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

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RESUMEN

Revisión de las serpientes neógenas y cuaternarias de Europa central y oriental. Parte I: Scolecophidia, Boidae, Colubrinae. Se estudian restos neógenos y cuaternarios de escolecofidios, boidos y colúbridos «colubrinos», incluyendo tanto formas ya descritas como inéditas, y procedentes de Polonia, Ucrania, Moldavia, Checoslovaquia, Austria, Hungría, Rumanía, Bulgaria y Grecia. Se reconocen los siguientes taxones: Scolecophidia indet.; Boidae: *Bransateryx septentrionalis, Bransateryx* sp., *Albaneryx volynicus,* cf. *Gongylophis* sp., *Eryx jaculus, Eryx* sp., cf. *Eryx* sp., Erycinae indet.; Colubridae: *Texasophis bohemiacus, Coluber dolnicensis, Coluber planicarinatus, Coluber viridiflavus,* cf., *Coluber viridiflavus, Coluber caspius, Coluber gemonensis,* cf. *Coluber gemonensis, Coluber* sp., *Coronella austriaca, Coronella* sp., cf. *Coronella* sp., *Elaphe kohfidischi,* cf. *Elaphe kohfidischi, Elaphe paralongissima, Elaphe longissima,* cf. *Elaphe longissima, Elaphe quatuorlineata,* cf. *Elaphe quatuorlineata,* cf. *Elaphe situla, Elaphe* sp., cf. *Malpolon* sp., *Telescopus* sp., «Colubrinae» indet.

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

ABSTRACT

Remains of Neogene and Quaternary scolecophidians, boids and «colubrine» colubrids, including snakes previously described and those undescribed yet, coming from Poland, Ukraine, Moldavia, Czechoslovakia, Austria, Hungary, Romania, Bulgaria, and Greece are discussed. The following taxa, including 7 extinct species, were recognized: Scolecophidia indet.; Boidae: *Bransateryx septentrionalis, Bransateryx* sp., *Albaneryx volynicus,* cf., *Gongylophis* sp., *Eryx jaculus, Eryx* sp., cf. *Eryx* sp., Erycinae indet.; Colubridae: *Texasophis bohemiacus, Coluber dolnicensis, Coluber planicarinatus, Coluber viridiflavus,* cf. *Coluber viridiflavus, Coluber caspius, Coluber gemonensis,* cf. *Coluber gemonensis, Coluber* sp., *Coronella austriaca, Coronella* sp., cf. *Coronella* sp., *Elaphe kohfidischi,* cf. *Elaphe kohfidischi, Elaphe paralongissima, Elaphe longissima,* cf. *Elaphe longissima, Elaphe quatuorlineata,* cf. *Elaphe quatuorlineata,* cf. *Elaphe situla, Elaphe* sp., cf. *Malpolon* sp., *Telescopus* sp., «Colubrinae» indet.

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

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 *Mesophis nopcsai* Bolkay, 1925. Identification of these finds as snakes cannot, however, be demonstrated with confidence (cf. Rage, 1987).

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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 paper 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 Szunyoghy (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 Sciencies, Sofia.
MHGI: Museum of the Hungarian Geological Institute, Budapest.
MNCN: Museo Nacional de Ciencias Naturales, Madrid.
NMW: Geol.-Paläont. Abteilung der Naturhistorisches Museum, Wien.
SMF: Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main.
TGPI: Tiraspol' State Normal School.
UUGI: Geological Institute of Utrecht University.
UWPI: Institut der Paläontologie der Universität Wien.
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 exists.

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) Przeworno 2 (upper Orleanian/middle Astaracian; MN 5-7).
(2) Opole 2 (middle Astaracian; MN 7).
(3) Podlesice (lower Ruscinian; MN 14).
(4) Węże 1 (upper Ruscinian; MN 15).
(5) Węże 2 (lower Villanyian; MN 16).
(6) Rębielice Królewskie 1A (Villanyian; MN 16).
(7) Rębielice Królewskie 2 (lower Villanyian; MN 16).
(8) Mała Cave (age uncertain) *.
(9) Polish Pleistocene.

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 Młynarski 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 speciments (ZZSiD, ZPUW, ZPPAN).

* The age of the layers 4 + 5 of Mała 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 Głazek 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; Bezimennoie; Bolshaya Kamyshevaha; Cherevichnoie, middle layer) and uppermost Pliocene sites (Morskoy; Zhevatova Gora, upper layer; Kairy; Kryzhanovka, upper layer; Tarhankut; Nogaysk; Cherevichnoie, 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):

(10) Gritsev (lower Vallesian; MN 9).
(11) Krivoy Rog (lower Turolian; MN 11).
(12) Novoelizabetovka, lower layer (lower Turolian; MN 11).
(13) Novaya Emetovka (middle Turolian; MN 12).
(14) Cherevichnoie, lower layer (middle Turolian; MN 12).
(15) Bielka (middle Turolian; MN 12).
(16) Novoelizabetovka, upper layer (middle Turolian; MN 12).
(17) Novoukrainka 1 (upper Turolian; MN 13).
(18) Andreievka (upper Turolian; MN 13).
(19) Frunzovka 2 (upper Turolian; MN 13).
(20) Kuchurgan (lower Ruscinian; MN 14).
(21) Kotlovina, lower layer (upper Ruscinian; MN 15).
(22) Kotlovina, middle and upper layer (lower Villanyian; MN 16).
(23) Bolurubince (age unknown).
(24) Ukrainian upper Pliocene.
(25) Ukrainian Pleistocene.

References: Basic data (age, location, preliminary faunistic lists) concerning all snake-bearing sites in Ukraine were summarized briefly by Zerova (1987). Moreover, a number of detailed papers dealing with some snake remains from the area was recently published or submitted for publication. A new species of Vipera from Kuchurgan was described by Zerova (in Zerova et al., 1987) and a new species of Albaneryx from Gritsev was described by the same author (Zerova, 1989). A detailed description of the snake fauna from Cherevichnoie is being prepared by Szyndlar and Zerova (in prep.) and elapid remains from Gritsev were described by the same authors (Szyndlar and Zerova, 1990).

Material examined: whole (IZAN) except for the classical material of von Meyer (1844) from Bolurubince that was lost (fide Rage, 1984).

USRR: Moldavia

Localities:

(26) Kalfa (lower Vallesian; MN 9).
(27) Buzhor (Vallesian; MN 9 or 10).
(28) Etuliya (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) Novye Tanatary (lower Villanyian; MN 16).
(34) Salchiya (lower Villanyian; MN 16).
(35) Chishmikioy (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).
(38) Děvínska Nová Ves [= Neudorf a.d. March] (lower Astaracian; MN 6).

References: The only snake materials described in detail come from the above two localities. Natricine remains from Dolcine were studied by Rage and Roček (1983); a description of the remaining snake material was given afterwards by Szyndlar (1987a). Of the latter locality, some snakes were briefly described by Wettstein-Westersheimb (1955).
Material examined: the available material from Dolcine (DPFNSP) and a part of the material from Děvínska Nová Ves (DPFNSP), other than that studied by Wettstein-Westersheimb (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 Szyndlar, 1985, 1987; Szyndlar 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 (Szyndlar 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

Localities: Datings follow Fejfar and Heinrich (1983), Jánossy (1986), and Kordos (1987):

(44) Polgárdi (upper Turolian; MN 13)
(45) Csarnóta 2 [= Csarnóta of Bolkay (1913) and of von Szunyoghy (1932)] (lower Villanyian: MN 16).
(46) Beremend 1 [= Beremend of Bolkay (1913) and of von Szunyoghy (1932)] (lower Villanyian; MN 16).

(47) Villány 3 [= Villány of Bolkay (1913) and Kalkberg near Villány of von Szunyoghy (1932)] (upper Villanyian; MN 17).
(48) Nagyharsány-hegy (upper Villanyian; MN 17).
(49) Villány 6 (upper Villanyian; MN 17).
(50) Csarnóta 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 Szunyoghy (1932). Kretzoi (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 Csarnóta 4 (ZZSiD). The examined collections are different from those described in the Hungarian classical papers (partly MHGI, partly probably lost).

Romania

Localities:

(52) Betfia [Püspökfürdö and Somlyó-hegy of Bolkay (1913) and von Szunyoghy (1932)] (lower Pleistocene).
(53) Braşov [Brassó of Bolkay (1913) and von Szunyoghy (1932)] (middle Pleistocene).

References: The previously cited papers devoted to Hungarian snakes (Bolkay, 1913, and von Szunyoghy, 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 Młynarski (1982), respectively:

(54) Dorkovo (lower Ruscinian; MN 14).
(55) Varbeshnitsa (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 (Młynarski, 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) Kimi (lower Miocene; MN ?).
(59) Pikermi 4 (middle or upper Turolian; MN 12 or 13).
(60) Maramena 1 (upper Turolian; MN 13).
(61) Ano Metochi 2 (upper Turolian; MN 13).
(62) Karabournu (upper Turolian or lower Ruscinian: MN 13 or 14).
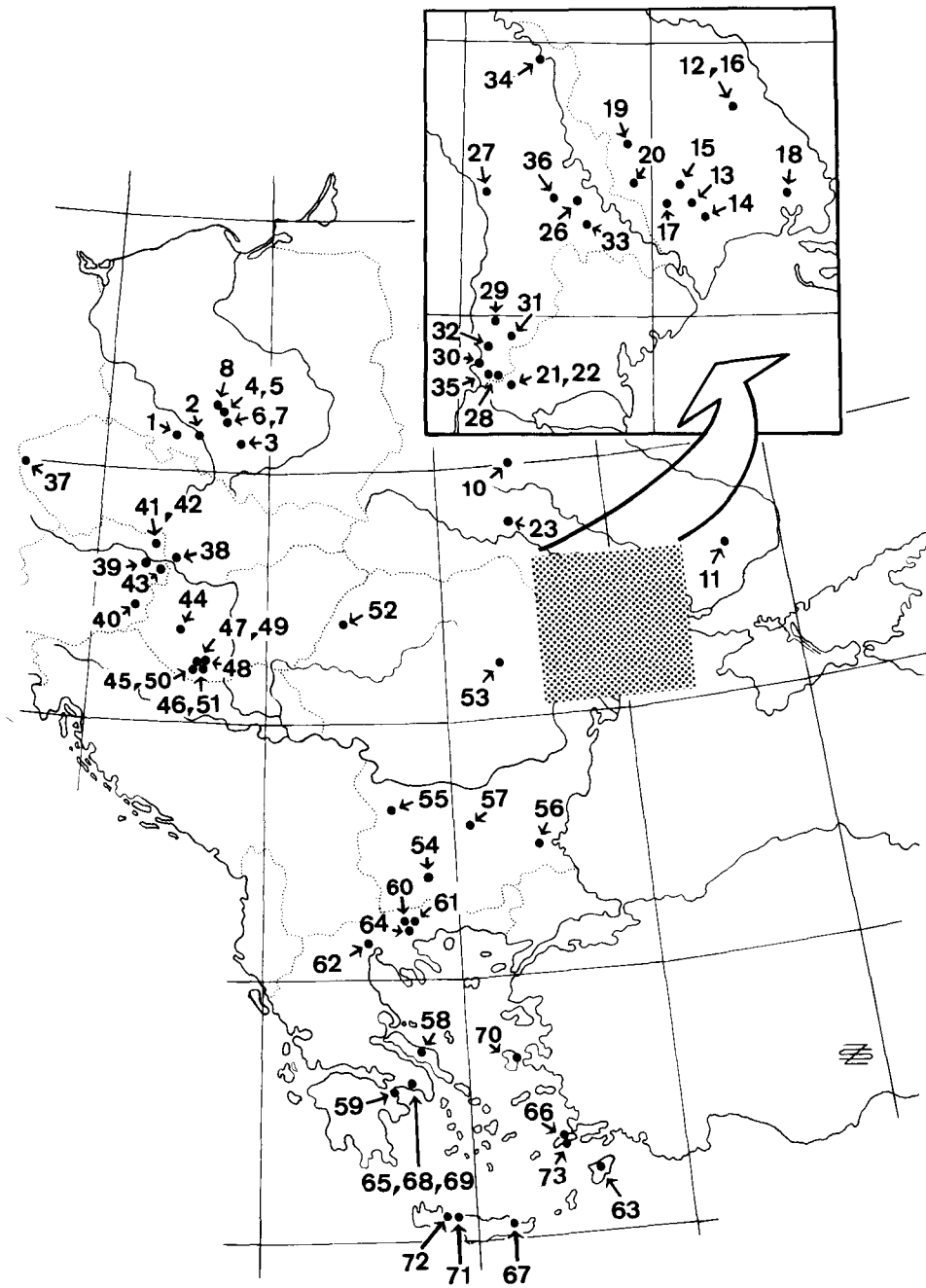(63) Maritsa (lower Ruscinian; MN 14).

