *Coro-nella austriaca*, *Elaphe paralongissima*, *E. quatuorlineata*, *Natrix natrix*, *N. tesselata*, *Vipera ammodytes* and *Vipera berus*. The fossil snake fauna of the locality Betfia 12/A is somewhat contrasting with those coming from the other localities, because the overwhelming part of the remains belonged to *Coluber viridiflavus* only, and just few remains of natricine snake were found here (Fig. 64). The locality of Subpiatră contained a single Mediterranean snake only (*Coluber viridiflavus*) (Fig. 68), while the upper layers from the locality complex Betfia 7 hasn't provided any Mediterranean snake . Except for *Elaphe paralongissima*, the remaining snakes (including Scolecophidia indet., which probably do not represent more than recent *Typhlops*) most probably belonged to extant species only. However in the morphology of cranial bones and even at the level of the axial skeleton few differences could be documented (see in the systematic part).

The Toringian snakes faunas are roughly contemporaneous with the Toringian land mammal age, or with the *Arvicola cantianus*, *A. terrestris* rodent zones of FEIFAR et al., 1998). All the forms reported from the localities of Toringian age (Chişcău 3, Râpa) belonged exclusively to recent snakes (Fig. 69, 70). However the presence of *Elaphe longissima* and *Natrix tesselata* in the above localities suggest that the accumulation of the vertebrate remains took place in rather mild climatic conditions. All the remains show close similarity with the recent comparative materials.

The Holocene snake remains belonged exclusively as in the case of Toringian faunas to recent species too. Except for Valea Morii (this locality yielding a somewhat diversified herpetofauna) the other localities usually yielded few vertebrae belonging to a single species only. No detectable differences in the morphology of skeletal elements of the studied material could be evidenced. Comparing the Holocene snake faunas to the recent one (which is somewhat diversified), may be concluded some mending tendency of the climate, despite the fact that the eurithermic species (the so called "cold trio", composed off by *Coronella austriaca*, *Natrix natrix* and *Vipera berus*) are more widely distributed than those of paramediterranean forms (*Elaphe longissima* and *Natrix tesselata*).

Discussion

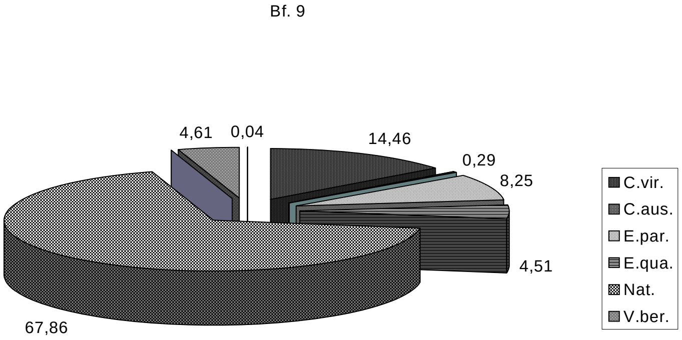


Figure 63. Relative frequency of snakes in locality of Betfia 9.

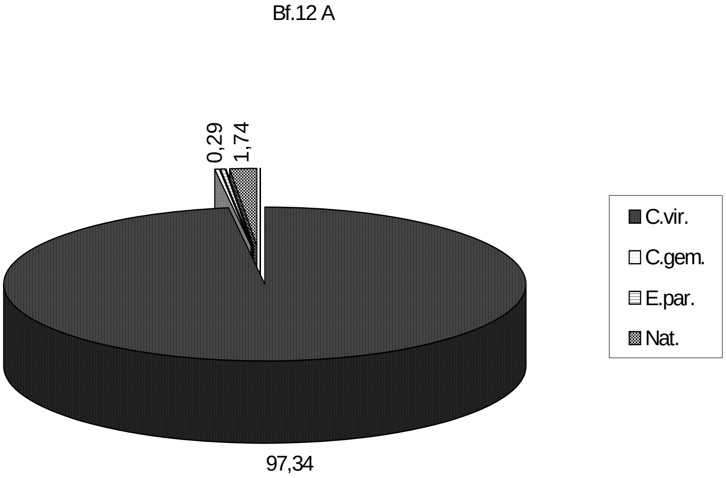


Figure 64. Relative frequency of snakes in locality of Betfia 12/A.

