A REVIEW OF NEOGENE AND QUATERNARY SNAKES OF CENTRAL AND EASTERN EUROPE. PART I: SCOLECOPHIDIA, BOIDAE, COLUBRINAE

Z. Szyndlar *

RESUMEN


Palabras clave: Serpentes, Scolecophidia, Boidae, Colubridae, Europa, Taxonomía, Paleofaunística, Morfología.

ABSTRACT


Key words: Serpentes, Scolecophidia, Boidae, Colubridae, Europe, Taxonomy, Paleofaunics, Morfology.

Introduction

The present study, consisting of two separate parts including this paper and the subsequent one (Szyndlar, in press), is devoted to fossil snakes found in the strip of Europe lying between the Baltic and Aegean Seas, hereafter referred to as Central and East Europe. The discussed fossils are of Neogene and Quaternary age. Contrary to the situation in West Europe, pre-Miocene snakes have never been reported from the area *. Although snake remains have been quite often found in fossil materials from

* Perhaps excepting for two Cretaceous fossils from Yugoslavia, Pachyophis woodwardi Nopcsa, 1923, and Metophis nopcsai Bolkay, 1925. Identification of these finds as snakes cannot, how­ever, be demonstrated with confidence (cf. Rage, 1987).

* Polish Academy of Sciences. Institute of Systematics and Evolution of Animals. Slawkowska 17, 31-016 Kraków, Poland.
Central and East European sites, most of them were rarely identified below subordinal level or described in detail. For example, a recent catalogue of Pleistocene vertebrate faunas from Hungary compiled by Jánossy (1986) lists 38 localities yielding snake remains. Materials from almost one third of the numbered sites were defined as either «abundant» or «common» or they counted thousands of bones. Of them, however, only the fossils from Villány 3 were identified to specific level (after Kretzoi, 1956; see below), while those from the remaining 37 localities were defined as «Ophidia indet.».

History of research

The history of previous studies of fossil snakes from Central and East Europe is brief. The first fossil snake described from the area was Coluber podolicus, found in Ukraine (von Meyer, 1844). Two other forms reported in the nineteenth century were Laophis crotaloides and Python euboicus; both described from the Miocene of Greece by Owen (1857) and Roemer (1870), respectively. According to Rage (1984), all these three snakes are nomina dubia.

Few next researches, resumed after forty years, were restricted to the area of Austro-Hungarian Empire (Kormos, 1911; Bolkay, 1913). Although somewhat surprising, the results included in Bolkay’s papers have not lost their value, because until almost the present time they have often been cited, especially by herpetologists not familiar with paleontology, as the only source of information on Central European Neogene snakes. In part it perhaps resulted from the fact that Bolkay’s paper was written in English, while most publications from the area were in German. A similar opinion can be addressed to the paper of von Szunyogh (1932); it has become famous not on account of its paleontological contents, but for a long time it has served as a useful key for determining fossil remains of modern snakes.

No other papers devoted to Central and East European fossil snakes were published prior to the early 1950s. Since that date, a number of papers were published in several Central European countries. Of them, Poland was the only country where the research on fossil snakes was undertaken on a larger scale, thanks to studies initiated by Młynarski (1960, and further papers) in the beginning of the 1960s. Few works with reference to other countries were published (see chapter «Localities» for full account). Among these papers, especially noteworthy is the work of Rabeder (1977), providing much data on the Pleistocene snake fauna of Austria. According to my best knowledge, fossil snakes have never been reported from Albania and Yugoslavia.

Prior to the beginning of the 1980s our knowledge on extinct snakes from the area was rather limited. It is to be noted that of more than forty papers devoted to Central and East European ophidian paleontology (i.e., those in which fossils were identified to generic level at least), about half were published after 1980. Most recent publications are those of Szyndlar, Zerova, and their co-authors (Szyndlar, 1984; Zerova et al., 1987, and other papers). Studies of Zerova are especially noteworthy because they cover the southwestern Soviet Union, an area unexplored since the time of von Meyer (1844).

Contents

In the present work I attempt to summarize all up-to-date knowledge about Central and East European fossil snakes. Fossils previously described in the literature as well as those hitherto not reported are considered. An overwhelming part of the discussed fossils have been personally examined; those unstudied are usually either of little importance or are lost. The only important collection not examined by me is the classical material of Bolkay (1913). Unfortunately, I have not received access to this collection; opinions referred to it in the following text are then exclusively based on Bolkay’s descriptions and illustrations.

Morphological descriptions included in this paper are rather parsimonious and they are focused mainly on ophidian vertebrae. Throughout the text they are, however, accompanied by references to the literature containing more detailed osteological descriptions of both living and fossil snakes. Despite these limitations, the chapters entitled «Systematic account», included in both parts of this study and containing descriptions of particular taxa and comments on their taxonomic status, are extensive enough. These chapters may be thought as reference-texts for ophidian paleontologists. The chapter «History of snakes in Central and East Europe», included in the subsequent part of this study (Szyndlar, 1991), summarizes the entire information about the composition and past distribution of the extinct snake fauna in the area, against the background of the recent fauna; this chapter is addressed to both paleoherpetologists and neoherpetologists.

Abbreviations of institutions housing the fossil collections

DPFNSP: Department of Paleontology of Charles University, Prague.
IZAN: Department of Paleozoology of the Institute of Zoology of the Academy of Sciences of Ukrainian SSR, Kiev.
IZBAN: Institute of Zoology of the Bulgarian Academy of Sciences, Sofia.

MHGI: Museum of the Hungarian Geological Institute, Budapest.

MNCN: Museo Nacional de Ciencias Naturales, Madrid.


SMF: Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main.

TGP: Tiraspol State Normal School.

UGUI: Geological Institute of Utrecht University.


ZPPAN: Institut of Paleozoology of the Polish Academy of Sciences, Warszawa.

ZPUW: Institut of Paleozoology of Wrocław University.

ZZSiD: Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences, Kraków.

**Localities**

Of more than one hundred fossil snake localities covered by the present study, collections from 92 sites were examined personally by the author. Of all the sites considered, seventy altogether are discussed in detail below. A number of upper Pliocene and Pleistocene localities of Poland and Ukraine, represented exclusively by living snake species occurring at present in these areas, are considered jointly throughout the text. Detailed descriptions of the Polish Pleistocene ophidian fauna can be found in Szyndlar (1984), while most upper Pliocene and Pleistocene snakes of Ukraine are currently being studied by Zerova (in prep.).

Below, the column «Localities» lists the sites from which fossil materials were discussed in the text. All these sites are mapped on figure 1. For Neogene localities, the European Land Mammal Ages (Fahlbusch, 1976) and Mammal Zones (Mein, 1975) are given. The zone MN 17 is regarded, according to currently accepted views, as uppermost Pliocene. References to dating of the localities are placed at the beginning of the column; in cases for which no papers are cited, information on their age comes from the articles listed in the column «References».

The column «References» lists papers devoted to local snake faunas, both detailed descriptions and short mentions, if such papers exist.

The column «Material examined» lists fossils studied by the author and indicates their repository.

**Poland**

Localities: The fossil sites listed below are exclusively of Neogene age. Younger localities, when they are mentioned in the present paper, are generally referred to as «Polish Pleistocene». All the sites discussed here were listed and briefly described by Szyndlar (1984). Dating of the localities follows Nadachowski et al. (1989):

1. Przeworsko 2 (upper Orleanian/middle Astartacian; MN 5-7).
2. Opole 2 (middle Astartacian; MN 7).
3. Podlesice (lower Ruscinian; MN 14).
4. Węże 1 (upper Ruscinian; MN 15).
5. Węże 2 (lower Villanyian; MN 16).
6. Rębielice Królewska 1A (Villanyian; MN 16).
7. Rębielice Królewska 2 (lower Villanyian; MN 16).
8. Mała Cave (age uncertain) *.

References: The basic and most up-to-date source of information on fossil snakes from Polish localities is the monograph by Szyndlar (1984); it also contains a critical review of all previous publications dealing with the subject. Of the two other papers published after 1984, i.e., Szyndlar in Mynarski et al. (1985) and Rage and Szyndlar (1986), the former merely repeats some information included in Szyndlar (1984), while the latter brings some new knowledge about *Natrix longivertebrata* from the Polish Pliocene.

Material examined: all specimens (ZZSiD, ZPUW, ZPPAN).

* The age of the layers 4 + 5 of Mala Cave, bearing remains of micromammals, was originally recognized as «Early (Turolian, Pannonian or Pontian) or Middle Pliocene» by Sulimski et al. (1979). The age of other strata of this site, especially the snake-bearing layers 7 + 8, was not discussed in the text of the above paper, however, in the accompanying Polish summary, it was stated that «sediments lying above the layers 7 + 9 are of considerably younger age» (ibidem, pág. 402). In a more recent paper of Gązek and Szymkiewicz (1987), the age of vertebrates found in the layers 7-22 is estimated as late Pleistocene.

**USSR: Ukraine**

Localities: The following list contains Neogene localities only. Most upper Pliocene sites (Kryzhanovka, lower layer; Bezimenko; Bolshaya Kamyshvah; Cherevchnica, middle layer) and uppermost Pliocene sites (Morskoy; Zhevatara Gora, upper layer; Kairy; Kryzhanovka, upper layer; Tarbantuk; Nogaysk; Cherevchnica, upper layer) are referred jointly to as «Ukrainian upper Pliocene»; all Pleistocene localities (Luzanovka; Bol’shevik; Tihonovka; Tihonovka 2; Morozovka; Ozernoie) are referred jointly to as «Ukrainian Pleistocene». The age of the below listed localities follows Zerova (1987):

1. Gritsev (lower Vallesian; MN 9).
2. Novoelizabetovka, lower layer (lower Turolian; MN 11).
3. Novoelizabetovka, lower layer (lower Turolian; MN 11).
4. Novaya Emcevka (middle Turolian; MN 12).
5. Cherevchnica, lower layer (middle Turolian; MN 12).
6. Bielka (middle Turolian; MN 12).
7. Novoelizabetovka, upper layer (middle Turolian; MN 12).
8. Novourainka 1 (upper Turolian; MN 13).
9. Andreievska (upper Turolian; MN 13).
10. Frunzovka 2 (upper Turolian; MN 13).
11. Kuchurgan was described by Zerova (in Zerova et al., 1990) and elapid remains from Gritsev were described by the same authors (Szyndlar and Zerova, 1990).
12. Kotlovina, lower layer (lower Ruscinian; MN 15).
13. Kotlovina, middle and upper layer (lower Villanyian; MN 16).
15. Ukrainian upper Pliocene.
16. Ukrainian Pleistocene.