Fig. 1.—Fossil snake localities of East Europe. Poland: (1) Przeworno 2, (2) Opole 2, (3) Podlesice, (4) Węże 1, (5) Węże 2, (6) Rębielice Królewskie 1A, (7) Rębielice Królewskie 2, (8) Mała Cave; Ukraine: (10) Gritsev, (11) Krivoy Rog, (12) Novoelizabetovka, lower layer, (13) Novaya Emetovka, (14) Cherevichnoie, lower layer, (15) Bielka, (16) Novoelizabetovka, upper layer, (17) Novoukrainka 1, (18) Andreievka, (19) Frunzovka 2, (20) Kuchurgan, (21) Kotlovina, lower layer, (22) Kotlovina, middle and upper layer (lower Villanyian; MN 16), (23) Bolurubince; Moldavia: (26) Kalfa, (27) Buzhor, (28) Etuliya, (29) Lucheshty, (30) Valeny, (31) Musait, (32) Dermendzhi, (33) Novye Tanatary, (34) Salchiya, (35) Chishmikioy, (36) Bachoy; Czechoslovakia: (37) Dolnice, (38) Dĕvínska Nová Ves; Austria: (39) Vösendorf, (40) Kohfidisch, (41) Bad Deutsch Altenburg 20, (42) Bad Deutsch Altenburg 2, (43) St. Margarethen; Hungary: (44) Polgárdi, (45) Csarnóta 2, (46) Beremend 1, (47) Villány 3, (48) Nagyharsány-hegy, (49) Villány 6, (50) Csarnóta 4, (51) Beremend 4; Romania: (52) Betfia, (53) Braşov; Bulgaria: (54) Dorkovo, (55) Varbeshnitsa, (56) Stoilovo, (57) Bacho Kiro; Greece: (58) Kimi, (59) Pikermi 4, (60) Maramena 1, (61) Ano Metochi 2, (62) Karabournu, (63) Maritsa, (64) Spilia 4, (65) Tourkobounia 1, (66) Laghada A and B, (67) Sitia 1 and 2, (68) Tourkobounia 2, (69) Tourkobounia 5, (70) Chios, (71) Gerani 1+4, (72) Rethymnon, (73) Pili B.

(64) Spilia 4 (upper Ruscinian; MN 15).
(65) Tourkobounia 1 (lower Villanyian; MN 16).
(66) Laghada A and B (lower Pleistocene).
(67) Sitia 1 and 2 (Pleistocene).
(68) Tourkobounia 2 (middle Pleistocene).
(69) Tourkobounia 5 (middle Pleistocene).
(70) Chios (middle Pleistocene).
(71) Gerani 1+4 (upper Pleistocene).
(72) Rethymnon (upper Pleistocene).
(73) Pili B (subrecent).

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 also 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-allocations 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.

Diagnoses 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 SCOLECOPHIDIA 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.

Scolecophidia indet. (fig. 2).

(37) 1987 Scolecophidia indet.: Szyndlar, p. 55, fig. 1.
(10) 1990 an unidentified scolecophidian: Szyndlar and Zerova, p. 54.

Material: (37) Lower Miocene (MN 4) of Dolcine: one vertebra (DPFNSP 1316). (10) Late Miocene (MN 9) of Gritsev: one vertebra (IZAN). (14) Upper Miocene (MN 12) of Cherevichnoie (lower layer): one vertebra (IZAN 45-6018). (63) Early Pliocene (MN 14) of Maritsa: 2 vertebrae. (65) Upper Pliocene (MN 16) of Tourkobounia 1: 5 vertebrae (UUGI). (68) Middle Pleistocene of Tourkobounia 2: 3 vertebrae (UUGI). (69) Middle Pleistocene of Tourkobounia 5: 2 vertebrae (UUGI).

Remarks: Except for the scolecophidian 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-
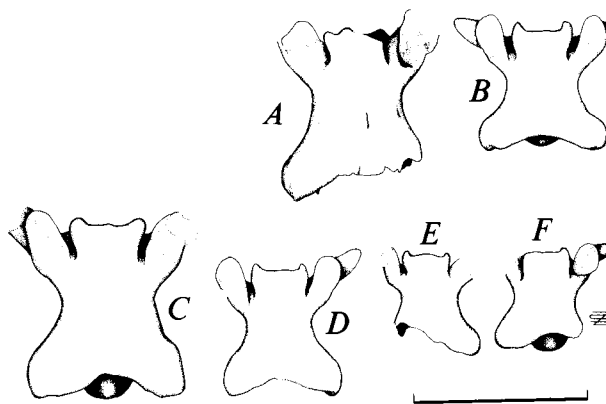

Fig. 2.—Trunk vertebrae of Scolecophidia indet., in dorsal view, from: A: lower Miocene of Dolnice (DPFNSP 1316); B: early Pliocene of Maritsa (UUGI); C and D: upper Pliocene of Tourkobounia 1; E: middle Pleistocene of Tourkobounia 2; F: middle Pleistocene of Tourkobounia 5. Scale equals 2 mm.

rence 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.
1939　*Heteropython euboicus* Roemer: Kuhn, p. 24.
1963　*Heteropython euboicus* (Roemer): Kuhn, p. 12.
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 thunk 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 *Charina* from North America; perhaps both genera represented the same evolutionary lineage (Szyndlar, 1987) or even they should be synonymized.

Bransateryx sp.

1987　*Bransateryx:* Zerova, p. 13.
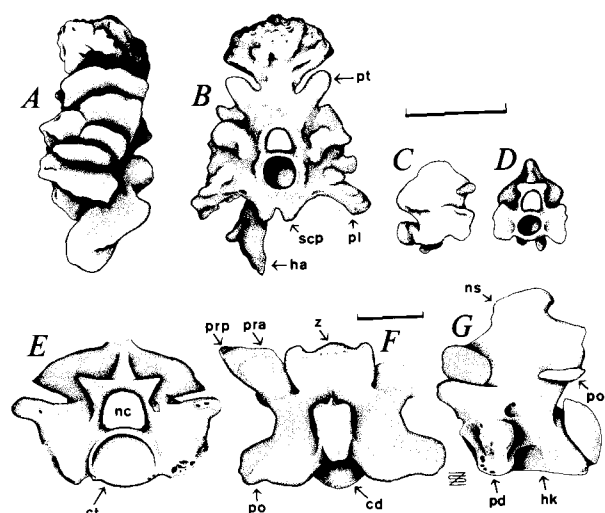1990　*Bransateryx* sp.: Szyndlar and Zerova, p. 54.

Fig. 3.—Vertebrae 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). A, C, G: lateral views; B, D, E: anterior views; F: dorsal view. Abbreviations: cd: condyle; ct: cotyle; ha: haemapophysis; hk: haemal keel; nc: neural canal; ns: neural spine; pd: paradiapophysis; pl: pleurapophysis; po: postzygapophysis; poa: postzygapophyseal articular surface; pra: prezygapophyseal articular surface; prp: prezygapophyseal process; pt: pterapophysis; scp: subcotylar process; z: zygosphene. Each scale equals 2 mm.

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

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

Genus *Albaneryx* Hoffstetter et Rage, 1972.

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).

1989　*Albaneryx volynicus* Zerova, pp. 30-35, figs. 1-12.

Material: (10) Late Miocene (MN 9) of Gritsev (type locality): 270 precaudal vertebrae (IZAN 11-1091, 11-1096, 22-1095), one caudal vertebra (holotype, IZAN 22-1089), 35 other caudal vertebrae (IZAN 22-1090, 22-1092, 22-1094).

Diagnostic vertebral characters: According to Zerova (1989: 31), posterior caudal vertebrae of *A. volynicus* differs from those of the type species by having, among others, «shorter vertebral centrum; hypapophyses longer and thickened distally; neural spine higher and more widened distally; (...) well developed pterapophyses (...)»; trunk vertebrae have shorter neural spines. The centrum length of trunk vertebrae ranges between 1.7 and
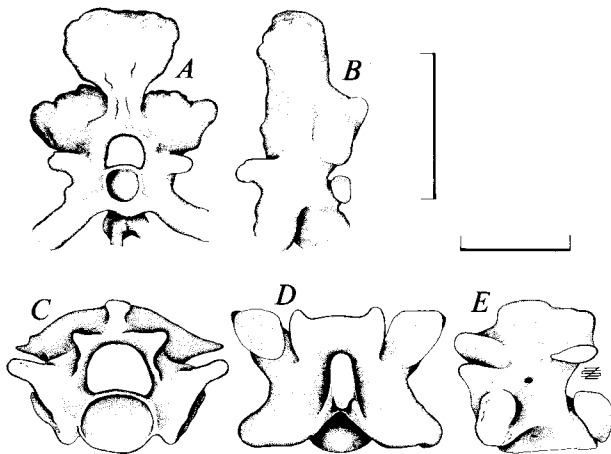
Fig. 4.—Vertebrae of *Albaneryx volynicus* from late Miocene of Gritsev. A and B: posterior caudal vertebra (holotype, IZAN 22-1089); C, D, E: trunk vertebra (IZAN 11-1091). A, C: anterior views; B, E: left lateral views; D: dorsal view. Each scale equals 2 mm.

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

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

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

Material: (70) Middle Pleistocene of Chios: (?13) 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
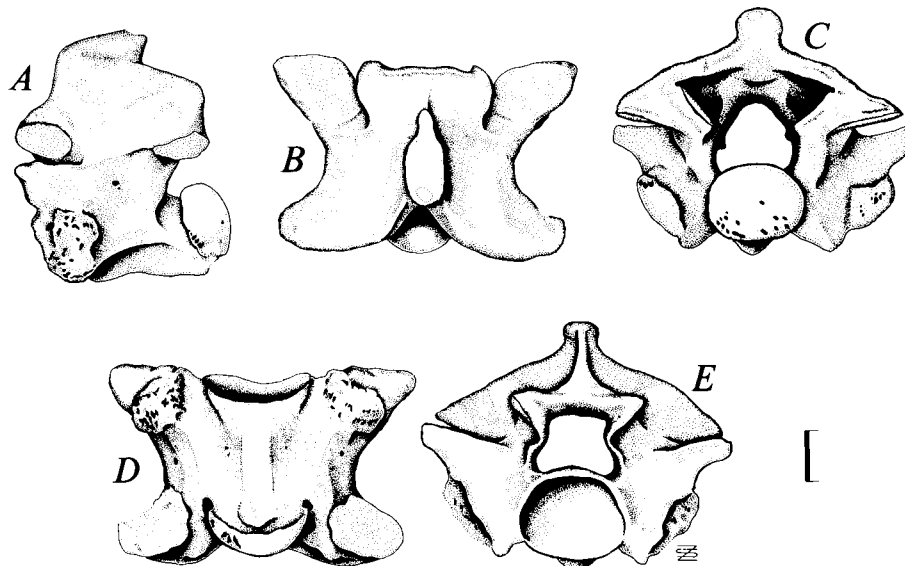

