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Z. Szyndlar. Fossil snakes from Poland — Kopalne węże Polski 1

POLSKA AKADEMIA NAUK
ZAKŁAD ZOOLOGII SYSTEMATYCZNEJ I DOŚWIADCZALNEJ

ACTA ZOOLOGICA CRACOVIENSIA

XXVIII
(Pars I)
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PAŃSTWOWE WYDAWNICTWO NAUKOWE
WARSZAWA—KRAKÓW 1984

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Adres redakcji: Zakład Zoologii Systematycznej i Doświadczalnej Polskiej Akademii Nauk, ul. Sławkowska 17, 31-016 Kraków
Address of the Editor: Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland

POLSKA AKADEMIA NAUK
Zakład Zoologii Systematycznej
i Doświadczalnej w Krakowie
BIBLIOTEKA
K.2787

Redaktor PWN
Maria Kaniowa

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ISBN 83-01-05852-8
ISSN 0065-1710

PAŃSTWOWE WYDAWNICTWO NAUKOWE — ODDZIAŁ W KRAKOWIE

Nakład 830 + 70 egz. — Ark. wyd. 13. — Ark. druk. $9^{13}/_{16}$ + 1 wklejka. Papier druk. sat. kl. III 70×100 90 g.
Oddano do skład. w lutym 1984 — Podpisano do druku w lipcu 1984 — Druk ukończono w lipcu 1984.
Zam. 195/84 Cena zł 140.—

DRUKARNIA UNIWERSYTETU JAGIELLOŃSKIEGO

D Akc. Nr 15/1989

ACTA ZOOL. CRACOV.	28	1	1—156	KRAKÓW, 31. VII. 1984

Zbigniew SZYNDLAR

Fossil Snakes from Poland

[With 62 text-figs]

Kopalne węże Polski *

Abstract. The present paper is a study of fossil snakes found in 27 Polish localities, dated from Middle Miocene into Holocene. The systematic part of the paper contains a review of 22 ophidian taxa, including description of four new species and redescription of one species. The following snakes have been recognized in the fossil materials: from the Miocene and Early Pliocene — *Ogmophis europaeus*, *Palaeonatrix silesiaca*, *Natrix parva* sp. n., *Zelceophis xenos* gen. sp. n., four members of the subfamily *Colubrinae* unidentified to generic level, and two unidentified members of the family *Viperidae*; from the Middle/Upper Pliocene — *Coluber robertmertensi*, *C.* cf. *robertmertensi*, *C.* cf. *viridiflavus*, *Elaphe paralongissima* sp. n., *Natrix longivertebrata* sp. n., *Natrix* cf. *longivertebrata*, and *Vipera ammodytes*; from the Quaternary — *Elaphe* aff. *longissima*, *E. longissima*, *Coronella austriaca*, *Natrix natrix*, and *Vipera berus*. Quantitative and qualitative changes in the snake fauna from Poland are discussed against a background of European paleo-ophiofaunas; moreover, dependence of the composition of Polish snake fauna upon climatic fluctuations during the Quaternary are pointed out. A general pattern of distributional history of modern European snakes, based both on paleontological evidence and zoogeographical analysis, completes the elaboration.

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* Praca wykonana w ramach problemu międzyresortowego MR. II. 3., wyróżniona nagrodą Sekretarza Naukowego Polskiej Akademii Nauk w 1982 r.

I. INTRODUCTION

European fossil snakes with the exception of Tertiary forms from France, have been little studied; moreover, a number of existing descriptions of fossil snakes are inadequate and need revision. In most publications concerning European fossil vertebrate faunas ophidian remains have been determined only to subordinal level.

Contrary to the situation in other Central European countries, fossil snakes from Poland have been fairly well recognized, mostly owing to several papers of MŁYNARSKI, who has given detailed description of snake faunas from four localities (MŁYNARSKI, 1961a, 1961b, 1964; MŁYNARSKI in KOWALSKI et al., 1963) and listed ophidian species from 9 other sites (MŁYNARSKI, 1962, 1977; MŁYNARSKI in BAŁUK et al., 1979). Recently, snake faunas from two Polish localities have been described by SZYNDLAR (1981, 1982).

However, the recovery of ophidian remains from 14 new sites, the necessity to describe materials presented previously in the form of lists only, and the necessity to revise materials already described contributed all to the present attempt to revise the fossil snakes of Poland.