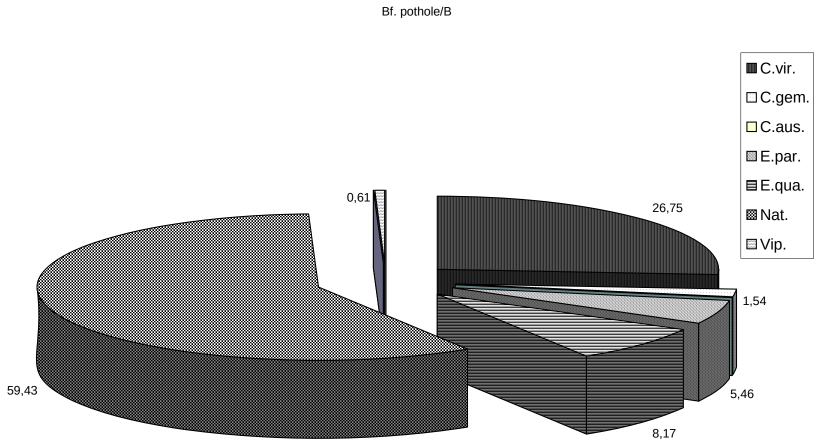


Figure 65. Relative frequency of snakes in locality of Betfia pothole/B

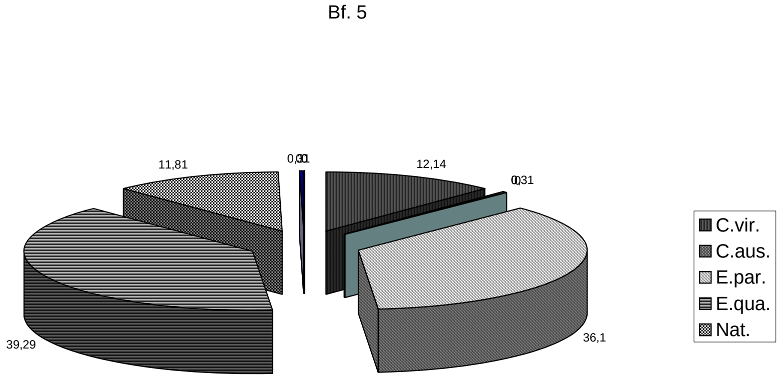


Figure 66. Relative frequency of snakes in locality of Betfia 5.

Discussion

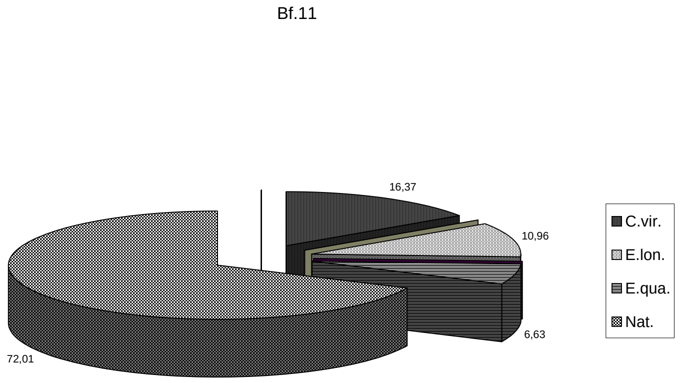


Figure 67. Relative frequency of snakes in locality of Betfia 11.