Fig. 5.—Trunk vertebra of cf. *Gongylophis* sp. from lower Miocene of Dolnice (DPFNSP 4005). A: left lateral view; B: dorsal view; C: posterior view; D: ventral view; E: anterior view. Scale equals 2 mm. (From Szyndlar, 1987. Copyright 1987 by the Society of Vertebrate Paleontology. Used with permission.)
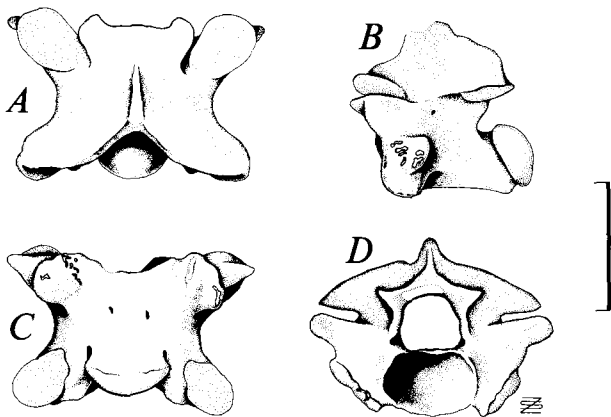
Fig. 6.—Trunk vertebra of *Eryx jaculus* from upper Quaternary of Pili B (UUGI). A: dorsal view; B: left lateral view; C: ventral view; D: anterior view. Scale equals 2 mm.
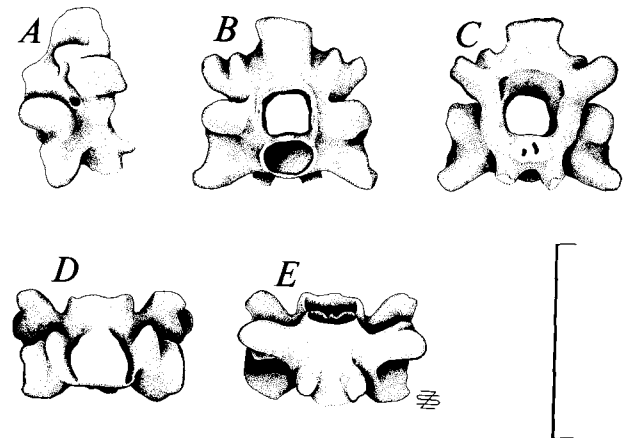

Fig. 7.—Posterior caudal vertebra of cf. *Eryx* sp. from lower Pliocene of Maritsa (UUGI). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm.

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

Eryx sp.

(14) 1987   *Eryx* sp.: Zerova, p. 13.
(21) 1987   Erycinae: Zerova, p. 15.
(22) 1987   Erycinae: Zerova, p. 16.

Material: (14) Upper Miocene (MN 12) of Cherevichnoie (lower layer): 9 precaudal vertebrae (IZAN 45-5021 and 45-5022), 2 caudal vertebrae (IZAN 45-5019 and 45-5020). (21) Middle Pliocene (MN 15) of Kotlovina (lower layer): precaudal vertebrae, one caudal vertebra (IZAN). (22) Upper Pliocene (MN 16) of Kotlovina (middle/upper layer): precaudal and caudal vertebrae (IZAN).

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)

(12) 1987   Erycinae: Zerova, p. 13.
(15) 1987   *Eryx* sp.: Zerova, p. 13.

Material: (12) Upper Miocene (MN 11) of Novoelizabetovka (lower layer): 2 fragmentary precaudal vertebrae (IZAN). (15) Upper Miocene (MN 12) of Bielka: one caudal vertebra (IZAN). (63) Lower Pliocene (MN 14) of Maritsa: one caudal vertebra (UUGI). (64) Middle Pliocene (MN 15) of Spilia 4: one fragmentary cervical vertebra (UUGI).

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 *Gongylophis*-like snake. The remains from particular localities presumably represented different species.

Erycinae indet.

(28) (32) (33)   1987   Erycinae: Redkozubov, p. 71.

Material: (28) Middle Pliocene (MN 15) of Etuliya: vertebrae (not seen, fide Redkozubov, 1987). (32) Middle Pliocene (MN 15) of Dermendzhi: vertebrae (not seen, fide Redkozubov, 1987). (33) Upper Pliocene (MN 16) of Novye Tanatary: vertebrae (not seen, fide Redkozubov, 1987).

Remarks: The only information provided by Redkozubov (1987:

71) is that the above listed localities yielded «... vertebrae of snakes of the subfamily Erycinae».

Family COLUBRIDADE 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. viridiflavus*, *Elaphe longissima*, *E. quatuorlineata*, and *Malpolon monspessulanus*. The remaining species, belonging to the genera *Coluber*, *Coronella*, *Eirenis*, *Elaphe*, and *Telescopus*, represent the small-sized colubrine group.

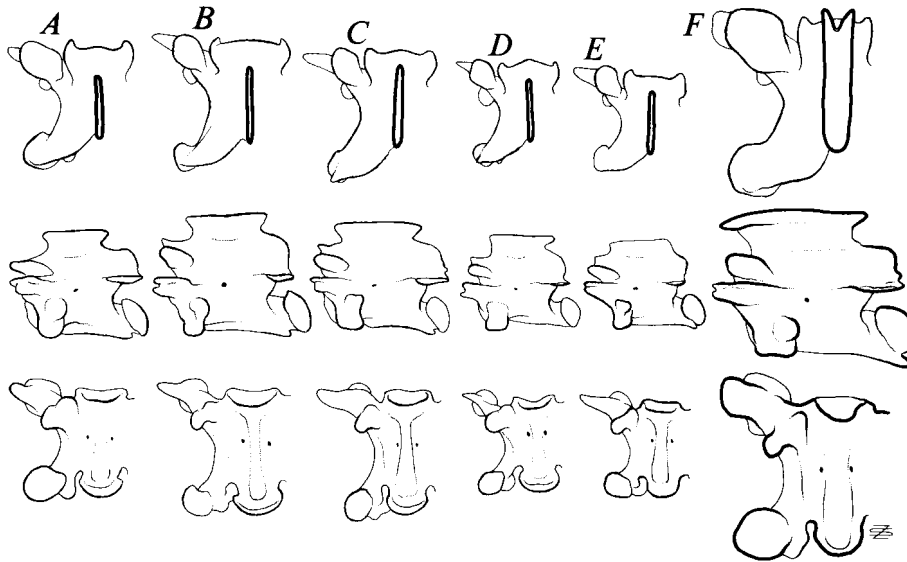The above remarks concern vertebrae of adult specimens. It

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 trigona-*

tum. 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 zygosphene (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 ocurring 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-
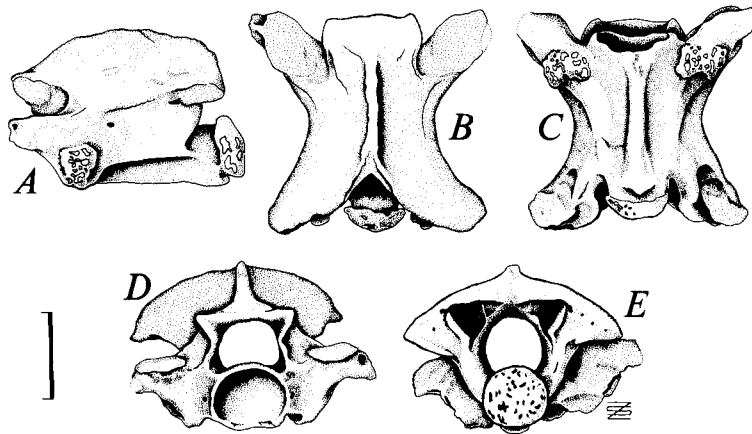
Fig. 9.—Trunk vertebra of *Texasophis bohemiacus* from lower Miocene of Dolnice (holotype, DPFNSP 1238). A: left lateral view; B: dorsal view; C: ventral view; D: anterior view; E: posterior view. Scale equals 2 mm. (From Szyndlar, 1987. Copyright 1987 by the Society of Vertebrate Paleontology. Used with permission.)
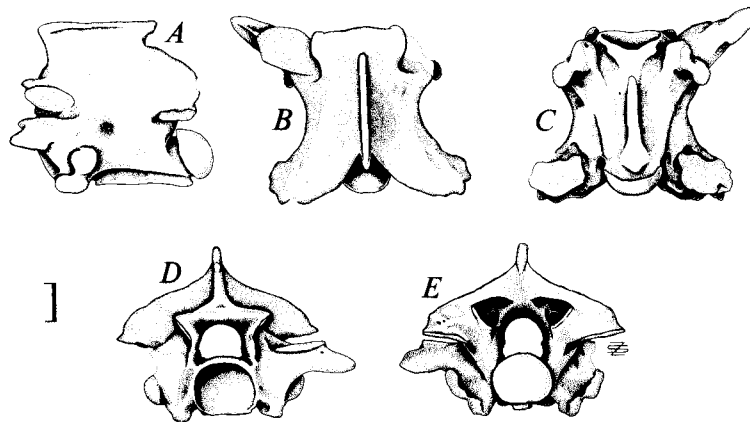

Fig. 10.—Trunk vertebra of *Coluber dolnicensis* from lower Miocene of Dolnice (holotype, DPFNSP 4558). A: left lateral view; B: dorsal view; C: ventral view; D: anterior view; E: posterior view. Scale equals 2 mm. (From Szyndlar, 1987. Copyright 1987 by the Society of Vertebrate Paleontology. Used with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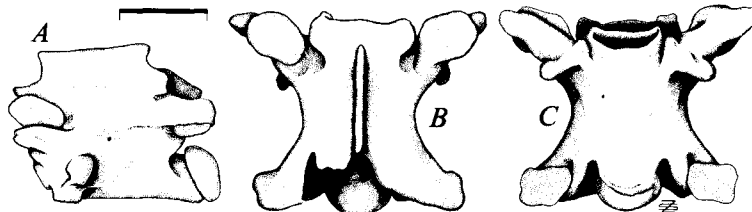

Fig. 11.—Trunk vertebra of *Coluber planicarinatus* from upper Miocene of Kohfidisch (holotype, NMW 1984/97). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.
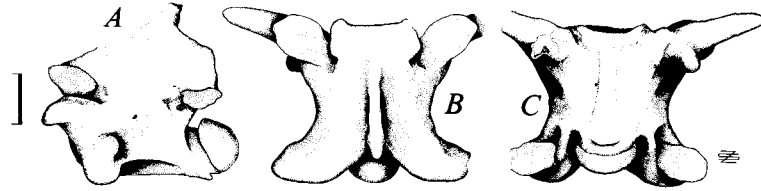
Fig. 12.—Trunk vertebra of *Coluber viridiflavus* from middle Pleistocene of Varbeshnitsa (IZBAN). A: left lateral view; B: ventral view; C: dorsal view. Scale equals 2 mm.
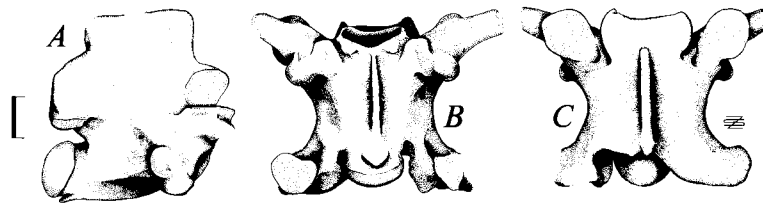
Fig. 13.—Trunk vertebra of *Coluber caspius* from middle Pleistocene of Varbeshnitsa (IZBAN). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.
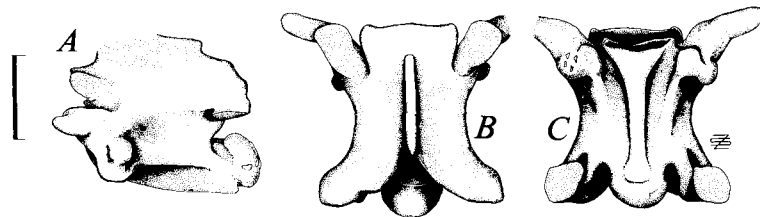
Fig. 14.—Trunk vertebra of cf. *Coluber gemonensis* from late Pleistocene of Stoilovo (IZBAN). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.
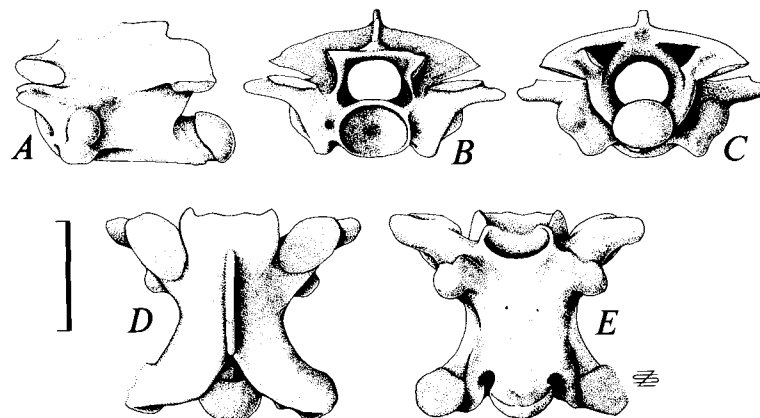
Fig. 15.—Trunk vertebra of *Coronella austriaca* from Polish Pleistocene (ZZSiD KG-8050). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm. (From Szyndlar, 1984.)