Acknowledgments. I am deeply indebted to Prof. Marian MŁYNARSKI (Cracow) for his guidance and encouragement throughout the course of the work presented herein. Thanks are due to Assoc. Prof. Teresa CZYŻEWSKA (Wrocław), Dr. Borja SANCHÍZ (Madrid), and Dr. Andrzej SULIMSKI (Warsaw) for allowing me to examine specimens in their care. I am grateful to reviewers of an earlier draft of this work *, Assoc. Prof. Teresa MARYAŃSKA (Warsaw) and Prof. Henryk SZARSKI (Cracow), for their helpful criticism and suggestions. Special acknowledgments are due to Dr. Richard ESTES (San Diego) and Dr. Jean-Claude RAGE (Paris), who have read the final draft, for critical comments on various parts of the manuscript. Dr. RAGE, during the development of the present study, has patiently answered my many questions on ophidian paleontology and Dr. ESTES has kindly revised the language of the manuscript.

MATERIAL AND LOCALITIES

Fossil materials described here, consisting of over 150 000 bones of snakes, originate from 27 localities situated in various regions of Poland, for the most part in the area of the Kraków—Wieluń Jurassic Upland in central Southern Poland. The age of snake-bearing deposits ranges from the Middle Miocene to Holocene. The majority of the materials date from the Upper Pliocene and Quaternary; older materials consist of only a few bones. All deposits are bone breccias found in karstic fillings and the material is entirely composed of disarticulated remains.

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* Submitted in partial fulfilment for the degree of Doctor of Science at the Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, Cracow (1982).

Table I

Assignation of Polish localities of snake fauna to the European Neogene and Quaternary zonation

Age (my BP)	General sub-division	Faunal sub-division of Kretzoi	Chrono-stratigraphic classification of the Pleistocene	Polish localities	Foreign localities	MN bio-zones of Mein
0	Holocene		Postglacial	JO, GI, DS		
	Pleistocene Upper	Turingian	Weichselian	NI, ZD, ND, ZS, RA, CI		
			Eemian	RZ, WA		
			Saalian	ZY		
			Holsteinian		Brásso=Braşov	
	Late		Elsterian	KG		
0.5	Middle	Biharian	Cromerian	ZA		
	Lower		Menapian	KI		
1.0			Waalian			
					Betfia	
1.5			Eburonian	KA, JZ	Nagyharsányhegy	
	Early				Osztramos 3	
		Villányan		KD	Villány 3	17
			Tiglian	(?)ZB		
2.0	Pliocene				Beremend 5	16
		Csarnótian		RK I, RK II, W II	Balaruc Deutsch Alt. 20	
					Csarnóta 2	15
		Ruscinian		W I	Séte Perpignan	
				PO	Osztramos 1	14
5.5					Polgárdi	13
	Miocene			MA		
				OP	La Grive Beni Mellal	7
15				PR	Sansan Dévinská Nová Ves	6
20					Lisboa	3
					St. Gérand	2
					Paulhiac	1
24					Rott	0

Most of the materials are stored in the Institute of Systematic and Experimental Zoology of the Polish Academy of Sciences in Cracow (abbreviation used in the text: ZZSiD), the remaining ones belong to the Institute of Paleozoology of the Polish Academy of Sciences in Warsaw (ZPPAN) and the Institute of Paleozoology of Wrocław University (ZPUW).

Geological time table of the Neogene and Quaternary (Table 1), showing correlation of Polish and some foreign localities of snake faunas with successive periods (after Van der MEULEN, 1973; JÁNOSSY, 1973; MEIN, 1975; RABEDER, 1981; and others), includes also faunal subdivision of the Plio- and Pleistocene (after KRETZOI, 1969, and earlier works of this author), chronostratigraphic classification of the Pleistocene (Van EYSINGA, 1975), and biozonation of the Neogene (MEIN, 1975). The Miocene-Pliocene boundary accepted here, agrees with the Western European system, formerly not used in Polish literature but being recently introduced in Germany (cf. FAHLBUSCH, 1981).