**USSR: Moldavia**

Localities:

1. Kalfa (lower Vallesian; MN 9).
2. Buzhor (Vallesian; MN 9 or 10).
3. Etulnya (upper Ruscinian; MN 15).
(29) Lucheshty (upper Ruscinian; MN 15).
(30) Valeny (upper Ruscinian; MN 15).
(31) Musait (upper Ruscinian; MN 15).
(32) Dermendzhi (upper Ruscinian; MN 15).
(33) Novy Tanatary (lower Villanyian; MN 16).
(34) Salchikya (lower Villanyian; MN 16).
(35) Chishimkicow (lower Villanyian; MN 16).
(36) Bachoy (lower Villanyian; MN 16).

References: The only detailed description from the area concerns a new species of *Vipera* from Kalfa (Chkhikvadze and Lungu, in Zerova et al., 1987). Moreover, Redkozubov (1987) listed snake faunas of several Pliocene localities. Some short notes on snakes remains from the Moldavian Neogene can be also found in papers of Chkhikvadze and Lungu (1973, 1984), David et al. (1988), and Redkozubov (1982, 1989).

Material examined: none.

Czechoslovakia

Localities:
(37) Dolnice (middle Orleanian; MN 4).

References: The only snake materials described in detail come from the above two localities. Natricine remains from Dolnice were studied by Rage and Roček (1983); a description of the remaining snake material can be also found in papers of Chkhikvadze and Lungu (1973, 1984), David et al. (1988), and Redkozubov (1982, 1989).

Material examined: the available material from Dolnice (DPFNSP) and a part of the material from Děvínška Nová Ves (DPFNSP), other than that studied by Wettstein-Westersheim (1955) (NMW).

Austria

Localities:
(39) Vösendorf (upper Vallesian; MN 10).
(40) Kohfidisch (lower Turolian; MN 11).
(41) Bad Deutsch Altenburg 20 (lower Villanyian; MN 16).
(42) Bad Deutsch Altenburg 2 (middle Pleistocene).
(43) St. Margarethen (middle Pleistocene).

References: Detailed descriptions of local snake faunas were given for Kohfidisch (Bachmayer and Syndlar, 1985, 1987; Syndlar and Zerova, 1990) and for St. Margarethen (Rabeder, 1977). Rabeder (1974) and Mais and Rabeder (1977) gave a preliminary list of snake assemblages from two other sites, Bad Deutsch Altenburg 2 and Bad Deutsch Altenburg 20, respectively. A detailed description of snakes from the latter locality is under preparation (Syndlar and Rabeder, in prep.).

The only mention concerning snakes from the oldest Austrian locality, Vösendorf, deals with remains incorrectly identified as aniliids (Papp et al., 1954).

Material examined: the whole material from Kohfidisch (NMW) and from Bad Deutsch Altenburg 20 (UWPI).

Hungary

(46) Beremend 1 [= Beremend of Bolkay (1913) and of von Szunyoghi (1932)] (lower Villanyian; MN 16).

(47) Villány 3 [= Villány of Bolkay (1913) and Kalkberg near Villány of von Szunyoghi (1932)] (upper Villanyian; MN 17).
(48) Nagyharsány-hegy (upper Villanyian; MN 17).
(49) Villány 6 (upper Villanyian; MN 17).
(50) Csanádta 4 (lower Pleistocene).
(51) Beremend 4 (lower Pleistocene).

References: Although Hungary possesses perhaps the highest number of snake-bearing sites in Central and East Europe, ophidian fossils were identified to generic or specific level in four papers only. In the first of them, Kormos (1911) recognized (erroneously) two snake genera in the material from Polgárdi. Bolkay (1913) described cranial remains of seven snake taxa from Polgárdi, Beremend 1, Nagyharsány-hegy and Villány 3; most of the Bolkay's material (with addition of a few new fossils) was then critically commented by von Szunyoghi (1932). Kreutzl (1956) listed three snake species from Beremend 4, and Villány 3 and 6.

Material examined: from Polgárdi (MHGI), Villány 3 and 6, Beremend 1 and Csanádta 4 (ZZSiD). The examined collections are different from those described in the Hungarian classical papers (partly MHGI), partly probably lost.

Romania

Localities:
(52) Befii (Puşşó-project of Somolyó-hegy of Bolkay (1913) and von Szunyoghi (1932)] (lower Pleistocene).
(53) Braşov (Brassó of Bolkay (1913) and von Szunyoghi (1932)] (middle Pleistocene).

References: The previously cited papers devoted to Hungarian snakes (Bolkay, 1913, and von Szunyoghi, 1932) covered also few fossils from the above listed sites, presently belonging to the territory of Romania. No new snake material has been reported from this country.

Material examined: none.

Bulgaria

Localities: Age of the following sites was given after Thomas et al. (1986), Popov (1988; and pers. comm., 1986), and Mýnarski (1982), respectively:
(54) Dorkovo (lower Ruscinian; MN 14).
(55) Varbeshtsitsa (middle Pleistocene).
(56) Stoilovo (late Pleistocene).
(57) Bacho Kiro (late Pleistocene).

References: The only hitherto described snake material comes from the archeological site of Bacho Kiro (Mýnarski, 1982); moreover, remains of a *Natrix* from Dorkovo were mentioned by Thomas et al. (1986).

Material examined: whole specimens (IZBAN and ZZSiD) except for that from Dorkovo.

Greece

Localities: The age of most of the following sites is given after Armour-Brown et al. (1977), de Bruijn (1976, and pers. comm., 1985), de Bruijn and van den Meulen (1975, 1979), Mayhew (1977), Symeonidis and Vos (1977), and other papers:
(58) Kymi (lower Miocene; MN ?).
(59) Pikermi 4 (middle or upper Turolian; MN 12 or 13).
(60) Maramena 1 (upper Turolian; MN 13).
(61) Ato Metochi 2 (upper Turolian; MN 13).
(62) Karabourni (upper Turolian or lower Ruscinian; MN 13 or 14).
(63) Maritsa (lower Ruscinian; MN 14).
References: The only four literature items concerning fossil snakes of the area are descriptions of a viperid and a python from the Greek Miocene, by Owen (1857) and Roemer (1870), respectively, as well as Schneider's (1975) study on the herpetofauna of Chios; the most recent publication is a short description of elapid remains from Tourkobounia 1 by Szyndlar and Zerova (1990).

Material examined: whole (UUGI) except for the fossils from Chios (SMF). The materials from Kimi and Karabournu, described by Roemer (1870) and Owen (1857), were probably lost (fide Rage, 1984).

Systematic account

This chapter summarizes basic data on snake fossils available from the discussed area; throughout the text, information about particular ophidian taxa is always arranged in the same format.

Information about fossil collections, their systematic identification, localities, and geological age are presented separately for each different taxon. When possible, the entire fossil material is listed in detail and followed by catalogue numbers. Unless the discussed collection is catalogued, only an abbreviated name of its repository is given. In cases when the material was previously described in any form, appropriate references and synonymy are cited; synonyms concern exclusively fossils coming from the discussed area. It is always indicated unless the material was seen only by the author. If fossils referred to the same taxa were recorded from more than one locality, they are listed in chronological order and each site is provided with a serial number concordant with those given in the chapter «Localities» and mapped on figure 1; both synonyms and comments concerning fossils from particular localities (in the column «Remarks») are then preceded by an appropriate serial number.

It should be stressed that all taxonomic re-allocation given in the present work refer almost exclusively to the fossils personally examined by me or, in a few cases, to those non-examined fossils for which descriptions given in the literature were sufficiently adequate. No changes were proposed in reference to those fossils quoted in the literature which were not described, not figured or described in an unsatisfactory manner. In most doubtful cases, however, critical comments are expressed in the column «Remarks» accompanying each taxon.

The usage of the qualifiers «cf.» follows Estes (1987). The qualifiers generally refer to structural similarities but sometimes they are also used on account of stratigraphic or geographical reasons.

Diagnostics of particular taxa are brief and they intend to indicate the most important differentiating features of vertebrae; there are also added references to the literature containing more detailed descriptions. Because one of the major purposes of the present paper is to serve as a guide to the East European fossils, it includes drawings of most species found in the area. Considering that the overwhelming majority of ophidian remains found wherever in fossil sites are vertebrae, the illustrations are almost exclusively of these elements.

Suborder SCOLECO-PHIDIA Duméril et Bibron, 1844.

Hitherto known fossil remains of scolecophidians are restricted to precaudal vertebrae. Because of the simple morphology of the vertebrae and of a great similarity of these elements even in members of different families, identification below the subordinal level is usually regarded as an impossible task. Scolecophidian vertebrae are of minute size, about 2 mm long or smaller, devoid of neural spines and hypapophyses, with undivided paradiapophyses, and have strongly flattened cotyles and condyles.

Scolecodinia indet. (fig. 2).

Suborder SCOLECO-PHIDIA Duméril et Bibron, 1844.

Hitherto known fossil remains of scolecophidians are restricted to precaudal vertebrae. Because of the simple morphology of the vertebrae and of a great similarity of these elements even in members of different families, identification below the subordinal level is usually regarded as an impossible task. Scolecophidian vertebrae are of minute size, about 2 mm long or smaller, devoid of neural spines and hypapophyses, with undivided paradiapophyses, and have strongly flattened cotyles and condyles.

Scolecodinia indet. (fig. 2).

Material: (37) Lower Miocene (MN 4) of Dolcine: one vertebra (DPFNSP 1316). (10) Late Miocene (MN 9) of Grisiev: one vertebr (IZAN). (14) Upper Miocene (MN 12) of Cherevichnoie (lower layer): one vertebra (IZAN 45-6018). (63) Early Pliocene (MN 14) of Maritsa: 2 vertebrae. (64) Upper Miocene (MN 16) of Tourkobounia 1: 5 vertebrae (UUGI). (65) Middle Pleistocene of Tourkobounia 2: 3 vertebrae (UUGI). (66) Late Miocene of Tourkobounia 3: 2 vertebrae (UUGI).

Remarks: Except for the scolecophilidan from Dolcine (37), characterized by a different morphology of the zygosphenal roof (Szyndlar, 1987), the remaining above listed fossils do not differ both from one another or from the living European species, Typhlops vermicularis. It is highly probable, especially with refe-

Fig. 2.—Trunk vertebrae of Scolecophidia indet., in dorsal view, from: A: lower Miocene of Dolcine (DPFNSP 1316); B: early Pliocene of Maritsa (UUGI); C and D: upper Pliocene of Tourkobounia 1; E: middle Pleistocene of Tourkobounia 2; F: middle Pleistocene of Tourkobounia 3. Scale equals 2 mm.
ence to the remains coming from youngest sites, that they belonged to *T. vermicularis* or to a closely related taxon. This opinion, however, cannot be demonstrated with confidence.