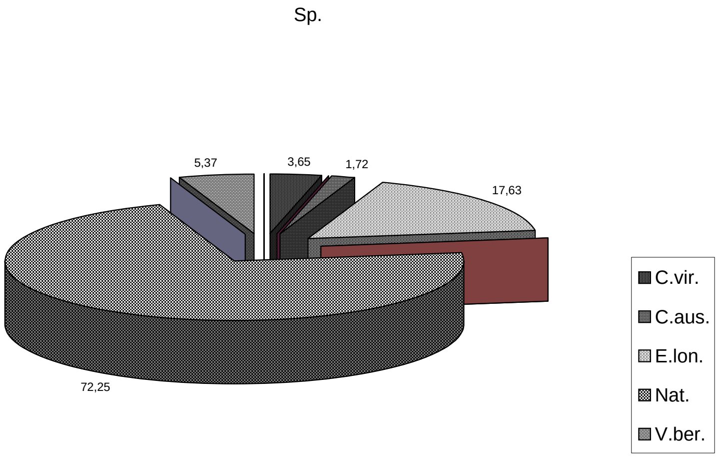


Figure 68. Relative frequency of snakes in locality of Subpiatră

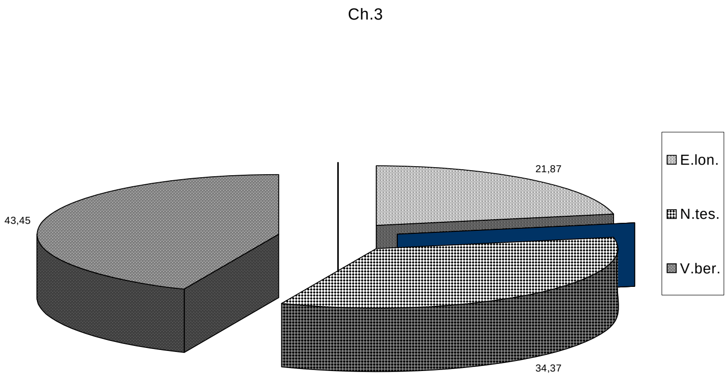


Figure 69. Relative frequency of snakes in locality of Chişcău 3.

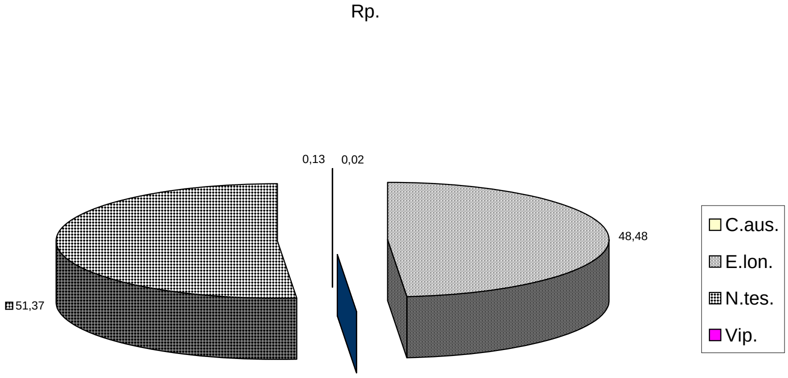


Figure 70. Relative frequency of snakes in locality of Râpa.