Below follows, in chronological order, a full list of all Polish localities from

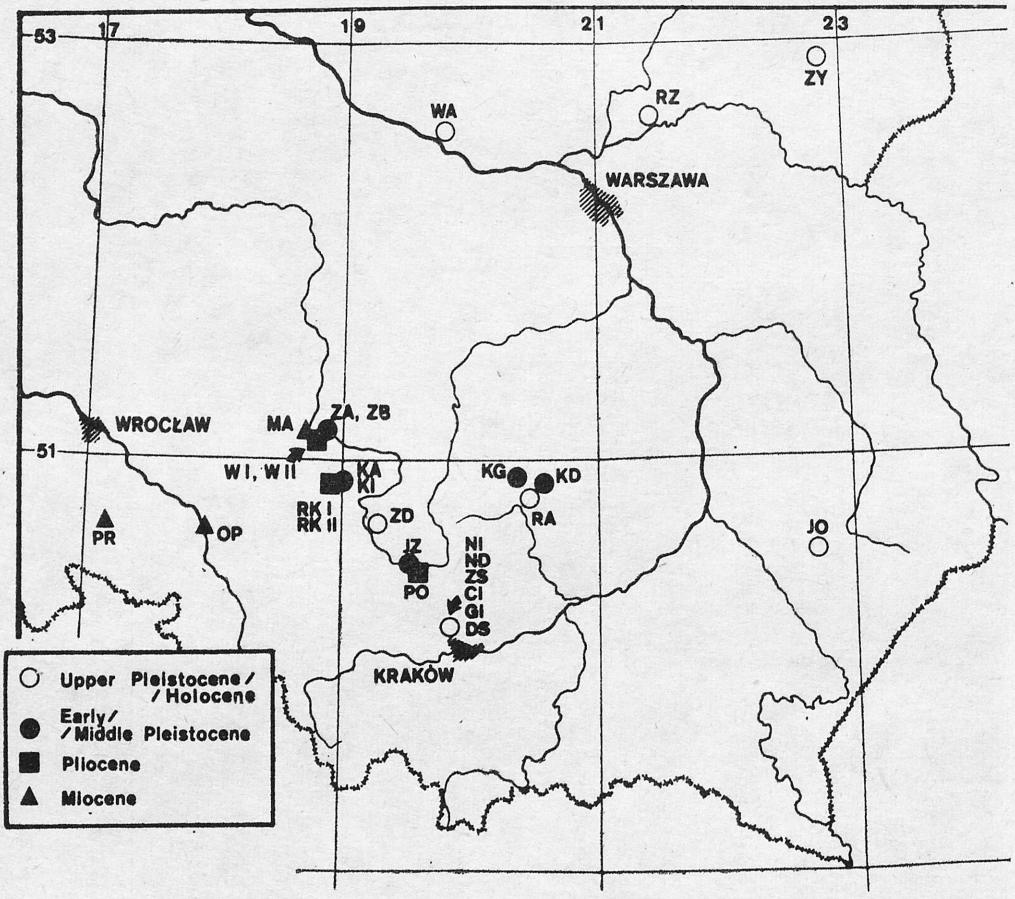

Fig. 1. Distribution of localities of fossil snake faunas in Poland. Abbreviations: CI — Ciasna Cave, DS — Dużej Sowy Cave, GI — Giebułtów, JO — Józefów, JZ — Żabia Cave, KA — Kamyk, KD — Kadzielnia, KG — Kozi Grzbiet, KI — Kielniki, MA — Mała Cave, ND — Niedostępna Cave, NI — Nietoperzowa Cave, OP — Opole, PO — Podlesice, PR — Przeworno, RA — Raj Cave, RK I — Rębielice Królewskie I, RK II — Rębielice Królewskie II, RZ — Rząśnik, W I — Węże I, W II — Węże II, WA — Wierzbica, ZA — Zalesiaki A, ZB — Zalesiaki B, ZD — Zamkowa Dolna Cave, ZS — Żytnia Skała, ZY — Zdrody

where snake remains have been studied *. Succeeding names of localities, accompanied (in parentheses) with abbreviations used in the text, are followed by references to geological description of the site (if such exists), age of the fauna, its correlation with other localities, paleoecology on the basis of known faunas, list of snake species with percentage of particular forms, and literature concerning the ophiofauna of a given locality. Age of particular localities given below agrees with internationally used current classification; local terminology used by previous authors is given in parentheses.

Distribution of the localities of snake faunas in the territory of Poland is shown on Fig. 1.

Przeworno 2 (PR)

Geological setting: GŁAZEK et al., 1971, 1977.
Age: Middle Miocene (Upper Vindobonian: GŁAZEK et al., 1971).
Correlation: La Grive, Sansan, Göriach (KUBIAK, 1982); MN biozone undetermined, presumably 6 or 7.
Paleoecology: warm subtropical climate; damp. scrub or forest environment with small reservoirs of stagnant water (GŁAZEK et al., 1971; MŁYNARSKI, 1976, 1978).
Material (ZZSiD): one fragmentary vertebra of *Colubrinae* indet. (form "A").
References: MŁYNARSKI, 1981, 1984.