Suborder ALETHINOPHIDIA Nopcsa, 1923.
Family BOIDAE Gray, 1825.
Subfamily Boinae Gray, 1825.

Genus *Python* Daudin, 1803.*

* Python euboicus Roemer, 1870.*

1870 *Python Euboicus* Roemer, p. 588, pl. XIII.
1880 *Heteropython euboicus* F. Roem.: de Rochebrune, p. 290.
1984 *Python euboicus* Roemer: Rage, p. 33.

Remarks: *Python euboicus*, described by Roemer (1870) from the lower Miocene of Kimi (Euboea, Greece) (58), is the only known fossil from Central and East Europe referred to the subfamily Boinae. Rage (1984) considered this (probably lost) fossil *a nomen dubium*. Based on Roemer’s description and figure (supra cit., pl. XIII), it can be stated that the discussed remains belonged indeed to a boid snake but not necessarily to a member of the subfamily Boinae. I thus agree with Rage’s opinion that the original description of *Python euboicus* is inadequate and little can be said about the diagnostic characters of the species.

Subfamily Erycinae Bonaparte, 1831.

Erycine snakes are characterized by highly complicated morphology of their caudal vertebrae and most diagnoses have been based on these elements. Precaudal vertebrae, as characteristic for most boid snakes, are always relatively very short (i.e., their centra are wider than long) and have reduced prezygapophyseal processes. Cranial elements have not been found in Central and East European fossil sites.

Genus *Bransateryx* Hoffstetter et Rage, 1972.

The type species of this extinct genus, *Bransateryx vireti*, was described from the Upper Oligocene and Lower Miocene of West Europe by Hoffstetter and Rage (1972). The diagnosis of the genus was then shortly summarized by Rage (1984: 24): the palatine retaining a medial process, the posterior caudal vertebrae high, very short, and provided with several complex additional processes. It should be noted, however, that homologous vertebrae of the living species *Eryx johni* from southern Asia may display a similar morphology.

*Bransateryx septentrionalis* Szyndlar, 1987 (fig. 3).

1987 *Bransateryx septentrionalis* Szyndlar, pp. 56-59, fig. 2.

Material: (37) Lower Miocene (MN 4) of Dolnice (type locality): 5 precaudal vertebrae (DPFNSP 3916, 3990, 4528, 4556, 4557), one caudal vertebra (holotype, DPFNSP 4555).

Diagnostic vertebral characters: The posterior caudal vertebrae of *Bransateryx septentrionalis* differ from those of the type species by having, among other characters, a spherical neural spine longer, pterapophyses, distinct subcotylar tubercles, and hypapophyses with strong lateral processes. Trunk vertebrae differ from those of the type species by having a zygosphene with three lobes in dorsal view (and not concave). The centrum length of trunk vertebrae ranges between 3.45 and 3.90 mm. For a more detailed description see Szyndlar (1987).

Remarks: This species displays morphology intermediate between that of *B. vireti* from the French Miocene and the living genus *Channa* from North America; perhaps both genera represented the same evolutionary lineage (Szyndlar, 1987) or even they should be synonymized.

*Bransateryx* sp.

1990 *Bransateryx* sp.: Szyndlar and Zerova, p. 54.

---

![Fig. 3. Vertebral Characters of Bransateryx septentrionalis from Lower Miocene of Dolnice. A and B: posterior caudal vertebra (holotype, DPFNSP 4555); C and D: anterior caudal vertebra (DPFNSP 4003); E: trunk vertebra (DPFNSP 4556); F and G: trunk vertebra (DPFNSP 4557).](image-url)

Material: (10) Lower Miocene (MN 9) of Grislev: trunk and caudal vertebrae (IZAN).

Remarks: This snake, apparently a distinct species, is currently being studied by Zerova (in prep.).


The type species of this extinct genus, *Albaneryx depereti*, was described from the French Middle Miocene by Hoffstetter and Rage (1972); the generic diagnosis was then briefly summarized by Rage (1984: 23). The caudal vertebrae, not shortened and devoid of additional processes, resemble those of the living genus *Lichanura* of North America. Zerova (1989: 30) recently extended a diagnosis of the genus *Albaneryx*, stating, among others, that posterior caudal vertebrae have «relatively long centra (...); the zygosphene [is] lacking; of additional processes [they] only possess small pterapophyses on the posterior surface of the neural canal; neural spine high, bifurcated towards the upper end and showing a flat plate on the top».

*Albaneryx volynicus* Zerova, 1989 (fig. 4).


Material: (10) Late Miocene (MN 9) of Grislev: trunk and caudal vertebrae (IZAN).


The type species of this extinct genus, *Albaneryx depereti*, was described from the French Middle Miocene by Hoffstetter and Rage (1972); the generic diagnosis was then briefly summarized by Rage (1984: 23). The caudal vertebrae, not shortened and devoid of additional processes, resemble those of the living genus *Lichanura* of North America. Zerova (1989: 30) recently extended a diagnosis of the genus *Albaneryx*, stating, among others, that posterior caudal vertebrae have «relatively long centra (...); the zygosphene [is] lacking; of additional processes [they] only possess small pterapophyses on the posterior surface of the neural canal; neural spine high, bifurcated towards the upper end and showing a flat plate on the top».

*Albaneryx volynicus* Zerova, 1989 (fig. 4).


Material: (10) Late Miocene (MN 9) of Grislev: trunk and caudal vertebrae (IZAN).


The type species of this extinct genus, *Albaneryx depereti*, was described from the French Middle Miocene by Hoffstetter and Rage (1972); the generic diagnosis was then briefly summarized by Rage (1984: 23). The caudal vertebrae, not shortened and devoid of additional processes, resemble those of the living genus *Lichanura* of North America. Zerova (1989: 30) recently extended a diagnosis of the genus *Albaneryx*, stating, among others, that posterior caudal vertebrae have «relatively long centra (...); the zygosphene [is] lacking; of additional processes [they] only possess small pterapophyses on the posterior surface of the neural canal; neural spine high, bifurcated towards the upper end and showing a flat plate on the top».

*Albaneryx volynicus* Zerova, 1989 (fig. 4).


Material: (10) Late Miocene (MN 9) of Grislev: trunk and caudal vertebrae (IZAN).


The type species of this extinct genus, *Albaneryx depereti*, was described from the French Middle Miocene by Hoffstetter and Rage (1972); the generic diagnosis was then briefly summarized by Rage (1984: 23). The caudal vertebrae, not shortened and devoid of additional processes, resemble those of the living genus *Lichanura* of North America. Zerova (1989: 30) recently extended a diagnosis of the genus *Albaneryx*, stating, among others, that posterior caudal vertebrae have «relatively long centra (...); the zygosphene [is] lacking; of additional processes [they] only possess small pterapophyses on the posterior surface of the neural canal; neural spine high, bifurcated towards the upper end and showing a flat plate on the top».

*Albaneryx volynicus* Zerova, 1989 (fig. 4).

Vertebrae of *Albaneryx volynicus* from late Miocene of Gritsev. A and B: posterior caudal vertebra (holotype, IZAN 22-1089); C, D, E: trunk vertebra (IZAN 11-1091). A, C: anterior views; B, E: left lateral views; D: dorsal view. Each scale equals 2 mm.

2.45 mm (ibid., table). For a full diagnosis of this snake see Ze­roya (1989).

Genus *Gongylophis* Wagler, 1830.

This living genus, at present occurring on the Indian Peninsula, closely resembles *Eryx* and has often been synonymized with the latter. Generic distinction of *Gongylophis* was demonstrated by Rage (1972) and recently confirmed by Tokar’ (1989). Vertebrae of *Gongylophis* were briefly described by Rage (1972) and carefully figured by Hoffstetter and Rage (1972, fig. 4). There are only minor differences in morphology of isolated vertebrae of both genera. However, the posterior caudal vertebrae of *Gongylophis* have relatively low neural spines in comparison with *Eryx*, while its trunk vertebrae differ from all but one members of *Eryx* by presence of a distinct haemal keel. The only keel-bearing member of the latter genus, *Eryx colubrinus* from Africa, also has very low neural spines on its posterior caudal vertebrae. Thus, identification of fossil remains as members of *Eryx* is possible, when both trunk and posterior caudal vertebrae are available.

**cf. Gongylophis** sp. (fig. 5).

1987 cf. *Gongylophis* sp.: Szyndlar, pp. 59-60, fig. 4.

Material: (37) Lower Miocene (MN 4) of Dolnice: 14 precaudal vertebrae (DPFNSP 1147, 1148, 1157, 1158, 1159, 1167, 1489, 1490, 3921, 3922, 4005, 4084, 4533, 5270).

Remarks: The allocation of trunk vertebrae in the genus *Gongylophis* was based on a set of various features, most important of them the presence of a distinct haemal keel. The centrum length of the largest trunk vertebra is 6.22 mm. No caudal vertebrae of this snake have been found in Dolnice. For further details see Szyndlar (1987).

Genus *Eryx* Daudin, 1803.

Vertebrae of members of this genus were described and discussed in a number of works (e.g., Sood, 1941; Bogert, 1968, and others). Caudal vertebrae of *Eryx*, provided with additional processes, display a similar complex pattern as in *Charina* and *Bransateryx*; the neural spine of *Eryx* is, however, distinctly lower (except in *Eryx johni*; see above).

Genus *Eryx* Daudin, 1803.

**Eryx johni** (Linnaeus, 1758) (fig. 6). (70) 1975 *Eryx turcicus* (Olivier): Schneider, pp. 193 and 195, fig. 4.

Material: (70) Middle Pleistocene of Chios: (713) caudal vertebrae (SMF; not seen, fide Schneider, 1975). (73) Upper Quaternary of Pili B: 4 trunk vertebrae (UUGI).

Remarks: (70): There is no significant difference between the caudal vertebrae from Chios figured by Schneider (1975, fig. 4) and those of the living *Eryx jaculus* (i.e., *E. turcicus* of Schneider). (73): Also, no differences can be noted in regard to the trunk vertebrae from Pili B. Although the fossils were not compared with all living members of the genus *Eryx*, the probability is low that the discussed remains may have belonged to another species.

**Eryx jaculus** (Linnaeus, 1758) (fig. 6).

Material: (70) Middle Pleistocene of Chios: (713) caudal vertebrae (SMF; not seen, fide Schneider, 1975). (73) Upper Quaternary of Pili B: 4 trunk vertebrae (UUGI).