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).

1987   *Coluber dolnicensis* Szyndlar, pp. 65,66, fig. 8.

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: Vertebrae 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» immediately behind the diapophyses); the neural spine is longer than high; the prezygapophyseal processes are obtuse 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 lenght 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.
1932   *Zamenis* cfr. *Dahli* Sav.: von Szunyoghy, pp. 10 and 49.
1939   *Zamenis hungaricus* Bolkay: Kuhn, p. 28.
1961   *Coluber cf. najadum* (Eichwald): Młynarski, p. 23.
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 quadrate (holotype, MHGI Ob-4464/Vt.76; not seen, fide Bolkay, 1913).

Remarks: Bolkay (1913: 223, 224) erected a new extinct species for the discussed quadrate 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 Szunyoghy (1913) who recognized the quadrate as comparable with the living *Zamenis dahli* (i.e., *Coluber najadum*). Mlynarski (1961), although retaining von Szunyoghy's allocation, observed that the quadrate is similar rather to that of *Natrix*. Rage (1984) then stated that the taxonomic status of the species is doubtful. Considering that a single quadrate 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.
1845   *Coluber Podolicus:* von Meyer, p. 41.
1880   *Periops podolicus* Meyer: de Rochebrune, p. 291.
1939   *Coluber podolicus* H. v. Meyer: Kuhn, p. 19.
1961   *Coluber podolicus* H. v. Meyer: Młynarski, p. 35.
1963   *Coluber podolicus* H. v. Meyer: Kuhn.
1984   *Coluber podolicus* Meyer: Rage, p. 52.
1984   *Coluber podolicus* H. v. Meyer: Zerova and Chkhikvadze, p. 322.

Remarks: The vertebra from Bolurubince (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 Szunyoghy, pp. 9 and 48-49, fig. 115.
(6)   1964   *Coluber robertmertensi* Młynarski, 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 robertmertensi* Młynarski: Rage, p. 45.
(6)   1984   *Coluber robertmertensi* Młynarski: Szyndlar, pp. 53-62, figs. 19-21.
       [For full synonymy of this snake from Rębielice Królewskie 1A see Szyndlar, 1984: 53.]
(28) (30) (31) (35) (36):
       1987   *Coluber robertmertensi:* Redkozubov, p. 71.

Material: (28) Middle Pliocene (MN 15) of Etuliya: trunk vertebrae (not seen, fide Redkozubov, 1987). (30) Middle Pliocene (MN 15) of Valeny: trunk vertebrae (not seen, fide Redkozubov, 1987). (31) Middle Pliocene (MN 15) of Musait: trunk vertebrae (not seen, fide Redkozubov, 1987). (6) Upper Pliocene (MN 16) of Rębielice Królewskie 1A: 8 basiparasphenoids (ZZSiD RKI-1, 13-19), 8 basioccipitals (ZZSiD RKI-5-12), one exoccipital, one premaxilla (ZZSiD RKI-58), 3 maxillary fragments (ZZSiD RKI-22-24), 3 pterygoid fragments (ZZSiD RKI-25-27), 3 ectopterygoids (ZZSiD RKI-3, 28, 29), one dentary (ZZSiD RKI-57), 18 compounds (ZZSiD RKI-2, 40-56), 11 quadrates (ZZSiD RKI-1, 30-39), 3 axes (ZZSiD RKI-59-61), 2209 precaudal vertebrae (ZZSiD RKI-62-2238, 2273-2306), one cloacal vertebra ZZSiD RKI-2239), 38 caudal vertebrae (ZZSiD RKI-2241-2272), ca. 10000 other vertebrae. (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen, fide Redkozubov, 1987). (36) Upper Pliocene (MN 16) of Bachoy: trunk vertebrae (not seen, fide Redkozubov, 1987). (47) Upper Pliocene (MN 16) of Beremend 1: one parietal, 2 quadrates, 12 compounds (not seen, fide von Szunyoghy, 1932). (43) Middle Pleistocene of St. Margarethen: 8 parietal fragments, 10 supraoccipitals, 6 basiparasphenoid fragments, 5 basioccipitals and basioccipital fragments, 19 prootics, 15 exoccipitals, 3 premaxillary fragments, 7 frontals and fron-

tal fragments, 4 ectopterygoid fragments, 33 quadrates and quadrate fragments, 17 compounds (UWPI 2350/3/1-61, 64-73, 68-89; not seen, fide Rabeder, 1977). (55) Middle Pleistocene of Varbeshnitsa: 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 Rębielice Królewskie 1A (formerly *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 Szunyoghy (1932: 18-19, 26-27, 31; figs. 31-36, 51, 63, 75, 88, 100; pl. II: 11, 12; pl. VI: 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) (6) Abundant cranial elements of this snake coming from two fossil localities, Rębielice Królewskie 1A and St. Margarethen, were described in detail and carefully figured by Rabeder (1977) and Szyndlar (1984), respectively.

(6) A few skull remains from Rębielice Królewskie 1A, closely resembling *C. viridiflavus*, were described by Młynarski (1964) 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 Mlynarski (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, in having concave and not straight zygosphene. 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 Rębielice Królewskie 1A are consistent with the latter subspecies. (46) The same similarities were previously pointed out by von Szunyoghy (1932), with reference to cranial remains from Beremend 1.

(28) (30) (31) (35) (36) Redkozubov (1987), who referred some colubrine trunk vertebrae from five 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.: Młynarski, pp. 10-12, pl. I-IV.
(42)   1974   cf. *Coluber viridiflavus* Lacépède: Rabeder, p. 148.

(7)   1977   *Coluber* sp.: Młynarski, p. 17.
(41)   1977   *Coluber viridiflavus* Lacépède: Mais and Rabeder, p. 85.
(7)   1984   *Coluber* cf. *robertmertensi* Młynarski: Szyndlar, pp. 62-63, fig. 22.
(4)   1984   *Coluber* cf. *viridiflavus* (Lacépède): Szyndlar, pp. 63-65, figs. 23, 24.

Material: (4) Middle Pliocene (MN 15) of Węże 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-11-553), 27 cloacal and caudal vertebrae (ZZSiD WI-554-580). (7) Upper Pliocene (MN 16) of Rębielice Królewskie 2: 57 precaudal and 3 caudal vertebrae (ZZSiD RKII-1-60). (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*; although vertebrae coming from these localities are of medium size, their zygosphenal roofs are often concave, moreover, a part of vertebrae from Węże 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 Szyndlar 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 prevailing 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 Szunyoghy (1932).

Coluber caspius Gmelin, 1789 (fig. 13).

(44) (45) (46) (47) (48) (52) (53):
       1932   *Zamenis jugularis* L. var. *caspia* Gmel.: von Szunyoghy, pp. 9 and 48, fig. 114.
(47)   1956   *Zamenis jugularis caspius* Gmelin: Kretzoi, p. 259.
(42)   1974   *Coluber jugularis* L. ?: Rabeder, p. 148.
(41)   1977   *Coluber jugularis* L.: Mais and Rabeder, p. 85.
(25)   1987   *Coluber jugularis*: Zerova, p. 17.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi: 2 compounds (not seen; fide von Szunyoghy, 1932). (41) Upper Pliocene (MN 16) of Bad Deutsch Altenburg 20: cranial bones and vertebrae (UWPI). (45) Upper Pliocene (MN 16) of Csarnóta 2: one compound (not seen; fide von Szunyoghy, 1932). (46) Upper Pliocene (MN 16) of Beremend 1: 2 frontals, 3 quadrates, 5 dentaries, 7 compounds (not seen; fide von Szunyoghy, 1932). (47) Uppermost Pliocene (MN 17) of Villány 3: one prefrontal (not seen; fide von Szunyoghy, 1932). (48) Uppermost Pliocene (MN 17) of Nagyharsány-hegy: one compound (not seen; fide von Szunyoghy, 1932). (49) Uppermost Pliocene (MN 17) of Villány 6: one right compound, 21 precaudal vertebrae (ZZSiD). (25) Ukrainian Pleistocene: precaudal vertebrae (IZAN). (52) Lower Pleistocene of Betfia: one compound (not seen; fide von Szunyoghy, 1932). (42) Middle Pleistocene of Bad Deutsch Altenburg 2: compounds (UWPI; not seen, fide Rabeder, 1974). (53) Middle Pleistocene of Braşov: one compound (not seen; fide von Szunyoghy, 1932). (55) Middle Pleistocene of Varbeshnitsa: 4 trunk vertebrae (IZBAN). (56) Late Pleistocene of Stoilovo: 2 trunk vertebrae (IZBAN).

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 zygosphene, even in smaller specimens, is concave in dorsal view; the haemal keel is distinctly high and sharp throughout 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-

cets) and acute. Mid-trunk vertebrae of the following two living specimens (ZZSiD 262, 10 vertebrae measured; and ZZSiD 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 that wide. Of few available fossil vertebrae, the largest one (from Varbeshnitsa) 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 Szunyoghy (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, 5: 2, 6: 3, 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 Szunyoghy, 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 only known compound of *C. dolnicensis* 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 Szunyoghy (1932) disregarded vertebrae throughout his study; the discussed compounds needs a prompt re-examination and it is also necessary to examine vertebrae from Polgárdi in order to confirm or refute von Szunyoghy'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).

(43) 1977 *Coluber gemonensis* (Laurenti): Rabeder, p. 92, pl. 1: 12; pl. 2: 17.
(28) (29) (31) (33) (35):
      1987 *Coluber gemonensis:* Redkozubov, p. 71.
(34) 1989 *Coluber gemonensis:* Redkozubov, p. 209.

Material: (28) Middle Pliocene (MN 15) of Etuliya: 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). (33) Upper Pliocene (MN 16) of Novye Tanatary: trunk vertebrae (not seen; fide Redkozubov, 1987). (34) Upper Pliocene (MN 16) of Salchiya: trunk vertebrae (not seen; fide Redkozubov, 1987). (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen; fide Redkozubov, 1987). (43) Middle Pleistocene of St. Margarethen: 2 supraoccipitals, 2 basioccipitals (UWPI 2350/3/61-63, 66-67; not seen; fide Rabeder, 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 os 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 keels 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. Margarthen 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 Szunyoghy (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).

(42) 1974 *Coluber* cf. *gemonensis* (Laurenti): Rabeder, p. 148, fig. 4.
(41) 1977 *Coluber gemonensis* (Laurenti): Mais and Rabeder, p. 85.

Material: (41) Upper Pliocene (MN 16) of Bad Deutsch Altenburg 20: vertebrae (UWPI). (42) Middle Pleistocene of Bad Deutsch Altenburg 2: one basiparasphenoid (UWPI 2271/18/2; not seen; fide Rabeder, 1974). (55) Middle Pleistocene of Varbeshnitsa: 3 trunk vertebrae (IZBAN). (56) Late Pleistocene of Stoilovo: 3 trunk vertebrae (IZBAN).