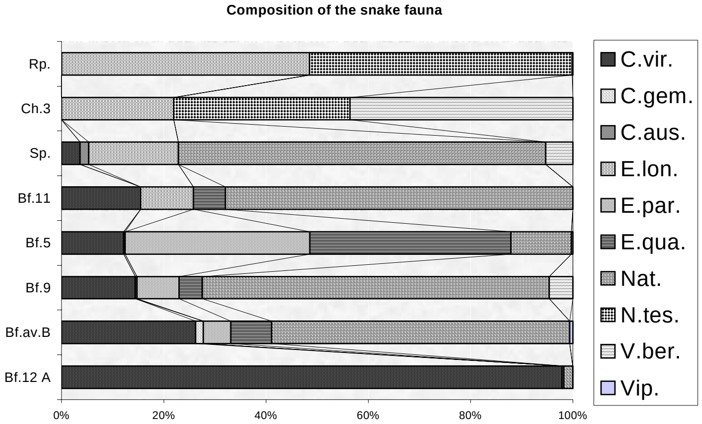


Figure 71. Composition of Pleistocene snake faunas from Bihor. Abbreviations: C. vir. – *Coluber viridiflavus*, C. gem. – *C. gemonensis*, C.aus. – *Coronella austriaca*, E. lon. – *Elaphe longissima*, E. par. – *E. paralongissima*, E. qua. – *E. quatuorlineata*, Nat. – *Natrix* sp., N. nat. – *Natrix natrix*, N. tes. – *N. tesselata*, T. fal. – *Telescopus fallax*, Vip. – *Vipera* sp., V. amm. – *Vipera ammodytes*, V. ber. – *V. berus*, Sco. – Scolecophidia indet., Bf – Betfia, Ch. – Chişcău, Rp. – Râpa, Sp. – Subpiatră.

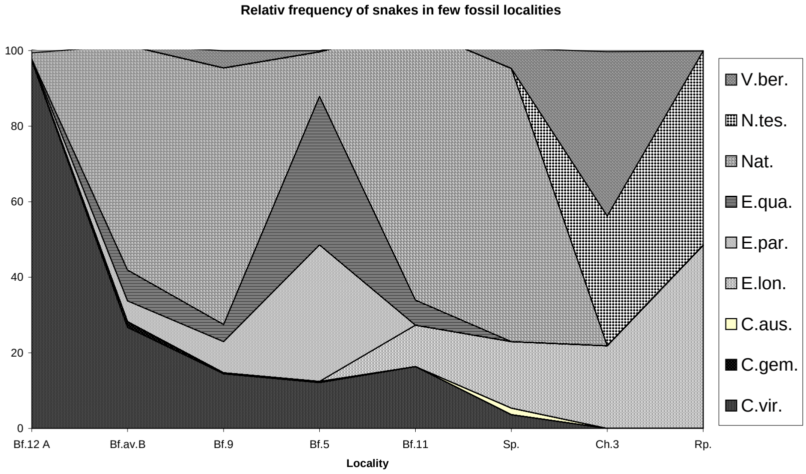


Figure 72. Relative frequency of snakes in few Pleistocene localities from Bihor. For abbreviations see Figure 62.

5. CONCLUSIONS

1. The Quaternary snake assemblages coming from 16 fossil localities of Bihor County, Romania were composed of extant genera and species only. The single extinct species found in few Lower Pleistocene (Biharian) localities was a colubrine snake: *Elaphe paralongissima*. All the skeletal remains studied show a close resemblance with those of recent species, and the few morphological differences observed never exceed the limits of intraspecific variations. However the morphological variations were wider in the case of Lower Pleistocene snakes than those in Upper Pleistocene or Holocene snakes.
2. The Lower Pleistocene (Biharian) snake faunas can be distinguished by those of Upper and Holocene snake faunas having in their composition a number of mediterranean species (e. g. *Coluber viridiflavus*, *C.* cf. *C. gemonensis*, *Elaphe quatuorlineata*, *Vipera ammodytes*, a. o.). The most abundant and diversified snake fauna is known from the locality Betfia 9/C, with few rarities in its composition (e.g. Scolecophidia indet., *Telescopus* cf. *T. fallax*). The fossil localities of Upper Pleistocene (Toringian) age are lacking any mediterranean snake in the faunal assemblages.
3. In Quaternary times the migrations of the ophidian faunas were rather reduced, when compared to those of Neogene times, and the direction of the migrations was north-south, as opposed to Neogene times in which the main direction of the migrations were east-west. Following the climatic fluctuations and environmental changes, the area of distribution of the ophidian assemblage in cold phases shrank southwards, and expanded northwards in warming periods.
4. The fossil ophidian assemblages may provide valuable paleoecological data, contributing substantially with other vertebrates (e. g. other reptiles, mammals, amphibians) to the paleoenvironmental reconstruction of the studied fossil localities.