Opole (OP) **

Age: Middle Miocene (Sarmatian: WEGNER, 1913; RYZIEWICZ, 1957; KOWALSKI, 1967).
Correlation: La Grive, Giggenheusen, Oggendorf (KOWALSKI, 1967); MN 7 (MEIN, 1975).
Paleoecology: climate intermediate between warm subtropical and mediterranean with high humidity; marshy and damp forest environment with small water reservoirs (KOWALSKI, 1967; MŁYNARSKI, 1983).
Material (ZPUW): 30 vertebrae altogether — (+) *Ogmophis europaeus* ***, (+) *Palaeonatrix silesiaca*, *Viperidae* indet. (form "A"); (?) *Coluber* sp. according to WEGNER (1913), material not traced.
References: WEGNER, 1913; SZYNDLAR, 1982; MŁYNARSKI, 1984.

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* Recently, 27 new sites containing vertebrate-bearing deposits, ranging in age from the Miocene till Mid-Pleistocene, have been discovered in the area of the Kraków—Wieluń Upland (GŁAZEK and SZYNKIEWICZ, 1980) and some from among them already have been partly exploited. Ophidian remains originating from these new localities are not discussed in the present work.

** Also known in German literature by names: Oppeln or Königliches Neudorf (= Nowa Wieś Królewska) (cf. WEGNER, 1913).

*** (+) means extinct species.

Mała Cave (MA)

Geological setting: SULIMSKI et al., 1979.
Age: Upper Miocene (Turolian/Pontian: SULIMSKI et al., 1979).
Correlation: Eichkogel, Kohfidisch, and other sites (SULIMSKI et al., 1979); MN biozone undetermined.
Paleoecology: (1) layer 22 — mediterranean climate; (2) below layers 7+9 — cool climate, resembling that existing in Central Europe at the present time.
Material (ZPUW): 11 vertebrae altogether — (+) *Zelceophis xenos* gen. sp. n., *Colubrinae* indet. (forms "B" and "C"), (+) *Natrix parva* sp. n.
References: no publication concerning ophiofauna.

Podlesice (PO)

Age: Early Pliocene (Lower Ruscinian: KOWALSKI, 1974). Note: the age of Podlesice has been defined previously as Early Pleistocene (KOWALSKI, 1956).
Correlation: somewhat younger than Eichkogel and Kohfidisch, and older than Osztramos-1 (KOWALSKI, 1974a); Osztramos-9,13 (JÁNOSSY and KORDOS, 1977); MN 14 (MEIN, 1975).
Paleoecology: mediterranean climate; environment presumably consisting of two types of vegetation, forests and open areas (KOWALSKI, 1964). Occurrence of *Gerbillinae (Mammalia: Rodentia)* is indicative of desert or semi-desert character of the open areas of Podlesice (KOWALSKI, 1974a).
Material (ZZSiD): 19 fragmentary vertebrae altogether — *Colubrinae* indet. (form "D"), *Viperidae* indet. (form "B").
References: MŁYNARSKI, 1962.

Węże I (W I)

Geological setting: SAMSONOWICZ, 1934; GŁAZEK et al., 1976.
Age: According to current studies of GŁAZEK et al. (1976) bone-bearing deposits of W I represented three different sequences, corresponding to (1) late Lower Pliocene (Brunssumian A — Ruscinian), (2) Upper Pliocene (Reuverian A — Lower Villa-franchian), and (3) Middle Pleistocene (Cromerian). This standpoint is discordant with KOWALSKI's (1964 and other works) opinion that the whole fauna from this site represented uppermost Pliocene (Upper Astian). The last view has been widely accepted by other paleontologists and the W I fauna has been treated in stratigraphic discussions as an individual biozone ("Wezeium"). Composition of snake remains, representing (1) Late/Upper Pliocene fauna (correlated with snake faunas of W II, RK I, and RK II), and (2) Pleistocene fauna (Recent snake species), supports the former opinion (GŁAZEK et al., 1976) about the separate cha-

racter of W I deposits. In the present study only the former (Pliocene) snake remains will be discussed *.

Correlation: Wölfersheim, Gundersheim (e.g. JÁNOSSY, 1973); MN 15 (MEIN, 1975).

Paleoecology: warm climate, of mediterranean type; prevailing habitat was steppe with scrubs and forests situated along rivers (SULIMSKI, 1959; KOWALSKI, 1960b, 1964).

Material (ZZSiD): 684 vertebrae and 12 skull bones — *Coluber* cf. *viridiflavus* (83%), (+) *Natrix* cf. *longivertebrata* (15%), *Vipera ammodytes* (2%).