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 basiparasphenoid 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.
(10) 1987 *Coluber* sp.: Zerova, p. 13.
(24) 1987 *Coluber* sp.: Zerova, p. 16.
(28) (29) (30) (31) (32) (33) (34) (35) (36):
      1987 *Coluber* sp.: Redkozubov, p. 71.
(10) 1990 *Coluber* sp.: Szyndlar and Zerova, p. 54.
(34) 1989 *Coluber* sp.: Redkozubov, p. 209.

Material: (10) Late Miocene (MN 9) of Gritsev: cranial bones and vertebrae (IZAN). (28) Middle Pliocene (MN 15) of Etuliya: trunk vertebrae (not seen; fide Redkozubov, 1987). (29) Middle pliocene (MN 15) of Lucheshty: trunk vertebrae (not seen, fide Redkozubov 1987). (30) Middle Pliocene (MN 15) of Valeny: trunk vertebrae (not seen; fide Redkozubov, 1987). (31) Middle Pliocene (MN 15) of Musait: trunk vertebrae (not seen; fide Redkozubov, 1987). (32) Middle Pliocene (MN 15) of Dermendzhi: trunk vertebrae (not seen; fide Redkozubov, 1987). (33) Upper Pliocene (MN 16) of Novye Tanatary: trunk vertebrae (not seen; fide Redkozubov, 1987). (34) Upper Pliocene (MN 16) of Salchiya: trunk vertebrae (not seen; fide Redkozubov, 1987). (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen; fide Redkozubov, 1987). (36) Upper Pliocene (MN 16) of Bachoy: trunk vertebrae (not seen; fide Redkozubov, 1987). (24) Ukrainian Upper Pliocene: precaudal vertebrae (IZAN).

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.).

(28) (29) (30) (31) (32) (33) (34) (35) (36): No additional remarks accompanied the statement of Redkozubov (1987: 71) that «... trunk vertebrae...» of «... *Coluber* sp. occurred in all [Moldavian] sites».

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.]
(35) 1987 *Coronella austriaca:* Redkozubov, p. 71.

Material: (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen; fide Redkozubov, 1987). (9) Polish Pleistocene (7 sites altogether; for detailes see Szyndlar, 1984: 102): 6 basioccipitals (ZZSiD KG-8001-8006), one frontal (ZZSiD KG-8007), one quadrate (ZZSiD KG-8008), 87 precaudal vertebrae (ZZSiD ZA-301-310, KG-8050, 8200). (53) Middle Pleistocene of Braşov: one basiparasphenoid, one fragmentary basioccipital, one quadrate, 4 fragmentary compounds (not seen; fide Bolkay, 1913).

Diagnostic vertebral characters: In its vertebral morphology, this living snake differs from other small-sized colubrines (cf. fig. 8) by a set of the following features: strongly depressed neural arch, very short prezygapophyseal processes (twice to three times shorter than the prezygapophyseal facets); zygosphene of variable shape in dorsal view, usually with two distinct outer lobes and an indistinct (or absent) median lobe; the haemal keel is usually weakly developed; in dorsal view, trunk vertebrae are strongly narrowed in the middle of the centrum length (Szyndlar, 1984). Of the material available, the centrum length of trunk vertebrae does not exceed 3.00 mm; in 60 vertebrae from the Polish Pleistocene, it ranges between 2.78 and 2.96 mm and the centra are 1.34-1.53 times longer than wide (mean 1.45 ± 0.05) (Szyndlar, 1984).

Remarks: Vertebrae of *C. austriaca,* although in most cases well differentiable from small-sized colubrines belonging to other genera, are very similar to those of another member of the genus *Coronella,* namely *C. girondica* from West Europe. Some differences between both species were observed by Szyndlar (1984, fig. 6), i.e., basal portion of prezygapophyses more strongly built and parapophyses longer than diapophyses in *C. austriaca.* These observations were based on limited comparative material. More clear differences can be observed in some cranial elements; (6) apart from vertebrae, skull bones were the basis of identification of *C. austriaca* from several Polish Pleistocene localities (see Szyndlar, 1984, for details). (53) Bolkay (1913: 225), in his report of this snake from Braşov, mentioned only that «the bones agree entirely with the recent and corresponding parts of *Coronella austriaca* Laur.»; the figure showing a basiparasphenoid (ibid. fig. 3) does not fully display features characteristic for *C. austriaca.* (35) Redkozubov (1987), who based his report exclusively on vertebrae, also only mentioned about the presence of *C. austriaca* in the Moldavian locality of Chishmikioy, providing no comments on his find.

All the above mentioned sites are located within the present range of *C. austriaca.*

The skull morphology of this snake was described in detail by von Szunyoghy (1932: 20, 28, 32; figs. 41-45, 58, 70, 82, 87, 106, 111, 112; pl. V: 23, 24; pl. VI: 11; pl. VII: 8).

Coronella sp.

(35) (36) 1987 *Coronella* sp.: Redkozubov, p. 71.

Material: (35) Upper Pleistocene (MN 16) of Chishmikioy: trunk vertebrae (not seen; fide Redkozubov, 1987). (36) Upper

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

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

cf. *Coronella* sp. (fig. 15).

(57) 1982 *Coronella* aff. *austriaca* (Laurenti) [part]: Mlynarski, p. 50.

Material: (55) Middle Pleistocene of Varbeshnitsa: 5 trunk vertebrae (IZBAN). (68) Middle Pleistocene of Tourkobounia 2: one trunk vertebra (UUGI). (57) Late Pleistocene of Bacho Kiro: 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).

1985 *Elaphe kohfidischi* Bachmayer et Szyndlar, pp. 80-84, fig. 1: 1-16, pl. 1: 1-3.
1987 *Elaphe kohfidischi* Bachmayer et Szyndlar: Bachmayer and Szyndlar, pp. 26-29, fig. 1, pl. 1: 1, 2.

Material: (40) Upper Miocene (MN 11) of Kohfidisch (type locality): 3 basiparasphenoids (NMW 1986/4/1, 2), one parietal fragment (NMW 1986/4/3), two basioccipitals (NMW 1986/4/4), two maxillary fragments (NMW 1986/4/5, 6), two dentary fragments (NMW 1986/4/7), one axis (NMW 1984/101/3), one trunk vertebra (holotype, NMW 1984/96), several hundred precaudal vertebrae (NMW1984/101/1, 2, 4), caudal vertebrae (NMW 1984/101/5).

Diagnostic vertebral characters: Trunk vertebrae of *E. kohfidischi* are characterized by a thin, high, spatulate-shaped haemal keel, with a characteristic «step» behind the cotylar rim; neural spine somewhat longer than high; zygosphene 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 basipterygoid 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 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 zygosphene (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).

cf. *Elaphe kohfidischi* Bachmayer et Szyndlar, 1985.

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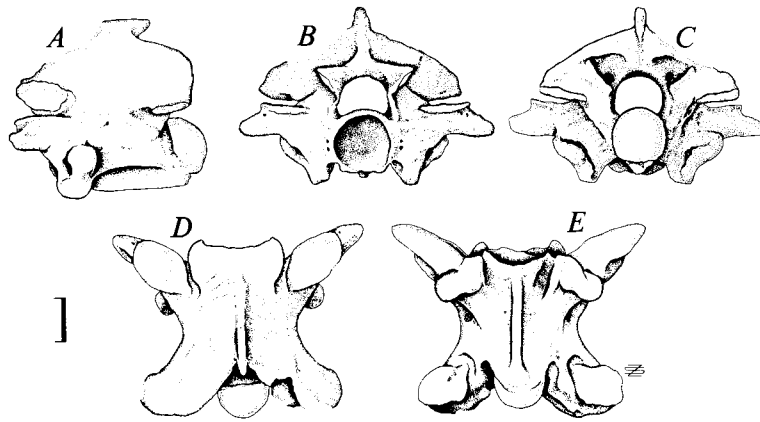
Fig. 16.—Trunk vertebra of *Elaphe kohfidischi* from upper Miocene of Kohfidisch (holotype, NMW 1984/96). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm. (From Bachmayer and Szyndlar, 1985.)
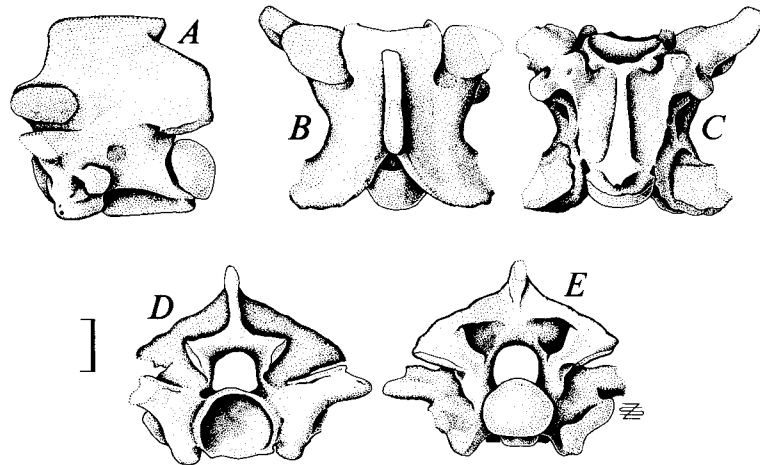

Fig. 17.—Trunk vertebrae of *Elaphe paralongissima* from Węże 2 (A, ZPPAN R-III/12; B-E, holotype, ZPPAN R-III/11). A: left lateral view; B: dorsal view; C: ventral view; D: anterior view; E: posterior view. Scale equals 2 mm. (From Szyndlar, 1984.)
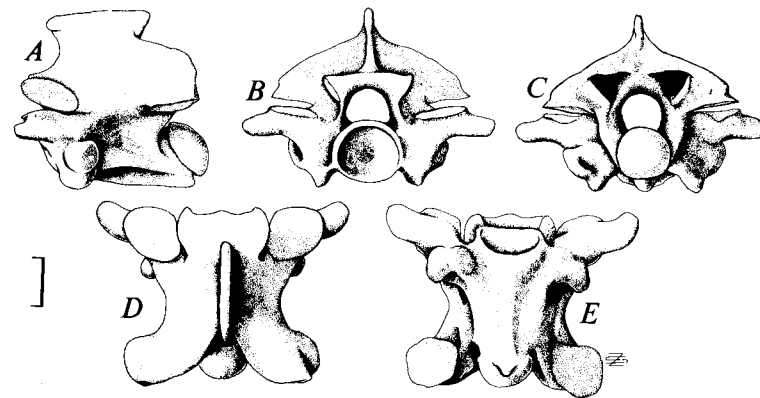

Fig. 18.—Trunk vertebra of *Elaphe longissima* from Polish Pleistocene (ZZSiD JO-201). A: left lateral view; B: anterior view; C: posterior view; D: dorsal view; E: ventral view. Scale equals 2 mm. (From Szyndlar, 1984.)

1939 *Coluber kormosi* Bolkay: Kuhn, p. 18.
1961 *Elaphe longissima* (Laurenti): Mlynarski, pp. 25-26.
1963 ? *«Coluber» kormosi:* Kuhn, p. 21.
1984 *Elaphe kormosi* (Bolkay): Rage, p. 46.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi (type locality): one fragmentary basiparasphenoid, one basioccipital, one premaxilla, one fragmentary palatine, 5 maxillary fragments, two ectopterygoids, 3 quadrates (syntypes, 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 Szunyoghy (1932) then synonymized the fossil species with *Elaphe longissima.* Mlynarski (1961), although retaining von Szunyoghy'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 palatine (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 occipitocondylar tubercle. Moreover, the basioccipital crest consists of two tubercles and is devoid of a median process (cf. 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).

1984 *Elaphe paralongissima* Szyndlar, pp. 67-71, fig. 26.
1985 *Elaphe paralongissima* Szyndlar: Szyndlar in Mlynarski *et al.,* p. 222, fig. 7: 1, 2.

Material: (5) Upper Pliocene (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).

(46) (52) (53):
　　　1932 *Elaphe longissima* Laur.: von Szunyoghy, pp. 10 and 49-50.
(43) 1977 *Elaphe longissima* (Laurenti): Rabeder, p. 92, fig. 11: 4, pl. 1: 11.
(9) 1984 *Elaphe longissima* (Laurenti): Szyndlar, pp. 86-97, figs. 34-37.
(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.]