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ŞERPI CUATERNARI DIN BIHOR (ROMÂNIA)

Rezumat

Resturile fosile de ofidieni sunt relativ comune în siturile neogene şi cuaternare, o bună parte a ocurenţelor fiind cunoscute din depozitele paleocarstice cu condiţii optime de conservare şi fosilizare pentru vertebrate şi moluşte. O altă sursă importantă de fosile pot fi săpăturile arheologice. Dimensiunea relativ mică a oaselor şi fiabilitatea lor, tehnicile neadecvate de colectare, precum şi lipsa de interes faţă de aceste animale "cu evoluţie lentă" au făcut ca, până în ultimul timp, grupul ofidienilor să rămână aproape necunoscut în urma cercetărilor paleofaunistice din ţara noastră. Referitor la cercetările paleoherpetologice, Zona Ţării Crişurilor poate fi considerată o excepţie, dat fiind faptul, că de aici provine marea majoritate a ocurenţelor şi sunt cunoscute şi cele mai multe publicaţii referitoare la faunele de amfibieni şi reptile cuaternare şi holocene din România. Existenţa numeroaselor depozite cuaternare din Bihor a fost o condiţie primordială pentru realizarea unei colecţii însemnate de paleoherpetologie (cu peste 30000 de resturi scheletice), depozitate în colecţiile de paleontologie (Secţia Ştiinţele Naturii) ale Muzeului Ţării Crişurilor din Oradea.

În acest volum sunt prelucrate datele referitoare asupra faunelor de ofidieni provenite din 16 puncte fosilifere (Complexul Betfia cu 10 situri diferite, Subpiatră, Chişcău 3, Râpa, Vadu Crişului, Valea Morii şi Galoşpetreu), începând din pleistocenul inferior până în holocen (vezi Fig.1 şi Fig. 2). Determinarea speciilor de şerpi fosili a fost realizat prin studiile morfologice şi micromorfologice, efectuate asupra tuturor resturilor de ofidieni (cu excepţia coastelor) descoperiţi în siturile fosilifere. Este de menţionat faptul, că marea majoritate a resturilor au constat din vertebre fragmentare şi mult mai rar din oase aparţinând craniului neural sau visceral. Oasele de ofidieni au fost colectate prin săpături paleontologice organizate de Muzeul Ţării Crişurilor (o parte fiind organizate în colaborare cu Institutul de Speologie "Emil Racoviţă" din Bucureşti şi cu Muzeul din Tinca), resturile fiind selectate din materialele de vertebrate fosile cu care au fost descoperite în amestec (micromamifere, păsări, amfibieni, etc.). Materialele comparative necesare în determinare au fost preparate prin macerarea sau fierberea specimenelor procurate (majoritatea exemplarelor au fost omorâte de localnici sau călcate de maşini, altele în schimb au murit în captivitate). Pe lângă acestea au fost studiate şi o serie de schelete aflate în colecţiile Academiei Poloneze din Cracovia, Muzeului de Istorie Naturală din Viena, Zoologische Forschungsinstitut şi Muzeul Alexander