Remarks: (70): There is no significant difference between the caudal vertebrae from Chios figured by Schneider (1975, fig. 4) and those of the living *Eryx jaculus* (i.e., *E. turcicus* of Schneider). (73): Also, no differences can be noted in regard to the trunk vertebrae from Pili B. Although the fossils were not compared with all living members of the genus *Eryx*, the probability is low that the discussed remains may have belonged to another species.

**Eryx jaculus** (Linnaeus, 1758) (fig. 6).

Material: (70) Middle Pleistocene of Chios: (713) caudal vertebrae (SMF; not seen, fide Schneider, 1975). (73) Upper Quaternary of Pili B: 4 trunk vertebrae (UUGI).

Remarks: (70): There is no significant difference between the caudal vertebrae from Chios figured by Schneider (1975, fig. 4) and those of the living *Eryx jaculus* (i.e., *E. turcicus* of Schneider). (73): Also, no differences can be noted in regard to the trunk vertebrae from Pili B. Although the fossils were not compared with all living members of the genus *Eryx*, the probability is low that the discussed remains may have belonged to another species.

**Eryx jaculus** (Linnaeus, 1758) (fig. 6).

Material: (70) Middle Pleistocene of Chios: (713) caudal vertebrae (SMF; not seen, fide Schneider, 1975). (73) Upper Quaternary of Pili B: 4 trunk vertebrae (UUGI).

Remarks: (70): There is no significant difference between the caudal vertebrae from Chios figured by Schneider (1975, fig. 4) and those of the living *Eryx jaculus* (i.e., *E. turcicus* of Schneider). (73): Also, no differences can be noted in regard to the trunk vertebrae from Pili B. Although the fossils were not compared with all living members of the genus *Eryx*, the probability is low that the discussed remains may have belonged to another species.
Fig. 6.—Trunk vertebra of *Eryx jaculus* from upper Quaternary of Pili B (UUGI). A: dorsal view; B: left lateral view; C: ventral view; D: anterior view. Scale equals 2 mm.

Fig. 7.—Posterior caudal vertebra of cf. *Eryx* sp. from lower Pliocene of Maritsa (UUGI). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm.

than *E. jaculus*. The islands Chios and Kos (where Pili B is situated), are presently inhabited by this snake (Wettstein, 1953).

*Eryx* sp.

(21) 1987 Erycinae: Zerova, p. 15.
(22) 1987 Erycinae: Zerova, p. 16.


Remarks: Lack of haemal keels on the trunk vertebrae indicates that the remains belonged to the genus *Eryx*. The vertebrae from particular localities may have belonged to different species; interrelationships among them and living species are currently being studied by Zerova (in prep.), while fossils from Cherevichnoie (lower layer) (14) by Szyndlar and Zerova (in prep.). All the fossil sites are located outside the present range of the genus.

cf. *Eryx* sp. (fig.7)


Remarks: Because of scarcity and/or fragmentary nature of the available material the allocation of the vertebrae to the genus *Eryx* cannot be fully demonstrated; it is not unlikely that the vertebrae may have belonged to a *Gongylisplis*-like snake. The remains from particular localities presumably represent different species.

Erycinae indet.


Remarks: The only information provided by Redkozubov (1987: 71) is that the above listed localities yielded «... vertebrae of snakes of the subfamily Erycinae».

Family COLUBRIDA Oppel, 1811, sensu lato.

Traditionally, ophidian paleontologists have subdivided the Colubridae into two subfamilies, Colubrinae and Natricinae. The only criterion of this subdivision is, respectively, absence or presence of hypapophyses on postcervical thoracic vertebrae. Since this arrangement is, at least in part, inconsistent with snake systematics accepted by neoherpetologists, below I use these names in informal forms, i.e., as «colubrines» and «natricines».

«Colubrines».

Colubrine snakes are most abundant in post-Paleogene fossil materials. It is very easy to distinguish «colubrine» vertebrae, devoid of hypapophyses throughout the postcervical precaudal region of the column, from other advanced snakes, yet proper identification to the generic level is in most cases hazardous. For instance, it is impossible to separate overall two of the most common European genera, *Coluber* and *Elaphe*, based on vertebral characters, unless they are closely similar to particular living members of these genera. Proper taxonomic allocation, based on similarity to living species, is possible with reference to relatively young fossils, but this is not the case of geologically older snakes. Fortunately, there are distinct differences between most skull bones of *Coluber* and *Elaphe* (cf. Szyndlar, 1985, 1988), in this case the taxonomic position of fossil colubrine species described on the basis of both cranial and axial elements is usually well grounded.

Regarding vertebrae, subdivision of colubrine snakes into two informal groups (disregarding their generic allocation), namely «small-sized colubrines» and «large-sized colubrines», may facilitate taxonomic allocation of fossils (Szyndlar, 1984, fig. 6). The former group includes snakes with total length rarely exceeding 100 cm (usually much smaller); trunk vertebral centra seldom reach a length of 5 mm and the vertebrae are relatively elongate. The latter group includes snakes with total length often reaching 200 cm (sometimes even more); centra of large trunk vertebrae exceed a length of 6 mm (or more) and they are almost as long as wide. The large-sized colubrines comprise the following living species, presently inhabiting Central and East Europe: *Coluber caspius*, *C. viridisflavus*, *Elaphe longissima*, *E. quatuorlineata*, and *Malpolon monspessulanus*. The remaining species, belonging to the genera *Coluber*, *Coronella*, *Eirenis*, *Elaphe*, and *Telecopus*, represent the small-sized colubrine group.

The above remarks concern vertebrae of adult specimens. It
Fig. 8.—Comparison of mid-trunk vertebrae of some living species of small-sized colubrines, in dorsal, left lateral, and ventral views. A: *Coronella austriaca* (ZZSiD 17); B: *Coluber gemonensis* (ZZSiD 350); C: *Coluber rubriceps* (ZZSiD 310); D: *Elaphe situla* (ZZSiD 349); E: *Eirenis collaris* (BMNH 44.7.13.50); F: *Telescopus fallax* (ZZSiD 412).

should be noted that vertebrae belonging to juveniles of large colubrines are easily distinguished from those of adults of small colubrines, among others on the basis of a relatively much higher diameter of their neural canals.

Identification of vertebrae of large-sized colubrines is usually easier than in the case of smaller species. Apart from morphological features, proportions of trunk vertebrae (or, strictly speaking, proportions of the length and width of vertebral centra) may be helpful in the identification process; I caution other workers, however, that setting too much weight on numerical (instead of morphological) features may lead to serious errors.

Identification of vertebrae belonging to small-sized colubrines is an especially difficult task, on account of their very similar morphology. Figure 8 shows a set of trunk vertebrae of some small colubrine species in dorsal, lateral and ventral views; it can be seen from the drawing that all vertebrae except that of *Telescopus* display very similar morphological patterns. The only possible differentiating features are the shape of the zygosphenal roofs along with the length and shape of the prezygapophyseal processes. On account of intraspecific variation, however, these slight differences may be obscure and, in consequence, differentiation at even generic level may be impossible. This is the main reason that in my own identifications of colubrine species, based on vertebrae only, in most cases I use the qualifiers «cf.» before (and not after) generic names.

**Genus Texasophis** Holman, 1977.

Remains of this extinct genus, known exclusively from precaudal vertebrae, have been reported from the Oligocene and Miocene of North America and Europe; up to the present, five species of *Texasophis* have been described. The basic differentiating features of the genus, given by Holman (1977), are an elongated vertebral form, moderately vaulted neural arch, low neural spine, a very robust distinct haemal keel, and very distinct subcentral ridges. The taxonomic status of *Texasophis* was recently questioned by Zerova (1987: 13) who placed, without any additional comments, *Texasophis meini* (originally described from the French Miocene by Rage and Holman, 1984) into the modern genus *Boiga*. According to Zerova (pers. comm., 1989), her decision resulted from comparison of *Texasophis* with the living *Boiga trigonatum*. Indeed, the later species is closely similar (though not identical with) to *Texasophis meini*; on the other hand, another species of *Boiga* examined by me, namely *B. dendrophila* strongly differs in its vertebral morphology from both *B. trigonatum* and *Texasophis*.

**Texasophis bohemiacus** Szyndlar, 1987 (fig. 9).

1987 *Texasophis bohemiacus* Szyndlar, pp. 62-65, fig. 7.

Material: (37) Lower Miocene (MN 4) of Dolnice (type locality): one trunk vertebra (holotype, DPFNSP 1238), 4 other trunk vertebrae (DPFNSP 1239, 3927, 3947, 4025).

Diagnostic vertebral characters: This extinct species, known exclusively from the type locality, is most similar to *T. meini* from the French Miocene, but differs from the latter by having a much narrower haemal keel; it differs from most members of the genus by having the zygosphen (in dorsal view) straight rather than provided with three lobes. The centrum length of the holotype vertebra is 3.60 mm. For more detailed morphological description see Szyndlar (1987).

**Genus Zelceophis** Szyndlar, 1984.

**Zelceophis xenos** Szyndlar, 1984.

1984 *Zelceophis xenos* Szyndlar, pp. 38-40, fig. 12.

Material: (8) Mala Cave (age uncertain) (type locality): one trunk vertebra (holotype, ZPUW IZ-6/R/1).

Remarks: Description of this extinct, species was based on a single fragmentary vertebra only. The bone displays a set of very peculiar features not occurring among colubrine snakes, among others a relatively very short centrum and lack of paracotylar foramina; these features can be, however, pathologic in nature (Szyndlar, 1984). Considering both the absence of any additional material and the fact that the age of the fossil may be much younger than originally ascertained (cf. remarks to *Natrix parva*, Szyndlar, 1991) the taxonomic status of this snake is uncertain.

**Genus Coluber** Linnaeus, 1758.

Up to the present, about 17 fossil species referred to this modern genus were described, all but one from the European Paleo-
Fig. 9.—Trunk vertebra of *Texasophis bohemiacus* from lower Miocene of Dolnice (holotype, DFFNSP 1238). A: left lateral view; B: dorsal view; C: ventral view; D: anterior view; E: posterior view. Scale equals 2 mm. (From Szyndlar, 1987. Copyright 1987 by the Society of Vertebrate Paleontology. Used with permission.)

Fig. 10.—Trunk vertebra of *Coluber dolnicensis* from lower Miocene of Dolnice (holotype, DFFNSP 4558). A: left lateral view; B: dorsal view; C: ventral view; D: anterior view; E: posterior view. Scale equals 2 mm. (From Szyndlar, 1987. Copyright 1987 by the Society of Vertebrate Paleontology. Used with permission.)