References: MŁYNARSKI, 1961a, 1962.

Węże II (W II)

Geological setting: SULIMSKI, 1962.

Age: Upper Pliocene.

Correlation: of the age of RK I, and younger than W I (SULIMSKI, 1962); MN biozone undetermined, presumably 16.

Material (ZPPAN): 645 vertebrae — (+) *Elaphe paralongissima* sp. n. (82%), (+) *Natrix* cf. *longivertebrata* (18%).

References: no publication concerning ophiofauna.

Rębielice Królewskie I (RK I)

Geological setting: MOSSOCZY, 1959.

Age: Upper Pliocene (Lower Villafranchian: KOWALSKI, 1960a).

Correlation: Csarnóta, Gundersheim, Séte (KOWALSKI, 1960a); Osztramos-7, Beremend 4-5 (JÁNOSSY, 1973); Hajnačka (RABEDER, 1981); MN 16 (MEIN, 1975).

Paleoecology: warm climate of mediterranean character, resembling that of W I, though somewhat cooler; vertebrate fauna contains many aquatic forms (KOWALSKI, 1960a, 1964, 1974b).

Material (ZZSiD): About 15 000 bones — (+) *Coluber robertmertensi* $\left(?\frac{2}{3}\right)$, (+) *Natrix longivertebrata* sp. n. $\left(?\frac{1}{3}\right)$, *Vipera ammodytes* (at least 3 vertebrae).

References: MŁYNARSKI, 1961a, 1962, 1964, 1977.

Rębielice Królewskie II (RK II)

Age: Upper Pliocene.

Correlation: RK I (KOWALSKI, 1974b; MŁYNARSKI, 1977).

Material (ZZSiD): 135 vertebrae — (+) *Coluber* cf. *robertmertensi* (44%),

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* Pleistocene ophidian material consists of dozens of vertebrae belonging to *Natrix natrix* and *Elaphe longissima* from a calcite layer (cf. MŁYNARSKI, 1961a, pl. 3 and 4: Fig. 1). MŁYNARSKI (supra cit.) has identified these remains as belonging to *Natricinae* indet. and *Coluber* cf. *viridiflavus* and defined their age as Pliocene.

(+) *Natrix* cf. *longivertebrata* (44%), *Vipera ammodytes* (12%).
References: MŁYNARSKI, 1977.

Zalesiaki B (ZB) *

Age and correlation: still undetermined, according to Prof. K. KOWALSKI's unpublished data, cited by MŁYNARSKI (1977) — Pliocene, correlated with W I. In MŁYNARSKI's (1977) opinion, the herpetofauna from this site was younger, resembling in age that of RK I. However, composition of ophidian fauna of ZB is completely different from these of all Pliocene localities and identical with snake faunas from the Early Pleistocene of KD and KA. Because of these reasons I provisionally place the ZB fauna in the Early Pleistocene.
Material (ZZSiD): 115 vertebrae — *Elaphe* aff. *longissima* (73%), *Coronella austriaca* (3%), *Natrix natrix* (23%), *Vipera berus* (1%).
References: MŁYNARSKI, 1977.

Kadzielnia (KD)

Age: Early Pleistocene (Tiglian Interglacial: KOWALSKI, 1973; Upper Villanyian: RABEDER, 1981; Villanyan/lower Biharian: BOSÁK et al., 1982).
Correlation: Villány-3, Osztramos-3 (RABEDER, 1981); KA, JZ (BOSÁK et al., 1982); MN 17 or Q 1 (MEIN, 1975). Note: Earlier the age of Kadzielnia has been determined as Cromerian (Günz/Mindel Interglacial) (KOWALSKI, 1958).
Paleoecology: Climate cooler than that of W I and RK I, but warmer than in the area at present, for the most part forest vegetation (KOWALSKI, 1964, 1974b).
Material (ZZSiD): 419 bones — *Elaphe* aff. *longissima* (66%), *Coronella austriaca* (4%), *Natrix natrix* (23%), *Vipera berus* (7%).
References: MŁYNARSKI, 1961a, 1962.

Kamyk (KA)

Geological setting: MOSSOCZY, 1959.
Age: Early Pleistocene (Eburonian — Lower Biharian: Van der MEULEN, 1973; BOSÁK et al., 1982).
Correlation: Betfia-2, Nagyharsányhegy-2 (Van der MEULEN, 1973); KD, JZ, Mokrá, Betfia (BOSÁK et al., 1982). Note: the age of KA has previously been determined as terminal Cromerian (Günz/Mindel Interglacial) and correlated with Nogaysk, Beftia and Villány-5 (KOWALSKI, 1960c); in another paper, KOWALSKI (1973) has defined the age of KA as Menapian (Günz Glaciation).