Koenig din Bonn, etc. Studiile morfologice efectuate asupra scheletului cefalic (Fig. 8-13.) şi cel axial au fost totdeauna urmate de măsurători efectuate asupra vertebrelor (Fig.14). În acest scop au fost selectate o serie de vertebre toracale mijlocii şi relativ bine conservate (măsurabile), pe care au fost făcute următoarele măsurători: lungimea centrului vertebral (CL), lăţimea centrului vertebral (CW), raportul dintre lungimea şi lăţimea centrului vertebral (CL/CW). Datele obţinute au fost reprezentate în diagrame şi interpretate în partea descriptivă. Totodată am încercat să evităm determinarea speciilor exclusiv pe baza vertebrelor, acest lucru fiind riscant mai ales în cazul colubrinelor mici, natricinelor şi viperelor, datorită variaţiilor foarte largi intra- şi interspecifice. Vertebrele fiind mult mai numeroase, raportate la numărul oaselor craniene, ne-a ajutat totuşi la estimarea corectă a numărului speciilor de ofidieni la siturile studiate. Pentru sprijinirea cercetărilor paleoherpetologice şi arheologice viitoare din ţara noastră, am întocmit pe baza vertebrelor şi chei de determinare pentru toate speciile de ofidieni existente la noi în ţară şi în zonele învecinate (Peninsula Balcanică), specii a căror prezenţă în timpul neogenului şi cuaternarului putea fi posibilă şi în România: *Typhlops vermicularis*, *Eryx jaculus*, *Coluber caspius*, *C. viridiflavus*, *C. gemonensis*, *C. najadum*, *Coronella austriaca*, *Elaphe longissima*, *E. quatuorlineata*, *E. situla*, *Malpolon monspessulanus*, *Natrix natrix*, *N. tesselata*, *Telescopus fallax*, *Vipera ammodytes*, *V. berus* şi *V. ursinii* (Fig. 15-20.).

Studiul faunelor fosile de ofidieni, descoperite în Bihor a cuprins mai multe etape: 1. estimarea pe baza vertebrelor a numărului de specii de ofidieni aflate în siturile studiate; 2. raportarea oaselor craniene (dacă erau prezente) la cele axiale pentru fiecare specie în parte; 3. măsurători biometrice efectuate asupra vertebrelor; 4. descrierea tuturor resturilor din staţiunea respectivă şi interpretarea rezultatelor; 5. reconstituirea paleomediului pe baza faunei de ofidieni.

În urma studiilor efectuate asupra siturilor fosilifere cuaternare şi holocene din Zona Ţării Crişurilor au fost găsite următoarele specii (taxoni) de ofidieni: Scolecophidia indet., *Coluber viridiflavus*, *C.* cf. *C. gemonensis*, *Coronella austriaca*, *Elaphe longissima*, *E.* cf. *E. longissima*, *E. paralongissima*, *E. quatuorlineata*, *Natrix natrix*, *N. tesselata*, *Natrix* sp., *Telescopus* cf. *T. fallax*, *Vipera ammodytes*, *Vipera berus*, *Vipera* sp. Toate speciile descrise, cu excepţia speciei dispărute *E. paralongissima*, aparţineau unor genuri şi specii recente. Câteva vertebre fragmentare aparţinând scolecofidienilor (foarte probabil de *Typhlops*, unicul reprezentant european al acestui subordin) sunt singurele ocurenţe din cuaternarul Europei Centrale (Fig. 21). Resturile osteologice fosile ale lui *Coluber viridiflavus* (Fig. 22-25), sunt comparabile cu cele cunoscute din pliocenul superior al Poloniei, de la Rebielice Królewskie 1A, descrise iniţial ca o nouă specie fosilă (*C.*