Fig. 11.—Trunk vertebra of *Coluber planicarinatus* from upper Miocene of Kohfidisch (holotype, NMW 1984/97). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.
Fig. 12.—Trunk vertebra of *Coluber viridiflavus* from middle Pleistocene of Varbeshnitsa (IZBAN). A: left lateral view; B: ventral view; C: dorsal view. Scale equals 2 mm.

Fig. 13.—Trunk vertebra of *Coluber caspius* from middle Pleistocene of Varbeshnitsa (IZBAN). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.

Fig. 14.—Trunk vertebra of cf. *Coluber gemonensis* from late Pleistocene of Stoilovo (IZBAN). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.

Fig. 15.—Trunk vertebra of *Coronella austriaca* from Polish Pleistocene (ZZSiD KG-8050). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm. (From Szyndlar, 1984.)
gene and Neogene; five of them were recognized nomina dubia by Rage (1984). The referral of the overwhelming majority of these fossils to the genus Coluber cannot be demonstrated (!). It should be noted that some authors used the generic name Coluber not in the strict systematic meaning but rather as a symbol indicating a 'typical' colubrine snake.

Coluber dolnicensis Szyndlar, 1987 (fig. 10).

Material: (37) Lower Miocene (MN 4) of Dolnice (type locality): one compound (DPFNSP 310), one precaudal vertebra (holotype, DPFNSP 4558), another precaudal vertebra (DPFNSP 4559).

Diagnostic vertebral characters: Vertebræ of this extinct species, known exclusively from the type locality, resemble those of larger members of the living genera Coluber and Elaphe. The diapophysis occurs posterior to the parapophysis; the haemal keel does not reach the subcotylar rim (it forms a distinct step); the prezygapophyseal facets are obverse and somewhat shorter than the prezygapophyseal facets; the zygosphene is slightly convex (in the larger vertebra slightly concave) in dorsal view. The centrum length of the holotype vertebra is 7.56 mm and is 1.35 times longer than wide; the centrum of the larger vertebra is as long as wide. For more detailed morphological description see Szyndlar (1987).

Remarks: The decisive evidence for referring the fossil to the former genus is presence of a prominent supraangular crest on its compound bone; this feature being characteristic of Coluber and absent in Elaphe. C. dolnicensis is therefore the oldest fossil that may be referred with certainty to the genus Coluber.

Coluber planicarinatus (Bachmayer et Szyndlar, 1985) (fig. 11).
1985 Nanus planicarinatus Bachmayer et Szyndlar, pp. 84-87, fig. 1: 17-22, pl. 1: 4-6.
1987 Coluber planicarinatus (Bachmayer et Szyndlar): Bachmayer and Szyndlar, pp. 29-30, fig. 2, pl. 1: 3-4.

Material: (40) Upper Miocene (MN 11) of Kohfidisch (type locality): a basiparasphenoid (NMW 1986/5), one trunk vertebra (holotype, NMW 1984/97), six other trunk vertebrae (NMW 1984/102/1).

Diagnosis: Trunk vertebrae of C. planicarinatus differ from those of small-sized European colubrines by having a very broad and flat haemal keel and minute paradiapophyses. The neural spine is very low (three times longer than high); the prezygapophyseal processes are very short (more than twice as short as the prezygapophyseal facets); the zygosphene is slightly convex in dorsal view. The centrum length of the holotype vertebra is 4.03 mm and is 1.44 times longer than wide.

Remarks: This extinct species, known exclusively from the type locality, was originally described by Bachmayer and Szyndlar (1985) as a distinct fossil genus, Nanus, on the basis of a peculiar morphology of the trunk vertebrae. Discovery of a basiparasphenoid, referred to this snake and closely resembling those of the recent C. najadum-C. rubriceps group, caused removal of the fossil to the genus Coluber (Bachmayer and Szyndlar, 1987). The fossil snake is perhaps closely related to the above mentioned recent species but, considering scantiness of the available materials, it is not clear. For detailed morphological description see Bachmayer and Szyndlar (1985, 1987).

Coluber hungaricus (Bolkay, 1913).
1913 Zamenis hungaricus Bolkay, pp. 223-224, pl. XII: 3.
1939 Zamenis hungaricus Bolkay, p. 28.
1963 Coluber hungaricus Bolkay: Kuhn, p. 20.
1984 Coluber hungaricus (Bolkay): Rage, p. 44.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi (type locality): one quadrat (holotype, MHGI Ob-446/VI:76; not seen, fide Bolkay, 1913).

Remarks: Bolkay (1913: 223, 224) erected a new extinct species for the discussed quadrat because he was unable to «... identify it with the spp. of Zamenis occurring in our monarchy». Specific distinction of this fossil was questioned by von Szunyogh (1913) who recognized the quadrat as comparable with the living Zamenis dahli (i.e., Coluber najadum). Mlynarski (1961), although retaining von Szunyogh's allocation, observed that the quadrat is similar rather to that of Natrix. Rage (1984) then stated that the taxonomic status of the species is doubtful. Considering that a single quadrat is an insufficient basis for erecting a new colubrine species, I agree with Rage's opinion. There are no significant differences in morphology of quadrates belonging to at least three European small members of Coluber, namely C. najadum, C. rubriceps, and C. gemonensis. Perhaps distinction of C. hungaricus may be confirmed by detailed research of other remains coming from the type locality, including vertebrae, which have never been investigated by the Hungarian authors.

Coluber podolicus von Meyer, 1844.
1844 Tropidonotus podolicus von Meyer, p. 564.
1880 Petrops podolicus Meyer: de Rochebrune, p. 291.
1939 Coluber podolicus: van Meersbergh, Kuhn, p. 19.
1984 Coluber podolicus Meyer: Rage, p. 52.

Remarks: The vertebra from Bolyburince (23) on which von Meyer (1844) based his description of Coluber podolicus was lost. Considering that the description provided by von Meyer is inadequate, Rage (1984) considered this species a nomen dubium.

Coluber viridiflavus Lacépède, 1789 (fig. 12).
(46) 1932 Zamenis viridiflavus Lacép. var. carbonaria Bonap.: von Szunyogh, pp. 9 and 48-49, fig. 115.
(6) 1964 Coluber robertmertensi Mlynarski, pp. 331-332, figs. 9-12.
(43) 1977 Coluber viridiflavus Lacépède: Rabeder, pp. 86-91, figs. 9: 6, 11: 2, pl. 1: 1, 5, 7, 8, 10; pl. 2: 15, 16, 20, 22, 23.
(6) 1984 Coluber viridiflavus Mlynarski: Rage, p. 45.
[For full synonymy of this snake from Rębielice Królewskie 1A see Szyndlar, 1984: 53.]

tal fragments, 4 ectopterygoid fragments, 33 quadrates and quadrate fragments, 17 compounds (UWPI 2350/3-1-6), 64-73, 68-89, not seen; fide Rabeder, 1977). (55) Middle Pleistocene of Varbushtsia: 9 trunk vertebrae (IZAN).

Diagnostic vertebral characters: Trunk vertebrae can be differentiated from those of other large-sized European colubrines on the basis of a distinctly flattened and widening posteriorly haemal keel and a straight zygosphene in dorsal view (Szyndlar, 1984, fig. 6); in very large snakes, the zygosphenal roof is concave in dorsal view. The prezygapophyseal processes are relatively long (almost as long as the prezygapophyseal facets) and acute; the neural spine is slightly longer than high. The centrum length of 60 largest trunk vertebrae from Rebieliece Króliewskie 1A (C. robertmertensi) ranges between 6.67 and 8.64 mm and it is 1:17 (±0.05) times longer than wide on average (Szyndlar, 1984); in 65 vertebrae from Bad Deutsch Altenburg 20 it ranges between 4.88 and 6.48 mm and is 1:15 (±0.05) times longer than wide. In absolute size and proportions, they closely resemble trunk vertebrae of most East European large-sized colubrines.

Remarks: Remains of this living species were reported from numerous European fossil sites (cf. Szyndlar, 1984, for review) and most of these reports were based on cranial elements. It should be stressed that a number of skull bones of C. viridiflavus display a distinct morphology and may be easily differentiated from the homologous elements of other European members of Coluber and Elaphe. A detailed description of the skull of C. viridiflavus was done by von Szunyogh (1932: 18-19, 26-27, 31; figs. 31-36, 51, 63, 75, 88; fide: pp. 11-11, 12; pl. 6: 3, pl. VII: 2). Moreover, differentiating features of some skull bones, especially those of the braincase were discussed and figured by Rabeder (1977; figs. 3: 2, 4: 1, 5: 4, 6: 1, 7: 1, 8: 1, 9: 1, 10: 1, 11: 1, 12: 1). (43) Abundant cranial elements of this snake coming from two fossil localities, Rebieliece Króliewskie 1A and St. Margarethen, were described in detail and carefully figured by Rabeder (1977) and Szyndlar (1984), respectively.

(6) A few skull remains from Rebieliece Króliewskie 1A, closely resembling C. viridiflavus, were described by Mynarski (1977) as a distinct extinct species, C. robertmertensi. Numerous both cranial and axial elements from the same locality were then reported by Szyndlar (1984), who referred them to C. robertmertensi, Szyndlar (1984), following the opinion of Mynarski (1964), noticed close similarities between the fossil species and the living C. viridiflavus; the most important difference was, however, the absolute larger size of the former snake; moreover, some minor morphological differences were observed in the premaxilla, maxillae, and quadrates. Trunk vertebrae of C. robertmertensi differed from those of C. viridiflavus then available, apart from greater dimensions of the zygosphene and not straight zygosphere. Recent studies reveal, however, that all these differences are exclusively of allometric nature because morphology of bones belonging to smaller specimens of C. robertmertensi is consistent with that of C. viridiflavus. Therefore, the fossil species is here synonymized with the living C. viridiflavus. It should be noted that there are some minor osteological differences observed between the nominative subspecies from West Europe and C. viridiflavus carbonarius inhabiting, among others, northwesternmost Yugoslavia and southern Italy; the fossils from Rebieliece Króliewskie 1A are consistent with the latter subspecies. (46) The same similarities were previously pointed out by von Szunyogh (1932), with reference to cranial remains from Beremend 1.

(28) (30) (31) (35) (36) Redkozubov (1987), who referred some coluberid vertebrae from Moldavian sites to C. robertmertensi, provided neither description nor explanation of his decision.

It should be stressed that all fossil sites discussed here are located outside the present range of this snake.

cf. Coluber viridiflavus Lacépède, 1789.

(4) 1961 Coluber viridiflavus Lacépède; Coluber cf. viridiflavus Lacépède; Coluber sp.; Colubrinae indet.: Mynarski, pp. 10-12, pl. I-IV.