Material: (46) Upper Pliocene (MN 16) of Beremend 1: one parietal (not seen; fide von Szunyoghy, 1932). (9) Polish Pleistocene (15 sites altogether; for details see Szyndlar, 1984: table XIII): three frontals, 21 parietals, 4 basioccipitals, 35 basiparasphenoids, above 21 maxillae, above 17 pterygoids, above 3 ectopterygoids, above 13 palatines, 3 squamosals, above 10 quadrates, above 15 quadrates, 141 dentaires, 2 nasals, 2 premaxillae, one septomaxilla, ca. 5700 vertebrae, ca. 300 ribs (ZZSiD ZA-1-300, KG-1-32, 5000-5050, 6000, 7001-7050, JO-1-938, GI-1-606; ZPPAN; ZPUW). (52) Lower Pleistocene of Betfia: one parietal (not seen; fide von Szunyoghy, 1932). (43) Middle Pleistocene of St. Margarethen: one basioccipital, one quadrate (UWPI 2350/5/1-2; not seen; fide Rabeder, 1977). (53) Middle Pleistocene of Braşov: one basisphenoid (not seen; fide von Szunyoghy, 1932). (55) Middle Pleistocene of Varbeshnitsa: 7 trunk vertebrae (IZBAN). (69) Middle Pleistocene of Tourkobounia 5: one trunk vertebrae (UUGI).

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 zygosphene 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). Vertebrae of this snake are relatively large; maximum centrum length of a vertebra recorded from the Polish Pleistocene is 7.97 mm and in a vertebra from Tourkobounia 1 it is 7.84 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 (ZZSiD 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. (9) Almost all kinds of cranial elements were recorded from the Polish Pleistocene; they are described in detailed and figured by Szyndlar (1984). (43) Of 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 Szunyoghy (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, 6: 4, 7: 3, 11: 3, 12: 3).

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

cf. *Elaphe longissima* (Laurenti, 1768).

(42) 1974 *Elaphe* sp. *(E. longissima?):* Rabeder, p. 148, fig. 1.
(28) (30) (32) (33) (35) (36):
　　　1987 [sic] *Elaph* cf. *longissima:* Redkozubov, p. 71.

Material: (28) Middle Pliocene (MN 15) of Etuliya: trunk vertebrae (not seen; fide Redkozubov, 1987). (30) Middle Pliocene (MN 15) of Valeny: trunk vertebrae (not seen; fide Redkozubov, 1987). (32) Middle Pliocene (MN 15) of Dermendzhi: trunk vertebrae (not seen; fide Redkozubov, 1987). (33) Upper Pliocene (MN 16) of Novye Tanatary: trunk vertebrae (not seen; fide Redkozubov, 1987). (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen; fide Redkozubov, 1987). (36) Upper Pliocene (MN 16) of Bachoy: trunk vertebrae (not seen; fide Redkozubov, 1987). (42) Middle Pleistocene of Bad Deutsch Altenburg 2: one basiparasphenoid, palatines (UWPI 2275/26/5; not seen; fide Rabeder, 1974). (68) Middle Pleistocene of Tourkobounia 2: 2 trunk vertebrae (UUGI). (71) Upper Pleistocene of Gerani 1: one trunk vertebra (UGGI). (73) Upper Quaternary of Pili B: one fragmentary trunk vertebra (UUGI).

Remarks: (68) (71) (73) Vertebrae 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 (Lacépède, 1789) (fig. 19).

(42) 1974 *Elaphe* cf. *quatuorlineata* (Lacépède): Rabeder, p. 148, fig. 3.
(41) 1977 [?] *Elaphe* sp.: Mais and Rabeder, p. 85.

Material: (41) Upper Pliocene (MN 16) of Bad Deutsch Altenburg 20: skull bones and vertebrae (UWPI). (50) Lower Pleistocene of Csarnóta 4: 3 trunk vertebrae (ZZSiD). (42) Middle Pleistocene of Bad Deutsch Albenburg 2: one basiparasphenoid (UWPI 2271/18/1; not seen; fide Rabeder, 1974). (55) Middle Pleistocene of Varbeshnitsa; 3 trunk vertebrae (IZBAN). (68) Middle Pleistocene of Tourkobounia 2: 9 trunk vertebrae, one fragmentary compound (UUGI). (69) Middle Pleistocene of Tourkobounia 5: 8 trunk vertebrae (UUGI). (56) Late Pleistocene of Stoilovo: 2 trunk vertebrae (IZBAN).

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 zygosphene is distinctly concave; 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 (ZZSiD 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 ± 2.33). 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. Szyndlar, 1984, fig. 6).

Remarks: Detailed description of skull morphology of this snake may be found in von Szunyoghy (1932: 19, 25, 30-31; figs. 53, 65, 77, 92, 103, 113; pl. II: 9, 10; pl. VI: 1; pl. VII: 1); some differentiating features were also presented by Rabeder (1977; figs. 5: 6, 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 Szyndlar an Rabeder (in prep.); the material from this locality includes, among others, highly characteristic cervical vertebrae.

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

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

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

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

Material: (55) Middle Pleistocene of Varbeshnitsa: 8 trunk vertebrae (IZBAN). (68) Middle Pleistocene of Tourkobounia 2: 7 trunk vertebrae (UUGI). (57) Upper Pleistocene of Bacho Kiro: 5 trunk vertebrae (ZZSiD). (71) Upper Pleistocene of Gerani 1: ca. 30 vertebrae (UUGI). (71) Upper Pleistocene of Gerani 4: one precaudal vertebra (UUGI). (72) Upper Pleistocene of Rethymnon: ca. 60 vertebrae (UUGI). (73) Upper Quaternary of Pili B: 3 trunk vertebrae (UUGI).

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 zygosphene is triangle-shaped (cf. fig. 8). The centrum length of 14 largest vertebrae from Rethymnon ranges between 3.73 and 4.63 mm (mean 4.10 ± 0.24). In comparison with other small colubrines, trunk vertebrae of *E. situla* 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. situla*.

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

Elaphe sp.

(10) 1987 *Elaphe* sp.: Zerova, p. 13.
(24) 1987 *Elaphe* sp.: p. 16.
(25) 1987 *Elaphe dione:* Zerova, p. 17.
(28) (31) (35) (36):
1987 [sic] *Elaph* sp.: Redkozubov, p. 71.
(10) 1990 *Elaphe* sp.: Szyndlar and Zerova, p. 54.

Material: (10) Late Miocene (MN 9) of Gritsev: cranial bones and vertebrae (IZAN). (28) Middle Pliocene (MN 15) of Etuliya: trunk vertebrae (not seen; fide Redkozubov, 1987). (31) Middle Pliocene (MN 15) of Musait: trunk vertebrae (not seen; fide Redkozubov, 1987). (24) Ukrainian Upper Pliocene: vertebrae (IZAN). (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen; fide Redkozubov, 1987). (36) Upper Pliocene (MN 16) of Bachoy: trunk vertebrae (not seen; fide Redkozubov, 1987). (25) Ukrainian Pleistocene: vertebrae (IZAN).

Remarks: (10) Abundant remains from Gritsev, 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 Europan 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: Vertebrae of *M. monspessulanus*, the only living European member of the genus, can be differentiated from other large-sized West Paleartic 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 zygosphene 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 8.70 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 (ZZSiD 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 is 4.73-5.47 mm and the centrum lenght/width ratio is 1.37-1.48. Vertebrae of *M. monspessulanus* coming from all regions of the column were figured by Szyndlar (1984; fig. 4).

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

The skull morphology of *M. monspessulanus* was described by von Szunyoghy (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 braincase elements considering intraspecific variation and comparisons with *Elaphe* and *Coluber* can be found in Szyndlar (1988). Another member of the genus, *M. moilensis* from Africa, displays completely different morphology in both its skull and vertebrae; most likely, *M. moilensis* does not represent the genus *Malpolon* (Szyndlar, 1988).
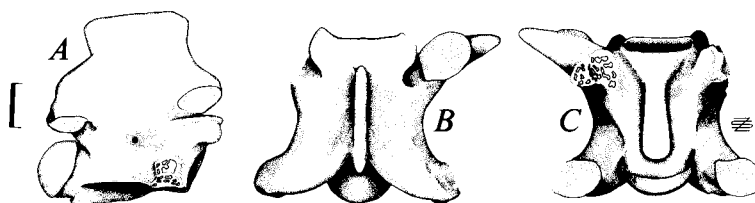
Fig. 19.—Trunk vertebra of *Elaphe quatuorlineata* from middle Pleistocene of Tourkobounia 2 (UUGI). A: right lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.
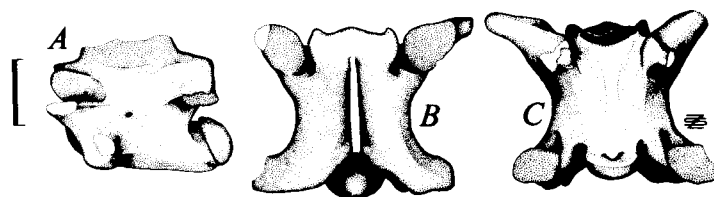

Fig. 20.—Trunk vertebra of *Elaphe situla* from middle Pleistocene of Tourkobounia 2 (UUGI). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.
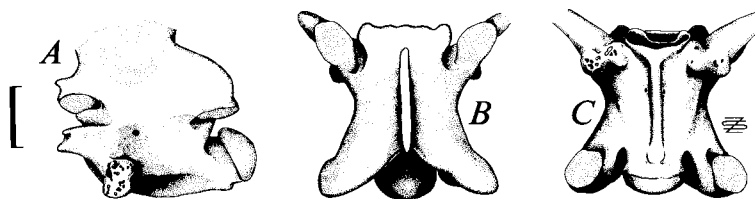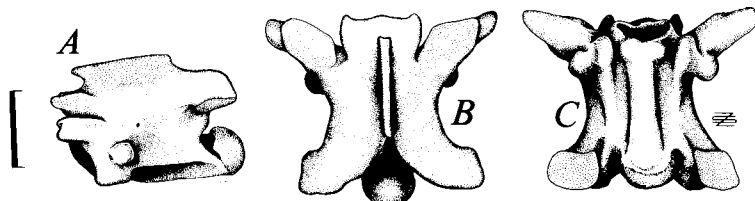

Fig. 21.—Trunk vertebra of cf. *Malpolon* sp. from upper Pliocene of Tourkobounia 1 (UUGI). A: left lateral view; B: dorsal view; C: ventral view. Scale equals 2 mm.

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.

(?) *Malpolon* sp.

1911   *Coelopeltis* ?: Kormos, p. 63 (187).

Material: (44) Uppermost Miocene (MN 13) of Polgárdi: vertebrae (not seen; fide Kormos, 1911).

Remarks: The presumed presence of *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 vertebrae on which Kormos' report was based. In any case, Kormos provided no description of his find and his identification is doubtful. Snake vertebrae from Děvínska Nová Ves, identified by Wettstein-Westersheimb (1955) as belonging to *Malpolon* (? *Malpolon* sp.), actually belong to another colubrine taxon (see below: Colubrinae indet. (38)).

Genus *Telescopus* Wagler, 1830.
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 *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 zygosphene is provided with three distinct lobes and the prezygapophyseal processes are very short and obtuse. The centrum of a trunk vertebra from Varbeschnitsa 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 *T. fallax*. However, considering that vertebrae of another member of the genus available for study, *T. dhara*, closely resemble those of *T. fallax*, proper identification of the fossils to the specific level seems impossible. Varbeshnitsa is situated at the northern boundary of the present range of this snake. *Telescopus* is for the first time recorded in fossil state.

The skull of *T. fallax* was described in detail by von Szunyoghy (1932: 20, 29, 33; figs. 60, 72, 84, 96, 108; pl. V: 25, 26; pl. VI: 9; pl. VII: 11).

«Colubrinae» indet.