robertmertensi), aceasta posedând caractere osteologice similare cu cele de la Betfia (ex. baziparasfenoid, bazioccipital, pătrat, articular, ş.a.). În schimb vertebrele de la Betfia şi Subpiatră sunt relativ mai mici şi cu raportul CL/CW mai mare, ceea ce sugerează condiţii paleoecologice diferite (condiţii mai favorabile în pliocenul superior). În schimb prezenţa lui *C. caspius* (deşi menţionat de la Betfia 2) nu a putut fi dovedită pe baza materialelor existente. Acest lucru ne lasă să credem, ca răspândirea acestei specii în Bazinul Carpatic să fi avut loc în epoca postglaciară, sau cel puţin după retragerea din zonă a lui *C. viridiflavus*. Resturile lui *C.* cf. *C. gemonensis* (Fig. 28.) sunt mult mai puţin numeroase. Bazioccipitalul este comparabil cu cel descris din pleistocenul mediu de la St. Margarethen, Austria. Vertebrele aparţinând acestei specii sunt de dimensiuni mici şi cu raportul CL/CW cuprins între 1,29-1,36. Fragmentele osteologice ale lui *Coronella austriaca* (Fig. 31.) nu diferă semnificativ de cele actuale, apropiindu-se morfologic de *C. miocaenica*, o specie dispărută, cunoscută de la Polgárdi 4, Ungaria. Vertebrele aparţinând speciei *E. paralongissima* (Fig. 36.) sunt comparabile cu cele de la Weze 2, Polonia (cu menţiunea că raportul CL/CW în cazul vertebrelor de la Betfia 7 au valori mai scăzute). O serie de resturi craniene atribuite cu oarecare incertitudine tot acestei specii (iniţial specia a fost descrisă exclusiv pe baza scheletului axial), prezintă deosebiri evidente faţă de cele aparţinând speciei recente *E. longissima* (Fig. 44-46.), specie cu morfologia axială apropiată de *E. paralongissima*. Fragmentele craniene atribuite lui *E. quatuorlineata* (Fig. 39-40) din punct de vedere morfologic sunt similare cu cele descrise din pliocenul superior de la Deutsch Altenburg 20, Austria. În schimb vertebrele toracale sunt comparabile cu cele din pleistocenul mediu de la Tourkobounia 2, Grecia (Fig. 40-41.). Este de menţionat, că aceasta este singura specie din Europa cu adaptări morfologice evidente la oofagie (hipapofiza vertebrelor cervicale sunt orientate anteroventral). Natricinele de la Betfia, pe cât sunt greu diferenţiabile pe baza morfologiei axiale (datorită conservării precare a caracterelor de diagnoză), pe atât sunt uşor identificabile pe baza resturilor craniene: baziparasfenoid, bazioccipital, pătrat, ectopterigoid, articular, etc.. Pe baza unor caractere morfologice ale baziparasfenoidului (ex. lungimea ductului carotic, aspectul proceselor pterigoidale, poziţia foramenului de ieşire a nervului constrictor internus dorsalis) şi ale prooticului (ex. aspectul laterosfenoidului şi modul de deschidere al foramenelor pentru ramura maxilară al nervului trigemen) specia *Natrix natrix* de la complexul Betfia şi Subpiatră (Fig. 49-50) se include perfect în linia evolutivă *N. longivertebrata* – *N. natrix*. Resturile scheletice aparţinând speciei *N. tesselata*, mai ales cele de la Chişcău 3 şi Râpa (Fig. 53-55.) sunt similare cu cele de la specia recentă. Câteva deosebiri observate (ex. mărimea foramenului vomeral, numărul dinţilor maxilari, dentari şi pterigoidieni) pot fi considerate ca şi variaţii intraspecifice. Fragmentul de basiparasfenoid aparținând speciei *Telescopus* cf. *T. fallax* este singurul specimen descoperit în stare fosilă din cuaternarul Europei (Fig. 57.). Față de Colubridae reprezentanții familiei Viperidae sunt mult mai slab reprezentate în depozitele studiate. Cele două specii găsite (*Vipera ammodytes* şi *V. berus*) pot fi diferențiate atât pe baza resturilor osteologice craniene (Fig. 59., Fig. 62.) cât şi pe baza celor axiale (de exemplu raportul CL/CW la *V. ammodytes* este mult mai scăzut față de *V. berus*) (Fig. 60, 61).