* Zalesiaki A (ZA) and Zalesiaki B (ZB) are a single locality; the whole fossil material has been divided into two groups by Prof. K. KOWALSKI after analysis of the fauna of micromammals. Samples 3, 6, 11, 12, 14, and 15 („older") are referred as ZB; samples 1, 2, 5, 7, 8, 9 and 10 („younger") compose ZA (cf. MŁYNARSKI, 1977). In his only published reference to the fauna from Zalesiaki KOWALSKI (1973) does not mention this division into ZA and ZB, dating the fauna as Cromerian.

Paleoecology: steppe habitat. Composition of microvertebrate fauna suggests the presence of much cooler climate than that of KD (KOWALSKI, 1960c, 1964, 1973); herpetological evidence, however, does not support this standpoint (MŁYNARSKI, 1962; also composition of ophiofauna is indicative of warm climate).

Material (ZZSiD): about 875 vertebrae — *Elaphe* aff. *longissima* (91%), *Coronella austriaca* (1%), *Natrix natrix* (6.5%), *Vipera berus* (0.5%).

References: MŁYNARSKI, 1961a, 1962.

Żabia Cave (JZ)

Geological setting: BOSÁK et al., 1982.

Age: Early Pleistocene (Lower Biharian: BOSÁK et al., 1982).

Correlation: KD, KA (BOSÁK et al., 1982).

Material (ZPUW): Snake remains from JZ, recently obtained by the author, so far have only been examined in part. Only remains of *Elaphe* aff. *longissima* (about 1000 bones) are discussed below; moreover, the material contains vertebrae of *Coronella* sp., *Natrix* sp., and *Vipera* sp.

References: BOSÁK et al., 1982.

Kielniki (KI)

Age: Lower Pleistocene — Menapian (Günz: unpublished data of Prof. K. KOWALSKI in STWORZEWICZ, 1975, 1981).

Paleoecology: Climate cooler and moister than in Preglacial period; forest habitat (STWORZEWICZ, 1981).

Material (ZZSiD): 248 vertebrae — *Coronella austriaca* (13%), *Natrix natrix* (85%), *Vipera berus* (2%).

References: MŁYNARSKI, 1977.

Zalesiaki A (ZA)

Age: Lower/Middle Pleistocene — Cromerian (MŁYNARSKI, 1977).

Material (ZZSiD): over 9000 bones — *Elaphe longissima* (4%), *Coronella austriaca* (2 vertebrae), *Natrix natrix* (34%), *Vipera berus* (62%).

References: MŁYNARSKI, 1977.

Kozi Grzbiet (KG)

Geological setting: GŁAZEK et al., 1976, 1977.

Age: Middle Pleistocene — Elsterian I/Elsterian II (Mindel I/Mindel II: GŁAZEK et al., 1976, 1977) *.

Paleoecology: composition of malaco- and herpetofauna indicates that the climate of KG site was warm (MŁYNARSKI, 1977; SZYNDLAR, 1981; STWORZEWICZ, 1981); this opinion agrees with the previous suggestion of GŁAZEK

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* In two previous descriptions of herpetofauna from KG (MŁYNARSKI, 1977; SZYNDLAR, 1981) the age of this site has been defined incorrectly as Cromerian.

et al. (1977) that the period between the first (premaximal) stage of Elsterian (Elsterian I) and its maximum stage (Elsterian II) was more similar to an interglacial than an interstadial. Fauna of snails and herpetofauna of KG were composed for the most part of forest forms. KOWALSKI (1975), however, based on micromammals, suggested that the site of KG was characterized by a cold steppe.

Material (ZZSiD): about 112 000 bones — *Elaphe longissima* (1.4%), *Coronella austriaca* (0.03%), *Natrix natrix* (98.5%), *Vipera berus* (0.07%).

References: MŁYNARSKI, 1977; SZYNDLAR, 1981.

Zdrody (ZY)

Geological setting: BAŁUK et al., 1979.

Age: Late Pleistocene — Saalian (North-Masovian Stadial of the Riss Glaciation: BAŁUK et al., 1979).