(2)   1913   *Tamnophis* sp.: Wegner, p. 212.
(39) 1954   ? Anilidae (= Tortricidae): Papp *et al.*, pp. 48-49, pl. 6: 23, 24.
(38) 1955   ? *Malpolon* (= *Coelopeltis*) spec.?: Wettstein-Westersheimb, p. 813, pl. 2: 4.
(70) 1975   Colubridae: Schneider, p. 193, fig. 3 A.
(2)   1982   *Ogmophis europaeus* Szyndlar (in Mlynarski *et al.*), pp. 112-114, fig. 9.
(28) (29) (30):
      1982   Colubridae: Redkozubov, p. 21.
(2)   1984   *Ogmophis europaeus* Szyndlar: Szyndlar, pp. 31-34, fig. 10.
(1)   1984   Colubrinae indet. (form «A»): Szyndlar, pp. 34-36, fig. 11.
(2)   1984   (?) *Coluber* sp. (= *Tamnophis* sp.): Szyndlar, pp. 37-38.
(8)   1984   Colubrinae indet. (form «B»): Szyndlar, pp. 40-41, fig. 13.
(8)   1984   Colubrinae indet. (form «C»): Szyndlar, pp. 42-43, fig. 14.
(3)   1984   Colubrinae indet. (form «D»): Szyndlar, pp. 43-44, fig. 15.
(27) 1984   *Coluber* (sensu lato): Chkhikvadze and Lungu, p. 82.
(37) 1987   Colubridae indet.: Szyndlar, p. 66, fig. 66.
(10) 1987   *Boiga* cf. *meini* (Rage, Holman): Zerova, p. 13.
(17) (18):
      1987   Colubridae: Zerova, p. 15.
(21) 1987   *Elaphe* sp.: Zerova, p. 15.
(24) 1987   Colubridae: Zerova, p. 16.

Material: (37) Lower Miocene (MN 4) of Dolnice: 7 vertebrae (DPFNSP 1374, 3938, 3964, 4200, 4530, 5207). (1) Middle Miocene (MN 5-7) of Przeworno 2: one fragmentary trunk vertebra (ZZSiD PR-1). (38) Middle Miocene (MN 6) of Děvínska Nová Ves: 32 vertebrae (not seen; fide Wettstein-Westersheimb); 32 other precaudal vertebrae (DPFNSP 5820-5834, 5836, 5838-5842, 5845-5854, 5856). (2) Middle Miocene (MN 7) of Opole: one vertebra (lost, fide Wegner, 1913); 20 other precaudal vertebrae (ZPUW OP 86/1-20). (10) Late Miocene (MN 9) of Gritsev: 3 vertebrae (IZAN). (27) Late Miocene (MN 9 or 10) of Buzhor: one vertebra (not seen; fide Chkhikvadze and Lungu, 1984). (39) Late Miocene of Vösendorf (MN 10): one vertebra (not seen; fide Papp *et al.*, 1954). (11) Upper Miocene (MN 11) of Krivoy Rog: one trunk vertebra (IZAN). (12) Upper Miocene (MN 11) of Novoelizabetovka (lower layer): numerous vertebrae (IZAN). (17) Uppermost Miocene (MN 13) of Novoukrainka 1: vertebrae (IZAN). (18) Uppermost Miocene (MN 13) of Andreievka: vertebrae (IZAN). (19) Uppermost Miocene (MN 13) of Frunzovka 2: vertebrae (IZAN). (44) Uppermost Miocene (MN 13) of Polgárdi: 5 fragmentary vertebrae (MHGI). (60) Uppermost Miocene (MN 13) of Maramena 1: fragmentary vertebrae (UUGI). (63) Lower Pliocene (MN 14) of Maritsa: fragmentary vertebrae (UUGI). (3) Lower Pliocene (MN 14) of Podlesice: 16 fragmentary vertebrae (ZZSiD PO 4-6). (21) Middle Pliocene (MN 15) of Kotlovina (lower layer): 3 precaudal vertebrae (IZAN). (28) Middle Pliocene (MN 15) of Etuliya: vertebrae and vertebral fragments (not seen; fide Redkozubov, 1982). (29) Middle Pliocene (MN 15) of Lucheshty: vertebrae and vertebral fragments (not seen; fide Redkozubov, 1982). (30) Middle Pliocene (MN 15) of Valeny: vertebrae and vertebral fragments (not seen; fide Redkozubov, 1982). (64) Middle Pliocene (MN 15) of Spilia 4: 31 fragmentary vertebrae (UUGI). (24) Ukrainian Upper Pliocene: vertebrae (IZAN). (65) Upper Pliocene (MN 16) of Tourkobounia 1: 14 fragmentary trunk vertebrae (UUGI). (68) Middle Pleistocene of Tourkobounia 2: 127 vertebrae and vertebral fragments, two fragmentary quadrates (UUGI). (69) Middle Pleistocene of Tourkobounia 5: ca. 405 vertebrae, 2 fragmentary dentaries, one maxillary fragment, 2 ribs (UUGI). (70) Middle Pleistocene of Chios: a trunk vertebra (SMF; not seen; fide Schneider, 1975). (8) Mala Cave (age uncertain): two fused vertebrae (ZPUW IZ-6/E/2), another trunk vertebra (ZPUW IZ-6/R/3). (73) Upper Quaternary of Pili B: 4 fragmentary precaudal vertebrae (UUGI).

Remarks: For various reasons, most often because of fragmentary preservation of the remains, unsufficient amount of the material, or owing to dissimilarity of the remains to other known fossil and living snakes, all the above-listed collections were not identified below the subfamilial level. In some cases, primary allocations were false, as stated by later authors.

(37): Of some unidentified colubrine vertebrae, reported by Szyndlar (1987) from Dolnice, two vertebral fragments (DPFNSP 3938 and 4200) perhaps belonged to *Texasophis*, while another one (DPFNSP 4530) closely resembles *Telescopus* (ibid., fig. 9).

(1): A unique ophidian remain from the locality of Przeworno 2, is a vertebral fragment of a medium-sized snake (centrum length 5.27 mm), similar to *Elaphe* or *Coluber* and not to *Malpolon* (Szyndlar, 1984).

(38): The presumed vertebrae of *Malpolon* reported by Wettstein-Westersheimb (1955) from Děvínska Nová Ves, based on Wettstein-Westersheimb's photo (ibid., pl. 2: 4) are not referable to this genus (cf. Szyndlar, 1984). Other vertebrae from the same locality, belonging to the DPFNSP collection, represented at least 2 different colubrine species: a small form (DPFNSP 5821, 5826, 5829, and others), similar to *Texasophis* but with indistinct haemal keel, and a large form, similar to recent medium-sized members of *Coluber* and *Elaphe* (DPFNSP 5820, 5845, 5848, 5854).

(2): A snake vertebra from Opole, referred by Wegner (1913) to *Tamnophis* (= *Coluber pouchetii* from the French Miocene; cf. Rage, 1984: 44), was never described nor figured and it is probably lost (Szyndlar, 1984); note that the locality of Wegner (1913), originally named Oppeln, is not identical with Opole 2. Vertebrae from Opole 2, described by Szyndlar (in Mlynarski *et al.*, 1982) as a new erycine species, *Ogmophis europaeus*, display

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., *Texasophis meini;* cf. comments to the genus *Texasophis*, 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)».

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

(11) (12) (17) (18) (19) (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): Few fragmentary vertebrae from Polgárdi belonged to snakes of very small size; they probably represent a single species.

(60): Fragmentary vertebrae from Maramena 1 belonged to at least 2 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 Maramena 1; caudal vertebrae present 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 downswept posterior portion of the haemal keel, deep furrows accompanying the lateral foraina and the condylar neck extending far behind the neural arch (Szyndlar, 1984).

(28) (29) (30): No explanation accompanies Redkozubov's (1982: 21) report of «... vertebrae and vertebral fragments» of «Colubridae» from three Moldavian sites.

(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 Mala 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

References

Armour-Brown, A.; Bruijn, H. de.; Maniati, C.; Siatos, G., and Niesen, P. (1977). The geology of the Neogene sediments north of Serrai and the use of rodent faunas for biostratigraphic control. *Proc. VI Coll. Geol. Aegean Region*, 2, 615-622.

Bachmayer, F. and Szyndlar, Z. (1985). Ophidians (Reptilia: Serpentes) from the Kohfidisch fissures of Burgenland, Austria. *Ann. Naturhist. Mus. Wien*, 87, 79-100.

Bachmayer, F. and Szyndlar, Z. (1987). A second contribution to the ophidian fauna (Reptilia: Serpentes) of Kohfidisch, Austria. *Ann. Naturhist. Mus. Wien*, 88, 25-39.

Bolkay, St. J. (1913). Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. *Mitt. Jb. Kgl. Ung. Geol. Reichsanst.*, 21, 217-230.

Bolkay, St. J. (1925). *Mesophis Nopcsai* n.g.n.sp. Ein neues, schlangenähnliches Reptil aus der unteren Kreide (Neocom) von Bilek-Selišta (Ost-Hercegovina). *Glasn. Zemal. Muz. Bosni Herceg.*, 37, 125-134.

Bogert, C. M. (1968). A new genus and species of dwarf boa from southern Mexico. *Amer. Mus. Novitates*, 2354, 1-38.

Bruijn, H. de (1976). Vallesian and Turolian rodents from Biota, Attica and Rhodes (Greece). I, II. *Proc. Konink. Nederl. Akad. Wetensch.*, ser. B, 79, 361-384.

Bruijn, H. de, and Meulen, A. J. van der (1975). The Early Pleistocene rodents from Tourkobounia-1 (Athens, Greece). I, II. *Proc. Konink. Nederl. Akad. Wetensch.*, ser. B, 78, 314-338.

Bruijn, H. de, and Meulen, A. J. van der (1979). A review of the Neogene rodent succession in Greece. *Ann. Géol. Pays Hellén.* (Tome hors série), 1979 (1), 207-217.

Chkhikvadze, V. M. and Lungu, A. N. (1973). Nekotorye dannye o gerpetofaune srednego sarmata Moldavii. [Some data on the herpetofauna of the middle Sarmatian of Moldavia.] Pp. 79-87. In: *Paleontologiya i stratigrafiya mezokaynozoya yuzhnykh okrain Russkoy platformy*. Izd. Shtiintsa, Kishinev.

Chkhikvadze, V. M. and Lungu, A. N. (1984). Novye dannye o miotsenovoy gerpetofaune Moldavii i Kavkava. [New data on the Miocene herpetofauna of Moldavia and the Caucasus.] Pp. 72-86. In: *Paleobiogeograficheskie issledovaniya mezozoya Dnestrovsko-Prutskogo mezhdurech'ya*. Izd. Shtiintsa, Kishinev.

David, A. I.; Bilinkis, G. M.; Shushpanov, K. I., and Redkozubov, O. I. (1988). Paleontologicheskaya kharakteristika neostratotipa fyrladyanskoy terrasy u s. Salchiya (MSSR) [Paleontological characteristics of the neostratotype of Fyrlandyan Terrace near the village of Salchiya (Moldavian SSR).] *Izv. Akad. Nauk Mold. SSR, Ser. biol. khim. nauk*, 1988, 72-74.

Estes, R. (1987). Lucas and Zidek on taxonomic syntax. *J. Vert. Paleont.*, 7, 101.

Fahlbusch, V. (1976). Report on the International Symposium on mammalian stratigraphy of the European Tertiary (München, April 11-14, 1975). *Newsl. Stratigr.*, 5, 160-167.

Fejfar, O. and Heinrich, W. D. (1983). Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. *Schriftenr. Geol. Wiss.*, 19/20, 61-109.

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

land and their paleogeographic implications. Pp. 113-130. In: *Problemy mlodszego neogenu i eoplejstocenu w Polsce*. Ossolineum, Wrocław.

Hoffstetter, R. and Rage, J. C. (1972). Les Erycinae fossiles de France (Serpentes, Boidae). Compréhension et histoire de la sous-famille. *Ann. Paléont. Vert.*, 58, 81-124.

Holman, J. A. (1977). Amphibians and reptiles from the Gulf Coast Miocene of Texas. *Herpetologica*, 33, 391-403.