Comparând distribuția actuală a speciilor descrise cu ocurențele lor fosile se conturează arealul lor de răspândire în decursul neogenului. Astfel distribuția actuală a lui *Coronella austriaca*, *Elaphe longissima*, *Natrix natrix*, *N. tesselata* şi *Vipera berus* practic se suprapune cu ocurențele fosile. În schimb în cazul speciilor mediteraneene (*Coluber viridiflavus*, *C. gemonensis*, *Elaphe quatuorlineata*, *Telescopus fallax* şi Scolecophidia indet.) distribuția lor în trecut era complet diferită de cea actuală. *Coluber viridiflavus* este singura specie vest europeană, care în timpul pliocenului şi pleistocenului inferior a avut o prezență largă şi în Europa Centrală şi de Est, răspândirea lui actuală fiind redusă doar la partea de sud-vest a continentului. Distribuția lui *Elaphe quatuorlineata*, *Coluber gemonensis*, *Telescopus fallax* şi probabil a lui *Typhlops vermicularis* era mult mai largă în timpul neogenului şi la începutul cuaternarului, față de răspândirea lor actuală. La *Vipera ammodytes* limita nordică a arealului actual de distribuție se află cam la 100 km sud de Betfia (singura localitate de unde a fost descris din pleistocenul inferior). Perioada decisivă în formarea faunelor actuale era cuaternarul. Oscilațiile climatice, care au devenit destul de frecvente încă din pliocenul superior, au produs transformări majore şi în compoziția faunelor de ofidieni. Astfel marea majoritate a speciilor termofile s-au retras înspre sud iar altele au dispărut complet.

În schimbările faunistice pot fi delimitate trei etape majore, care în linii mari corespund cu diviziunea generală a cuaternarului: 1. Etapa faunelor de ofidieni pleistocene inferioare (Bihariene); 2. Etapa faunelor de ofidieni pleistocene superioare (Toringiene); 3. Etapa faunelor de ofidieni holocene. În prima etapă faunele sunt încă destul de diversificate, având în compoziția lor cel puțin 1-2 specii mediteraneene. Aici pot fi incluse toate faunele din cadrul complexului faunistic Betfia (în afara punctului fosilifer Betfia 13, aceasta având o vârstă Villafranchiană) şi Subpiatră (Fig. 63-68 şi 71, 72). În decursul acestei etape pe lângă fluctuațiile climatice evidente (reflectate şi în compoziția faunistică: ex. în fauna de la Betfia 9/B predomină elementele de stepă, iar în cea de la Betfia 9/C elementele de pădure), tendința generală era o continuă scădere a temperaturii medii anuale. În fauna de la Subpiatră singurul element mediteranean era *Coluber viridiflavus*, iar în straturile superioare de la Betfia 7 nu mai găsim nici o urmă a speciei respective. În etapa faunelor Toringiene din compoziția faunistică lipsesc speciile mediteraneene, dar de regulă sunt prezente 1-2 specii termofile paramediteraneene (*Elaphe longissima* şi/sau *Natrix tesselata*). Aici pot fi încadrate faunele de la Chişcău 3 şi Râpa (Fig. 69-72). Faunele de ofidieni de vârstă holocenă (ex. Vadu Crişului, Valea Morii, Galoşpetreu) sunt oarecum similare cu cele actuale, cu o compoziție mai puțin diversificată. Compoziția faunei actuale reflectă o uşoară ameliorare climatică, cu toate că elementele euriterme (*Coronella austriaca*, *Natrix natrix* şi *Vipera berus*) au o răspândire mai largă, față de elementele termofile para-mediteraneene (*Elaphe longissima* şi *Natrix tesselata*). Trebuie menționat şi faptul, că faunele de ofidieni de vârstă pleistocenă din siturile de mai sus în bună parte s-au depozitat în perioade interglaciare, când procesele de acumulare a sedimentelor erau mult mai intense decât în cele glaciare. În schimb se poate presupune că cel puțin trei specii de ofidieni ("trioul rece", format din *Coronella austriaca*, *Natrix natrix* şi *Vipera berus*) au supraviețuit în zonă şi în cadrul celor mai aspre condiții climatice.