(7) 1977 Coluber sp.: Mynarski, p. 17.

(4) 1977 Coluber viridiflavus Lacépède; Mais and Rabeder, p. 85.


Material: (4) Middle Pliocene (MN 15) of Wećze 1: two maxillary fragments (ZZSiD WI-3, 10), one palatine fragment (ZZSiD WI-4), one pterygoid fragment (ZZSiD WI-2), 5 dentary fragments (ZZSiD WI-5, 9), one quadrate (ZZSiD WI-1), 542 precaudal vertebrae (ZZSiD WI-11, 53), 27 clavical and caudal vertebrae (ZZSiD WI-554, 580). (7) Upper Pliocene (MN 16) of Rebieliece Króliewskie 2: 57 precaudal and 3 caudal vertebrae (ZZSiD RK11-160). (41) Upper Pliocene (MN 16) of Bad Deutsch Altenburg 20: skull bones and vertebrae (UWPI). (42) Middle Pleistocene of Bad Deutsch Altenburg 2: compounds and palatines (UWPI; not seen, fide Rabeder, 1974).

Remarks: (4) (7) Remains from the Polish Pliocene differ in some details from C. viridiflavus; those vertebrae coming from these localities are of medium size, their zygosphenal roofs are often concave, moreover, a part of vertebrae from Wećze 1 does not possess flattened haemal keels.

(41) Abundant remains from Bad Deutsch Altenburg 20, consisting of numerous braincase bones, jaw elements and vertebrae, are currently being studied by Szynar and Rabeder (in prep.); it should be noted that although morphology of most bones is consistent with that of the living C. viridiflavus, haemal keels of a pre-vesting part of trunk vertebrae available for study are not (or weakly) flattened.

(42) Rabeder (1974) gave neither detailed description nor figures of the fossils from Bad Deutsch Altenburg 2; he only stated that in his determination he followed von Szunyogh (1932).

Coluber caspius Gmelin, 1789 (fig. 13).


(55) Middle Pleistocene of Várbushtsia: 4 trunk vertebrae (IZAN). (56) Late Pleistocene of Stylovo: 2 trunk vertebrae (IZAN).

Diagnostic vertebral characters: Trunk vertebrae of C. caspius are usually well differentiated from those of other large-sized European colubrines by the following features: the centra are distinctly elongated (cf. below); the zygosphere, even in smaller specimens, is concave in dorsal view; the haemal keel is distinctly high and sharp through most of its length. Its height diminishes immediately behind the cotyle rim and the keel becomes wider and flattened immediately before the condyle; the prezygapophyseal processes are relatively long (as long as the prezygapophyseal fa-
NEOGENE AND QUATERNARY SNAKES OF CENTRAL AND EASTERN EUROPE...

...and acute. Mid-trunk vertebrae of the following two living species, ZZZSD 262, 10 vertebrae measured; and ZZZSD 326, 30 vertebrae measured) have a centrum length of 5.86-6.01 mm (mean 5.90 ± 9.23) and 6.70-7.12 mm (mean 6.97 ± 0.11), respectively; the ratio centrum length/width is 1.36-1.42 (mean 1.39 ± 0.02) and 1.29-1.42 (mean 1.34 ± 3.68), respectively. It should be stressed that vertebrae of similar (and even smaller) absolute dimensions of other large-sized species of Coluber and of Elaphe usually have the centra only a little longer than that wide. Of few available fossil vertebrae, the largest one (from Varsheshtina) has the centrum length 6.55 mm; considering that C. caspius is the largest European snake, the absolute size of its vertebrae can be certainly much higher.

Remarks: Detailed morphological description of the skull of this living species (named by previous authors C. jugularis) was provided by von Szunyogh (1932: 18-19, 26-27, 31; figs 5-8, 27-30, 50, 62, 74, 89, 99; pl. III: 15, 16; pl. VI: 12; pl. VII: 4); Rabeder (1977; figs: 3, 5, 7, 30, 8, 3, 9, 8, 12; 4) discussed and figured differentiating features of some skull elements, while Szyndlar (1984, figs 2, 3) illustrated all isolated cranial bones of this snake. Most records of C. caspius from the area were based on cranial elements. (44) (45) (48) (52) (53) Nevertheless, some records from Hungarian and Romanian sites, based exclusively on compounds (von Szunyogh, 1932), are not credible and cannot be accepted. Of them, of special importance is the presumed presence of C. caspius in the Miocene of Polgárdi. This element is, however, very similar to those of some other species of the genus Coluber. For example, the known compound of C. dolichnus from the Czech Miocene (see above) closely resembles that of the living C. caspius, but there are significant differences between the vertebral morphology of both snakes. Unfortunately, von Szunyogh (1932) disregarded vertebrae throughout his study; the discussed compound necessitates a prompt re-examination and it is also necessary to examine vertebrae from Polgárdi in order to confirm or refute von Szunyogh's determination.

(41) Abundant fossil materials from Bad Deutsch Altenburg 20, consisting of numerous cranial elements and vertebrae, are currently being examined by Szyndlar and Rabeder (in prep.); the bones closely resemble those of the living C. caspius. Except for the Austrian and Romanian localities, all remaining fossil sites of C. caspius are located either within the present range of the species or in the close vicinity of it.

Coluber gemonensis (Laurenti, 1768) (fig. 14).

(34) 1977 Coluber gemonensis (Laurenti): Rabeder, p. 92, pl. 1: 12; pl. 2: 17.


Material: (28) Middle Pliocene (MN 15) of Etiulya: trunk vertebrae (not seen; fide Redkozubov, 1987). (29) Middle Pliocene (MN 15) of Lucheshty: trunk vertebrae (not seen; fide Redkozubov, 1987). (31) Middle Pliocene (MN 15) of Musait: trunk vertebrae (not seen; fide Redkozubov, 1987). (32) Upper Pliocene (MN 16) of Salchiva: trunk vertebrae (not seen; fide Redkozubov, 1987). (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen; fide Redkozubov, 1987). (34) Middle Pleistocene of St. Margarethen: 2 supraoccipitals, 2 basioccipitals (UWPI 2350/361-63, 66-67; not seen; fide Redkozubov, 1977). Diagnostic vertebral characters: Trunk vertebrae of this living species are characterized by a slightly convex (almost straight) zygosphene in dorsal view and by relatively long and acute prezygapophyseal processes; these are the only features differentiating C. gemonensis from most other small-sized colubrines. Vertebrae of C. gemonensis are closely similar to those of C. rubriceps, C. najadum, and Eirenis; it is then very difficult to discriminate properly from one another fossil remains of all these snakes. In a pictorial key placed in one of my previous papers (Szyndlar, 1984; fig. 6), I suggested that the main feature differentiating trunk vertebrae of C. gemonensis from other small-sized colubrines is the presence of a well-developed haemal keel, the structure being absent or weakly developed in the remaining small colubrines. Unfortunately, this statement, based on a limited comparative collection, was largely untrue; absence of the keel is characteristic for younger specimens, while in older examples of most small-sized colubrines the structure is usually clearly visible. Therefore, the haemal keel is not useful for identifying particular species. The centrum length of trunk vertebrae of cf. C. gemonensis from two Bulgarian sites (see below) ranges between 3.42 and 4.58 mm, while the ratio centrum length/width is between 1.29 and 1.50.

Remarks: (28) (29) (31) (33) (34) (35) The only finds of C. gemonensis, based exclusively on vertebrae, were reported by Redkozubov (1987, 1989) from six Moldavian sites. Unfortunately, this author provided neither description nor any other explanation of his decision.

(43) Rabeder (1977) based his report of C. gemonensis from St. Margarethen on two kinds of cranial bones. Of them, the basioccipitals only are clearly referable to C. gemonensis (ibid., pl. 1: 12), while the supraoccipital figured by Rabeder (ibid., pl. 2: 17) belonged most likely to C. caspius.

Detailed morphological description of the skull of C. gemonensis was provided by von Szunyogh (1932: 17-18, 27, 32; figs. 9-12, 37-40, 40, 61, 73, 90, 101; pl. IV: 19, 20; pl. VI: 2; pl. VII: 5); also Rabeder (1977; figs: 3, 4; 5, 3, 6; 2, 8, 2, 9, 7, 12: 2) discussed differentiating features of some skull elements of this snake.

cf. Coluber gemonensis (Laurenti, 1768).


Remarks: (41) (55) (56) A few vertebrae, belonging to small-size colubrines are most similar to those of the living C. gemonensis, but this allocation is not quite certain (cf. remarks for C. gemonensis, above).

(42) The basi-parasphenoid from Bad Deutsch Altenburg 2, figured by Rabeder (1974, fig. 4), resembles that of C. gemonensis in the presence of a vast frontal crest above the parasphenoid process; the disposition of openings of the Vidian canals is, however, somewhat different from the comparative material at hand.

Coluber sp.

(34) 1985 Coluber sp.: David et al., p. 73.


(28) 1987 Coluber sp.: Zerova, p. 16.


(10) 1990 Coluber sp.: Szyndlar and Zerova, p. 54.


Remarks: (10) The remains from Gritsev, owing to the presence of abundant cranial remains, belonged undoubtedly to a new extinct species of the genus Coluber. (24) Trunk vertebrae coming from some younger Ukrainian sites are comparable with a number of living species of the genus Coluber. All these fossils are currently being studied by Zerova (in prep.).


Genus Coronella Laurenti, 1768.
Coronella austriaca Laurenti, 1768.

(53) 1913 Coronella austriaca Laur.: Bolkay, p. 225, fig. 3.
(9) 1984 Coronella austriaca Laurenti: Szyndlar, pp. 102-105, figs. 41, 42.

[For full synonymy of C. austriaca from Polish sites see Szyndlar, 1984: 102.]


Coronella austriaca: (MN 16) of Bachoy: trunk vertebrae (not seen; fide Redkozubov, 1987).

Remarks: No comments on these finds were provided by Redkozubov (1987).

Coronella austriaca (Laurenti) [part]: Młynarski, p. 50.

Material: (55) Middle Pleistocene of Barbeshnitsa: 5 trunk vertebrae (IZBAN). (68) Middle Pleistocene of Tourkobounia 2: one trunk vertebra (UUGI). (57) Upper Quaternary of Pili B: two trunk vertebrae (ZZSiD). (73) Upper Quaternary of Pili B: one trunk vertebra (UUGI).

Remarks: Generic allocations of these vertebrae, usually strongly damaged, is not fully demonstrated.

Genus Elaphe Fitzinger, 1833.
Elaphe kohfidischi Bachmayer et Szyndlar, 1985. (fig. 16).