Paleoecology: Basing exclusively on geological data, BAŁUK et al. (1979) have presented an improbable opinion that the abundant invertebrate and vertebrate faunas of ZY (ibidem described) existed in the direct vicinity of dead ice during the deglaciation period! Considering the composition of the fauna from ZY, including the herpetofauna, this view is untenable. Indeed, it now appears that the dating of ZY has been doubtful (Dr. A. BAŁUK, pers. comm., 1981)

Material (ZPPAN): 7 fragmentary vertebrae of *Natrix natrix*.

References: MŁYNARSKI in BAŁUK et al., 1979.

Rząśnik (RZ)

Age: Late/Upper Pleistocene. First dating of the deposit as Saalian (Riss) has later been questioned (Dr. A. BAŁUK, pers. comm., 1981). Considering the presence and large size of numerous bones of *Elaphe longissima*, together with the occurrence of this locality far in the north of Poland, I have provisionally dated the deposit as Eemian (Riss/Würm Interglacial)

Material (ZPPAN): 234 bones of *Elaphe longissima* and 2 vertebrae of *Natrix natrix*.

References: No data have been published on the RZ fauna.

Wierzbica I (WA)

Age: Late/Upper Pleistocene. Primarily the age of WA has been correlated with Weichselian (Würm), but the dating has afterwards been questioned (Dr. A. BAŁUK, pers. comm., 1981). For reasons similar to those in the case of the previous locality (RZ) I have provisionally accepted the age of WA as Eemian.

Material (ZPPAN): 240 bones of *Elaphe longissima*.

References: No data have been published on the WA fauna.

Table II

Correlation of Polish Upper Quaternary localities of snake fauna (after BOCHEŃSKI, 1974, and NADACHOWSKI, 1982; simplified). Abbreviations of specific names: (C) — *Coronella austriaca*, (E) — *Elaphe longissima*, (N) — *Natrix natrix*, (V) — *Vipera berus*. For abbreviations of locality names see Fig. 1

Period \ Localities			NI	ZD	ND	ZS	RA	CI	JO	GI	DS
Holocene					E		E, N, V	E	E, N	E, N	N
Weichselian (Würm)	Late Glacial				C, E, V	E		E, V			
	Pleniglacial	Upper		E							
		Middle	N								
		Lower					N, V				
	Early Glacial		V								

Nietoperzowa Cave (NI)

Geological setting: CHMIELEWSKI, 1959.

Age *: Upper Pleistocene — Weichselian (Würm): (1) Early Glacial (Prebrørup) (layer 12), (2) Middle Pleniglacial (layer 8) (KOWALSKI, 1961; NADACHOWSKI, 1982).

Paleoecology: For both layers climate rather warm, similar to that in the area at the present time, forest habitat (KOWALSKI, 1961).

Material (ZZSiD): one vertebra of *Natrix natrix* (layer 8) and one vertebra of *Vipera berus* (Layer 12).

References: no publication.

Zamkowa Dolna Cave (ZD)

Age: Upper Pleistocene — Weichselian (Würm): Upper Pleniglacial (NADACHOWSKI, 1982).

Material (ZZSiD): 10 vertebrae of *Elaphe longissima*.

References: no publication.

Niedostępna Cave (ND)

Age: Upper Quaternary: (1) Weichselian (Würm), Late Glacial (layer 4), (2) Holocene (layers 5, 5/6) (NADACHOWSKI, 1982).

Paleoecology: the avifauna suggests moderately cool or cool climate in Late Glacial, and the climatic optimum in Holocene (BOCHEŃSKI, 1974).

* For detailed data on the age of this site and all next ones see also Table II.

Material (ZZSiD): 25 bones of *Elaphe longissima* (layers 5 and 5/6), 3 vertebrae of *Coronella austriaca* (layer 4), 7 vertebrae of *Vipera berus* (layer 4).
References: no publication.

Żytnia Skała (ZS)

Geological setting: KOWALSKI et al., 1967.
Age: Upper Pleistocene — Weichselian (Würm): Upper Glacial. Correlation of sediments doubtful (NADACHOWSKI, 1982).
Paleoecology: climate similar to these existing today in Lithuania or Southern Finland; afforestation of taiga-type with water reservoirs (BOCHEŃSKI, 1974).
Material (ZZSiD): 26 bones of *Elaphe longissima*.
References: KOWALSKI et al., 1967.