Jánossy, D. (1986). *Pleistocene vertebrate faunas of Hungary*. Akadémiai Kiadó, Budapest.

Kordos, L. (1987). Neogene vertebrate biostratigraphy in Hungary. *Ann. Inst. Geol. Publ. Hung.*, 70, 393-396.

Kormos, T. (1911). A Polgárdi pliocén csontlelet. *Földt. Közl.*, 41, 48-64.

Kretzoi, M. (1956). A Villányi hegység Alsó-Pleisztocén gerinces-faunái. *Geol. Hung.* (Ser. Paleont.), 27, 1-264.

Kuhn, O. (1939). *Squamata: Lacertilia et Ophidia. Fossilium Catalogus, I: Animalia, pars 86*. Verlag Gustva Feller, Neubrandenburg.

Kuhn, O. (1963). *Serpentes (Supplementum I). Fossilium Catalogus, I: Animalia, pars 103*. W. Junk, The Hague.

Mais, K. and Rabeder, G. (1977). Eine weitere pliozäne Höhlenfauna aus dem Steinbruch Hollitzer bei Bad Deutsch Altenburg (Niederösterreich). *Die Höhle*, 28, 84-86.

Mayhew, D. F. (1977). The endemic Pleistocene murids of Crete. I. *Proc. Konink. Nederl. Akad. Wetensch.*, ser. B, 80, 182-214.

Mein, P. (1975). Biozonation du Néogène méditerranéen à partir des Mammifères. *Proc. VIth Congr. Reg. Comm. Medit. Neogene Stratigr.*, Bratislava, unpaginated.

Meyer, H. von (1844). [Untitled.] *N. Jb. Min. Geognos. Geol. Petrefakt.*, 12, 564-567.

Młynarski, M. (1960). Pliocene amphibians and reptiles from Rębielice Królewskie (Poland). *Acta Zool. Cracov.*, 5, 131-153.

Młynarski, M. (1961). Serpents pliocènes et pléistocènes de la Pologne avec la revue critique des Colubridés fossiles. *Folia Quatern.*, 4, 1-45.

Młynarski, M. (1964). Die jungpliozäne Reptilienfauna von Rębielice Królewskie, Polen. *Senck. Biol.*, 45, 325-347.

Młynarski, M. (1977). New notes on the amphibian and reptilian fauna of the Polish Pliocene and Pleistocene. *Acta Zool. Cracov.*, 22, 13-36.

Młynarski, M. (1982). Amphibian and Reptilia. Pp. 29-31. In: *Excavation in the Bacho Kiro Cave (Bulgaria). Final report* (K. Kozχowski, ed.) Pánstw. Wyd. Nauk., Warszawa.

Młynarski, M.; Szyndlar, Z.; Estes, R., and Sanchiz, B. (1982). Lower vertebrate fauna from the Miocene of Opole (Poland). *Estudios Geol.*, 38, 103-119.

Młynarski, M.; Szyndlar, Z.; Estes, R., and Sanchiz, B. (1985). 1984. Amphibians and reptiles from the Pliocene locality of Węże II near Dziaχoszyn (Poland). *Acta Palaeont. Polon.*, 29, 209-227.

Nadachowski, A.; Pawlowski, J., and Stworzewicz, E. (1989). Charakterystyka stanowisk i ich korelacja stratygraficzna. [Characteristics of localities and their stratigraphic correlation.] In: Historia i ewolucja lądowej fauny Polski (K. Kowalski, ed.). *Folia Quatern.*, 59-60, 5-19.

Nopcsa, F. (1923). *Eidolosaurus* und *Pachyophis*. Zwei neue Neocom-Reptilien. *Palaentographica*, 65, 97-154.

Owen, R. (1857). On the fossil vertebrae of a serpent (*Laophis crotaloïdes*, Ow.) discovered by Capt. Spratt, R. N., in a Tertiary Formation at Salonica. *Quart. J. Geol. Soc. London*, 13, 196-199.

Papp, A.; Thenius, E.; Berger, W., and Weinfurter, E. (1954). 1953. Vösendorf-ein Lebensbild aus dem Pannon des Wiener Beckens. *Mitt. Geol. Ges. Wien*, 46, 1-109.

Popov, V. V. (1988). Middle Pleistocene small mammals (Mammalia: Insectivora, Lagomorpha, Rodentia) from Varbeshnitsa (Bulgaria). *Acta Zool. Cracov.*, 31, 193-234.

Rabeder, G. (1974). Fossile Schlangenreste aus den Höhlenfüllungen des Pflaffenberges bei Bad Deutsch Altenburg (NÖ). *Die Höhle*, 25, 145-149.

Rabeder, G. (1977). Wirbeltierreste aus einer mittelpleistozänen Spaltenfüllung im Leithakalk von St. Margarethen im Burgenland. *Beitr. Paläont. Österr.*, 1977, 79-103.

Rage, J. C. (1972). *Eryx* Daudin et *Gongylophis* Wagler (Serpentes, Boidae). Étude ostéologique. *Bull. Mus. Natn. Hist. Nat.*, 78, 893-898.

Rage, J. C. (1974). Les Serpents des Phosphorites du Quercy. *Palaeovertebrata*, 6, 274-303.

Rage, J. C. (1984). *Serpentes. Handbuch der Paläoherpetologie, Part 11*. Gustav Fischer Verlag, Stuttgart-New York.

Rage, J. C. (1987). Fossil history. Pp. 51-76. In: *Snakes: ecology and evolutionary biology* (R. A. Seigel et al., eds.) MacMillan, New York.

Rage, J. C. and Holman, J. A. (1984). Des Serpents (Reptilia, Squamata) de type Nord-Américain dans le Miocène francais. Evolution parallèle ou dispersion? *Geobios*, 17, 89-104.

Rage, J. C. and Roček, Z. (1983). *Dolniceophis lehmani* (Serpentes, Colubridae), a new fossil snake from the Lower Miocene of Czechoslovakia. *Čas. Mineral Geol.*, 28, 17-21.

Rage, J. C. and Szyndlar, Z. (1986). *Natrix longivertebrata* from the European Neogene, a snake with one of the longest known stratigraphic ranges. *N. Jb. Geol. Paläont. Mh.*, 1986, 56-64.

Redkozubov, O. I. (1982). Nakhodki ostatkov kholodnokrovnykh pozvonochnykh v pliotsene Moldavii. [Finds of remains of cold-blooded vertebrates in the Pliocene of Moldavia.] Pp. 20-21. In: *Faunisticheskie kompleksy, biostratigrafiya pliotsena i pleystotsena Moldavii*. Izd. Shtiintsa, Kishinev.

Redkozubov, O. I. (1987). Novye svedeniya o zmeyakh pliotsena Moldavii. [New data on snakes of the Pliocene of Moldavia.] *Izv. Akad. Nauk Moldav. SSR, Ser. biol. khim. nauk.*, 1987, 71.

Redkozubov, O. I. (1989). Iskopaemye ostatki reptiliy iz verkhnepliotsenovogo mestonakhozhdeniya u s. Salchiya. [Fossil remains of reptiles from the upper Pliocene locality near the village of Salchiya.] Pp. 209-210. In: *Vopr. Gerp., Sed'm. Vsesoy. Gerp. Konf.*, Kiev.

Rochebrune, A. T. de (1880). Revision des Ophidiens fossiles du Muséum d'Histoire Naturelle. *Nouv. Arch. Mus. Hist. Nat.*, sér. 2, 271-296.

Roemer, F. (1870). Ueber *Python Euboïcus*, eine fossile Riesenschlange auf tertiärem Kalkschiefer von Kumi auf

der Insel Euboea. *Zeitschr. Deutsch Geol. Ges.*, 22, 582-590.

Schneider, B. (1975). Eine mittelpleistozäne Herpetofauna von der Insel Chios, Ägäis. *Senck. Biol.*, 56, 191-198.

Sood, M. S. (1941). The caudal vertebrae of *Eryx johnii* (Russell). *Proc. Ind. Acad. Sci.*, ser. B, 14, 390-394.

Sulimski, A.; Szynkiewicz, A., and Woloszyn, B. (1979). The Middle Pliocene micromammals from Central Poland. *Acta Palaeont. Polon.*, 24, 377-403.

Symeonidis, N. and Vos, J. de (1977). Grossäuger-funde aus den Pleistozänen Spaltenfüllungen von Turkovunia in Athen. *Ann. Géol. Pays Hellén,* 46, 135-144.

Szunyoghy, J. von (1932). Beiträge zur vergleichenden Formenlehre des Colubridenschädels, nebst einer kranialogischen Synopsis der fossilen Schlangen ungarns mit nomenklatorischen, sytematischen und phyletischen Bemerkungen. *Acta Zool.*, 13, 1-56.

Szyndlar, Z. (1984). Fossil snakes from Poland. *Acta Zool. Cracov.*, 28, 1-156.

Szyndlar, Z. (1985). Ophidian fauna (Reptilia, Serpentes) from the Uppermost Miocene of Algora (Spain). *Estudios Geol.*, 41, 447-465.

Szyndlar, Z. (1987). Snakes from Lower Miocene locality of Dolnice (Czechoslovakia). *J. Vert. Paleont.*, 7, 55-71.

Szyndlar, Z. (1988). Two new extinct species of the genera *Malpolon* and *Vipera* (Reptilia, Serpentes) from the Pliocene of Layna (Spain). *Acta Zool. Cracov.*, 31, 687-706.

Szyndlar, Z. (in press). A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part. II: Natricinae, Elapidae, Viperidae. *Estudios Geol.*

Szyndlar, Z. and Zerova, G. A. (1990). Neogene cobras of the genus *Naja* (Serpentes, Elapidae) of East Europe. *Ann. Naturhist. Mus. Wien.*, 91, 53-61.

Thomas, H.; Spassov, N.; Kodjumdgieva, E.; Poidevin, J. L.; Popov, V.; Sen, S.; Tassy, P., and Visset, D.

(1986). Résultats préliminaires de la première mission paléontologique franco-bulgare à Dorkovo (arrondissement de Pazardjik, Bulgarie). *C. R. Acad. Sci. Paris,* 302, 1037-1042.

Tokar', A. A. (1989). Reviziya roda *Eryx* (Serpentes, Boidae) po osteologicheskim dannym. [Revision of the genus *Eryx* (Serpentes, Boidae) on the basis of osteological data.] *Vest. Zool.*, 46-55.

Wegner, N. (1913). Tertiär und umgelagerte Kreide bei Oppeln (Oberschlesien). *Palaeontographica,* 60, 175-274.

Wettstein, O. (1953). Herpetologia aegaea. *SB Österr. Akad. Wiss., Math.-naturw. Kl.,* Abt. I, 162, 651-833.

Wettstein-Westersheimb, O. (1955). Die Fauna der miozänen Spaltenfüllung von Neudorf a.d. March (ČSR.). Amphibia (Anura) et Reptilia. *SB Österr. Akad. Wiss., Math.-naturw. Kl.,* Abt. I, 164, 805-815.

Zerova, G. A. (1987). Mestonakhozhdeniya pozdnemiotsenovykh rannepleystotsenovykh yashcherits i zmey Ukrainy. [Localities of the late Miocene-early Pleistocene lizards and snakes of the Ukraine.] Pp. 12-18. In: *Materialy po nekotorym gruppam pozdnekaynozoyskikh pozvonochnykh Ukrainy.* Inst. Zool. AN USSR, Kiev.

Zerova, G. A. (1989). The first find of a fossil Sand Boa of the genus *Albaneryx* (Serpentes, Boidae) in the USSR. *Vest. Zool.*, 1989, 30-35.

Zerova, G. A. and Chkhikvadze, V. M. (1984). Review of Cenozoic lizards and snakes of the USSR. *Izv. Akad. Nauk GSSR, Ser. biol.*, 10, 319-326.

Zerova, G. A.; Lungu, A. N. and Chkhikvadze, V. M. (1987). 1986. Large fossil vipers from northern Black Seaside and Transcaucasus. *Trudy Zool. Inst. (Leningrad),* 158, 89-99.