1987 Elaphe kohfidischi Bachmayer et Szyndlar: Bachmayer and Szyndlar, pp. 26-29, fig. 1, pl. 1: 1, 2.


Diagnostic vertebral characters: Trunk vertebrae of E. kohfidis-chi are characterized by a thin, high, spatulate-shaped haemal keel, with a characteristic «step» behind the cotylar rim; neural spine somewhat longer than high; zygapophyses straight or slightly convex (in small specimens) or slightly concave (in largest specimens); and moderately developed prezygapophyseal processes (shorter than the prezygapophyseal facets). The centrum length of 20 trunk vertebrae ranges between 5.83 and 7.31 mm. They are more elongate than those of most large-sized colubrines: the centrum length/width ratio is 1.18-1.45 (mean 1.29 ± 0.08).

Remarks: This extinct species, described on the basis of both cranial and axial elements, displays a number of features characteristic for the genus Elaphe, among others; the basipetrosphenoid processes reaching the lateral margins of the basiparasphenoid (condition unknown among members of Coluber except for C. viridiflavus); the prefrontal process of the maxilla slanting posteriorly (conditions restricted to the genus Elaphe). The basioccipital of E. kohfidischi, with a peculiar basioccipital crest, does not resemble those of other European colubrines. The vertebrae, however, in the opinion of Bachmayer and Szyndlar (1985) being closest to those of the living E. longissima and extinct E. paralongissima, are actually more similar to Coluber caspius, especially in their elongation, morphology of the haemal heel and the concave zygapophyseal (but this structure displays a different pattern of allometric variation than in the living C. caspius). The allocation of the remains to the genus Elaphe, although most probable, is not fully demonstrated. For more detailed morphological description of this snake see Bachmayer and Szyndlar (1985, 1987).


Material: (14) Upper Miocene (MN 12) of Cherevichnoie (lower layer): ca. 400 precaudal vertebrae (IZAN 45-5026).

Remarks: The vertebrae from Cherevichnoie most resemble those of E. kohfidischi from the type locality; on account of poor preservation, their systematic allocation cannot be fully demonstrated (Szyndlar and Zerova, in prep.).

Elaphe kormosi (Bolkay, 1913).
1913 Coluber kormosi Bolkay, s. 224, pl. XII: 4-8.
1932 Elaphe longissima Laur.: (Coluber Kormosi By.): von Szunyoghy, pp. 10 and 49-50.
Fig. 16.—Trunk vertebra of *Elaphe kohfidischi* from upper Miocene of Kohfidisch (holotype, NMW 1984/96). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm. (From Bachmayer and Szyndlar, 1985.)

Fig. 17.—Trunk vertebrae of *Elaphe paralongissima* from Węże 2 (A, ZPPAN R-III/12; B-E, holotype, ZPPAN R-III/11). A: left lateral view; B: dorsal view; C: ventral view; D: anterior view; E: posterior view. Scale equals 2 mm. (From Szyndlar, 1984.)

Fig. 18.—Trunk vertebra of *Elaphe longissima* from Polish Pleistocene (ZZSD JO-201). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm. (From Szyndlar, 1984.)
Material: (44) Uppermost Miocene (MN 13) of Polgárdi (type locality): one fragmentary basioccipital, one basioccipital, one premaxilla, one fragmentary palate, 5 maxillary fragments, two ectopterygoids, 3 quadrates (synotypes, MHGI Ob-4465/Vt. 75; not seen; fide Bolkay, 1913).

Remarks: Bolkay (1913) noticed that his Coluber kormosi closely resembles the living Coluber longissimus i.e., Elaphe longissima; von Szunyogh (1932) then synonymized the fossil species with Elaphe longissima. Mlynarski (1961), although retaining von Szunyogh's (1932) re-allocation, observed some differences in the morphology and number of the palatine teeth between the Polgárdi fossil and the living Elaphe longissima; Mlynarski did not notice, however, that the lower number of teeth of kormosi resulted from absence of the anterior portion of the palate (cf. Bolkay, 1913; pl. XII: 5). Rage (1984) supposed that E. kormosi is perhaps a distinct species.

The ectopterygoid and basioccipital figured by Bolkay display indeed features characteristic for Elaphe: the external ramus of the ectopterygoid is of subquadrate shape (cf. Bolkay, 1913; pl. XII: 6), while the basioccipital possesses a distinct median crest forked before the occipitochondyreal tubercle. Moreover, the basioccipital crest consists of two tubercles and is devoid of a median process (ibid., pl. XII: 8). These features can be observed indeed in E. longissima, however, also in some other members of the genus. Regarding the palatine and quadrate, their allocation in the genus Elaphe is not demonstrable. Palatines of Elaphe and Coluber differs from each other by morphology of the vomerine process, the structure missing in the Polgárdi fossil (cf. ibid., pl. XII: 5). The quadrate, shown in the inner view (cf. ibid., pl. XII: 7), does not display the quadrate crest (lying on the outer side of the bone), the feature especially helpful for distinguishing Elaphe and Coluber from each other. The bones may have belonged to various snake taxa, thus the status of E. kormosi remains an open question.

Elaphe paralongissima Szyndlar, 1984 (fig. 17).


Elaphe paralongissima Szyndlar: Szynlar in Mlynarski et al., p. 222, fig. 7: 1, 2.

Material: (5) Upper Pleistocene (MN 16) of Węże 2 (type locality): one trunk vertebra (holotype, ZPPAN R-III/11), above 350 vertebrae (ZPPAN).

Diagnostic vertebral characters: The vertebrae of this extinct snake, known exclusively from the type locality, most resemble those of the living E. longissima, but differ from them, among other features, by having a strongly flattened haemal keel (condition very rarely observed in E. longissima) and paired distinct subcotylar tubercles (structures observed usually in natricines but not in colubrines). Szyndlar (1984) supposed that both species were closely related. In vertebral size and proportions, this species resembles E. longissima; the centrum length of 27 trunk vertebrae ranges between 4.61 and 6.48 mm, while the centrum length/width ratio is 1.08–1.23 (mean 1.15 ± 0.04). For more detailed morphological description see Szyndlar (1984).

Elaphe longissima (Laurenti, 1768) (fig. 18).


(47) 1977 Elaphe longissima (Laurenti): Rabeder, p. 92, fig. 11: 4, pl. 1: 11.


(9) 1984 Elaphe aff. longissima (Laurenti, 1768): Szyndlar, pp. 97-100, fig. 38.

[For full synonymy of E. longissima from Polish sites see Szyndlar, 1984: 86.]


Diagnostic vertebral characters: Trunk vertebrae of this living snake are characterized by a distinct spatulate-shaped haemal keel, usually rounded, very rarely sharp or (exceptionally) flattened. The zygodont has three distinct lobes, in large examples it is more or less straight in dorsal view. The prezygapophyseal processes are of moderate length (somewhat shorter than the prezygapophyseal facets), in large specimens usually obtuse, rarely acute; the neural spine is almost as high as long. For more details see Szyndlar (1984). Vertebralia of this snake are relatively large; maximum centrum length of a vertebra recorded from the Polish Pleistocene is 7.9 mm, and in a vertebra from Tourkobouenia 5: 7.8 mm. Centra of large specimens are little longer than wide. In 240 vertebrae from four Upper Pleistocene Polish localities, with the centrum length ranging between 4.47 and 7.97 mm, the average centrum length/width ratio fluctuates about 1.15; on the other hand, 60 vertebrae belonging to a recent example (ZZS5 291), with the centrum length 5.85-6.25 mm, display the value 1.34-1.47 (mean 1.40 ± 0.03) of the centrum length/width ratio (Szyndlar, 1984).

Remarks: E. longissima was described on the basis of cranial bones from a number of localities. Almost all kinds of cranial elements were recorded from the Polish Pleistocene; they are described in detailed and figured by Szyndlar (1984). (43) Two bones reported by Rabeder (1977) from St. Margarethen, allocation of the quadrate (ibidem, fig. 11: 4) to E. longissima is doubtful, while the basioccipital (ibid., pl. 1: 11; in the caption recognized as E. cf. longissima) is clearly referable to this species.

Skull morphology of E. longissima was described in detail and figured by von Szunyogh (1932: 19, 25, 30; figs. 55, 67, 79, 93, 104, 109, 110; pl. III: 13, 14, pl. VI: 8; pl. VII: 3); differentiating features of some cranial elements were also discussed by Rabeder (1977); figs. 5: 7, 6c, 4: 7, 3: 11, 3: 12. 3.

Except for the Polish sites, all remaining localities lie within the present range of E. longissima.


Remarks: (68) (71) (73) Vertebræ from the Greek sites, because of poor preservation, do not display fully all diagnostic features of the species. (28) (30) (32) (33) (35) (36): No comments accompanied Redkozubov's (1987) report of this snake from the six Moldavian sites.

*Elaphe quatuorlineata* (Lacépéde, 1789) (fig. 19).

(42) 1974 *Elaphe* cf. *quatuorlineata* (Lacépéde): Rabeder, p. 148, fig. 3.

(41) 1977 [?]. *Elaphe* sp.: Mais and Rabeder, p. 85.


Diagnostic vertebral characters: In most cases, this living snake may be easily distinguished from other large-sized European colubrines on the basis of vertebral morphology: the haemal keel is strongly flattened and it is not widened before the condyle; the prezygapophyseal processes are very short (twice shorter than the prezygapophyseal facets) and acute. Its trunk vertebrae display the lowest centrum length/width ratio among European colubrines and even smaller vertebrae are relatively short, e.g., in a living specimen (ZZSd 231; 10 vertebrae measured), with the centrum length ranging between 4.35 and 4.55 mm, the centrum length/width ratio is 1.09-1.16 (mean 1.12 ± 0.23). In largest fossil vertebrae (four examples), coming from Tourkobounia 2, the centrum length ranges between 6.00 and 7.68 mm and the centrum length/width ratio ranges between 1.06 and 1.18. *E. quatuorlineata* is the only European snake with hypapophyses (in cervical region of the column) directed forward and not backward (cf. Szyniadr, 1984, fig. 6).

Remarks: Detailed description of skull morphology of this snake may be found in von Szunyogh (1932: 19, 25, 30-31; figs. 53, 55, 77, 92, 103, 115, pl. II: 9, 10, pl. VI: 1; pl. VII: 1); some differentiating features were also presented by Rabeder (1977; figs. 5, 6, 8, 8, 4, 9, 4).

(42) Based on the Rabeder's figure (1974; fig. 3), the basiparasphenoid from Bad Deutsch Altenburg 2 is clearly referable to *E. quatuorlineata*. (41) Abundant cranial and axial elements from Bad Deutsch Altenburg 20 are currently being studied by Zerova (in prep.); the material from this locality includes, among others, highly characteristic cervical vertebrae.

cf. *Elaphe quatuorlineata* (Lacépéde, 1789).

Material: (47) Uppermost Pliocene (MN 17) of Villány 3: one trunk vertebra (ZZSd).

Remarks: Systematic allocation of this single vertebra, somewhat damaged, cannot be fully demonstrated.

cf. *Elaphe situata* (Linnaeus, 1758) (fig. 20).


Diagnostic vertebral characters: The main difference between this living European snake and other small-sized colubrines are very short and acute prezygapophyseal processes; the central lobe of the zygodine is triangle-shaped (cf. fig. 8). The centrum lengths on the last vestige vertebrae from heral keel are 3.73 and 4.63 mm (mean 4.10 ± 0.24). In comparison with other small colubrines, trunk vertebra of *E. situata* are less elongate: the centrum length/width ratio of the above vertebrae is 1.15-1.37 (mean 1.27 ± 0.83).

Remarks: All the localities are located within the present range of *E. situata*.

No cranial remains have been found in fossil sites. The skull morphology of this snake was described by von Szunyogh (1932: 19, 25, 30; figs. 54, 66, 78, 94, 105; pl. V: 21, 22; pl. VI: 10; pl. VII: 10).

*Elaphe* sp.


(24) 1987 *Elaphe* sp.: p. 16.


(10) 1990 *Elaphe* sp.: Syzgndlar and Zerova, p. 54.


Remarks: (10) Abundant remains from Grisev, clearly referable to the genus *Elaphe* owing to the presence of a number of cranial elements, are currently being studied by Zerova (in prep.); this is the oldest certain record of this genus in Europe. (24) (25) Younger fossils from other Ukrainian sites tentatively referred to *Elaphe* by Zerova (1987), are at least in part referable to some living European members of this genus.

(28) (31) (35) (36) Redkozubov (1987), who referred some vertebrae from four Moldavian sites to this genus, provided no description nor explanation of his decision.

Genus *Malpolon* Fitzinger, 1826.

cf. *Malpolon* sp. (fig. 21).

Material: (65) Upper Pliocene (MN 16) of Tourkobounia 1: 7 trunk vertebrae (UUGI).

Diagnostic vertebral characters: Vertebræ of *M. monspessulana*, the only living European member of the genus, can be differentiated from other large-sized West Palearctic colubrines by the following features: usually a thin and sharp haemal keel, weakly widening before the condyle; prezygapophyseal processes relatively long (as long as the prezygapophyseal facets or somewhat longer) and acute; a straight zygodine in dorsal view (in small individuals with three lobes), often with a minute median notch; parapophyses distinctly longer than diapophyses. Trunk vertebrae of this species can reach very large size; the largest specimen available (MNCN 820943) has the centrum length 9.70 mm. Moreover, they are more elongated than those of other large-sized European colubrines (except for *Coluber caspius*). Of 30 trunk vertebrae of a living example (ZZSd 244), with the centrum length 6.70-7.40 mm (mean 7.17 ± 0.21), the centrum length/width ratio is 1.24-1.45 (mean 1.31 ± 0.06). The vertebrae from Tourkobounia 1 (4 specimens) are smaller; the centrum length 4.73-5.47 mm and the centrum length/width ratio is 1.37-1.48. Vertebrae of *M. monspessulana* coming from all regions of the column were figured by Syndlar (1984; fig. 4).

Remarks: The vertebrae from Tourkobounia 1 do not display fully the differentiating features of *M. monspessulana*. The locality is situated within the recent range of this species.

The skull morphology of *M. monspessulana* was described by von Szunyogh (1932: 20, 28-29, 33; figs. 46-48, 59, 71, 83, 95, 107; pl. IV: 17, 18; pl. VI: 5; pl. VII: 7). A description of brain-case elements considering intraspecific variation and comparisons with *Elaphe* and *Coluber* can be found in Syndlar (1988). Another member of the genus, *M. moliensis* from Africa, displays completely different morphology in both its skull and vertebrae; most likely, *M. moliensis* does not represent the genus *Malpolon* (Syndlar, 1988).
Fig. 19.—Trunk vertebra of *Elaphe quatrolineata* from middle Pleistocene of Tourkobounia 2 (UUGI). A: right lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.

Fig. 20.—Trunk vertebra of *Elaphe situla* from middle Pleistocene of Tourkobounia 2 (UUGI). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.

Fig. 21.—Trunk vertebra of cf. *Malpolon* sp. from upper Pliocene of Tourkobounia 1 (UUGI). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.

Fig. 22.—Trunk vertebra of *Telescopus* sp. from middle Pleistocene of Varbeshnitsa (IZBAN). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.
Material: (44) Uppermost Miocene (MN 13) of Polgárdi: vertebræ (not seen; fide Kormos, 1911). Remarks: The presumed presence of \textit{Malpolon} in Polgárdi reported by Kormos (1911) was not confirmed by later students of the Polgárdi herpetofauna (i.e., Bolkay, 1913, and von Szunyoghy, 1932). On the other hand, neither Bolkay nor von Szunyoghy examined vertebræ on which Kormos' report was based. In any case, Kormos provided no description of his find and his identification is doubtful. Snake vertebrae from Devínska Nová Ves, identified by Wettstein-Westersheimb (1955) as belonging to \textit{Malpolon} (? \textit{Malpolon} sp.), actually belong to another colubrine taxon (see below: \textit{Colubrinae indet.} (38)).

\textbf{Genus \textit{Telescopus} Wagler, 1830.}
\textit{Telescopus} sp. (fig. 22).

Material: (55) Middle Pleistocene of Varbeshnitsa: 2 trunk vertebrae (IZBAN).

Diagnostic vertebral characters: Unlike other small-sized colubrines, trunk vertebrae of \textit{Telescopus fallax}, the only living European member of the genus, can be easily differentiated on the basis of their peculiar morphology. The most important feature is that its parapophyses are twice longer than diapophyses; moreover, the neural spine is extremely low, the zygosphenium is provided with three distinct lobes and the prezygapophyseal processes are very short and obtuse. The centrum of a trunk vertebra from Varbeshnitsa has the length 3.82 mm and is 1.44 times longer than wide.

Remarks: The features displayed by the vertebrae from Varbeshnitsa are clearly consistent with those of the living \textit{T. fallax}. However, considering that vertebrae of another member of the genus available for study, \textit{T. dhara}, closely resemble those of \textit{T. fallax}, proper identification of the fossils to the specific level seems impossible while another (ibid., fig. 9).


the presence of paracotylar foramina, previously overlooked, therefore they represent a colubrine and not a boid snake.

(10): Three minute vertebrae from Gritsev, compared by Zerova (1987) with Boiga meini (i.e., Taenosphyx meini; cf. comments to the genus Taenosphyx, above) actually belong to a snake of different vertebral morphology than the above two genera.

(27): According to Chkhikvadze and Lungu (1984: 82), the fossil reported by them from Buzhor is a «... Coluber (sensu lato). A vertebra of a small Whip Snake (without hypapophysis)».

(29): An ophidian vertebra from Vösendorf, shortly described and figured by Papp et al. (1954), does not belong to an anhiliid snake as stated by these authors, but actually is a colubrine (Rage, 1974).

(13) (17) (18) (21) (24): Generic allocation of colubrine vertebrae from several Ukrainian sites is uncertain; the entire material is currently being studied by Zerova (in prep.).

(44): Four fragmentary vertebrae from Polgárdi belonged to snakes of very small size; they probably represent a single species.

(50): Fragmentary vertebrae from Maramea 1 belonged to at least two very small colubrine species; one trunk vertebra belongs to a very large snake (centrum length about 9 mm). (63): The material from Maritsa contains vertebral fragments belonging to 2 small colubrines, both closely resembling those from Maramea 1; caudal vertebrae represented in the material may have also represented natricine snakes.

(3): Several small vertebral fragments (centrum length less than 4 mm) from Podlesice display a peculiar morphology in having a strongly downturned posterior portion of the haemal keel, deep furrows accompanying the lateral foramina and the condylar neck extending far behind the neural arch (Szyndlar, 1984).


(64): Vertebrae from Spilia 4 are very small and strongly damaged; caudal vertebrae may have also belonged to Natrix.

(65) (68) (69): Most unidentified vertebral fragments from Tourkobounia 1, 2, and 5 probably belong to the colubrine species reported above from these sites; caudal vertebrae may have also belonged to non-colubrine snakes.

(70): A single colubrine trunk vertebra from Chios was figured by Schneider (1975, fig. 3 A) but not discussed in the text.

(8): Of three unidentified vertebrae from Mata Cave, two belong to a very small (but adult) snake, while another one is a juvenile; the generic allocation is uncertain (Szyndlar, 1984).

(73): The few strongly damaged vertebral fragments from Pili B belong to a small-sized snake.

ACKNOWLEDGEMENTS

I am especially grateful to the persons and institutions that loaned fossil materials in their care for the present study; to most of them I am also greatly indebted for their cordial hospitality: the late Friedrich Bachmayer and Ortwin Schultz (Naturhistorisches Museum, Vienna), Hans de Bruijn (Utrecht University), Teresa Gams (Cenozoic Research Institute, Budapest), Vasil V. Popov (Institute of Zoology, Bulgarian Academy of Sciences, Sofia), Gernot Rabeder (Vienna University), Zbyněk Roček (Charles University, Prague), Andrzej Sulinski (Institute of Paleozoology, Polish Academy of Sciences, Warsaw), Galina A. Zerova (Institute of Zoology, Academy of Sciences of Ukrainian SSR, Kiev). A number of other friends and colleagues contributed in various ways to this work, by loans and gifts of comparative materials, providing literature not accessible to me or by other means: Wolfgang Böhme (Biologische Staatssammlung, Munich), Olga Büchel (Sorbonne, Paris), László Kordos (Hungarian Geological Institute, Budapest), Zdeněk Krček (Charles University, Prague), Zdeněk Krček (Charles University, Prague), Imre Németh (Central Institute of Geology, Budapest), Börja Sanchiz (Madrid), Miriam Wollberg (Tel-Aviv). I am very grateful to all of them. I thank also the reviewers, Richard Estes (San Diego), Jean-Claude Rage (Paris), and Börja Sanchiz (Madrid), for their useful comments on the manuscript. The research was supported by the CPBN 04.06.01-7 project.

References


Glazek, J. and Szynkiewicz, A. (1987). Stratigraphy of the Late Tertiary and Early Quaternary karst deposits in Po-


Roemer, F. (1870). Ueber Python Euböicus, eine fossile Riesenslange auf tertiärem Kalkschiefer von Kumi auf