Raj Cave (RA)

Geological setting: KOWALSKI et al., 1972.
Age: Upper Quaternary: (1) Weichselian (Würm), Early Glacial (Brørup)/Lower Pleniglacial (layers 4—6), (2) Holocene (layer 11) (NADACHOWSKI, 1982).
Paleoecology: In Early Weichselian taiga and wet meadows, mean July temperature about 14—15°C (layer 4); afterwards open areas (tundra), July temperature 10—14°C (layer 6); in Holocene forest fauna, presumably correlated with Atlantic climatic optimum (layer 11) (KOWALSKI et al., 1972; BOCHEŃSKI, 1974).
Material (ZZSiD): 2 vertebrae of *Elaphe longissima* (layer 11), 10 vertebrae of *Natrix natrix* (layers 4 and 11), 8 vertebrae of *Vipera berus* (layers 4, 6, and 11).
References: no publication.

Ciasna Cave (CI)

Age: Upper Quaternary: (1) Weichselian (Würm), Late Glacial (layer 6, 7), (2) Holocene (layer 8). Correlation doubtful, probably the whole fauna originates from the Holocene (NADACHOWSKI, 1982).
Material (ZZSiD): 10 vertebrae of *Elaphe longissima* (layers 6/7, 7, and 8), one vertebra of *Vipera berus* (layers 6/7—7).
References: no publication.

Józefów (JO)

Age: Holocene — Atlantic period (KOWALSKI et al., 1963).
Paleoecology: forest habitat (probably deciduous forests), climate somewhat warmer than that existing in the area today (KOWALSKI et al., 1963).
Material (ZZSiD): 1087 bones — *Elaphe longissima* (88%), *Natrix natrix* (12%).
References: MŁYNARSKI in KOWALSKI et al., 1963.

Giebułtów (GI)

Age: Holocene, presumably Atlantic period (MŁYNARSKI, 1961b).
Material (ZZSiD): 2199 bones — *Elaphe longissima* (36%), *Natrix natrix* (64%).
References: MŁYNARSKI, 1961b.

Dużej Sowy Cave (DS)

Age: Holocene (NADACHOWSKI, 1982).
Material (ZZSiD): 48 vertebrae of *Natrix natrix*.
References: no publication.

III. METHODS

Fossil snake materials described in the present paper primarily consist of vertebrae. Most taxa described below have been recognized on the basis of vertebrae only; skull bones form a relatively small part of all fossil material. Twenty two different forms of snakes have been recognized; among these one new genus and four new species have been described. In several cases in which ophidian taxa are represented only by solitary and/or fragmentary vertebrae, I have refrained from describing them as new species in spite of their distinctive character. However, some of these fossils most likely will be supplemented by new materials as the deposits from where the remains origin have not been yet entirely exhausted.

The fossil materials have been identified for the most part with use of skeletons of modern species. For this purpose I have examined skeletons of all European mainland snakes except *Telescopus fallax* as well as a number of Holarctic species from beyond Europe. All comparative materials used in this work are housed in the Institute of Systematic and Experimental Zoology of the Polish Academy of Sciences in Cracow (ZZSiD) and the Museo Nacional de Ciencias Naturales of the Consejo Superior de Investigaciones Científicas in Madrid (MNCN). Comparing the fossils with extinct species of snakes, I have used exclusively original descriptions of these taxa. Unfortunately, the majority of these descriptions, being either incomplete or indistinct and provided with inadequate figures (in classical papers usually showing complete skeletons and not details), make the comparison impossible. In particular, since many descriptions of fossil snakes are based exclusively on skull bones, therefore any comparisons with material consisting exclusively of vertebrae are impossible.

Identifying fossils I have used all bones except ribs since the latter elements can be identified at most to familial level. In spite of the widespread opinion among paleoherpetologists about the questionable taxonomic value of snake vertebrae or even their usefulness for identifying fossils, in my study just vertebrae have provided basic qualitative and quantitative data. As far as possible, I have examined vertebrae from all sections of the column; identification to the specific level, based only on trunk vertebrae, is often difficult

and conclusions from such a procedure are hazardous. The probability of correct determination, however, distinctly increases by use in addition of cervical vertebrae; caudal vertebrae usually seem to be of little importance, at least with reference to European colubroid snakes. Identifying materials from particular localities I have first determined a number of ophidian species based on their vertebrae and afterwards referred skull bones (if present) to the vertebrae. The disregard of vertebrae — a practice particularly common among Central European students of fossil snakes — can easily cause identification of taxa actually absent in the fossil material. Such a false determination can be caused owing to the great intraspecific variability of some skull bones (in practice still largely unknown), then these elements, if different from comparative materials at hand, can be described as another species or even a new taxon. On the other hand, if a sample indeed contains a new taxon, its remains can be described as several different forms because — at least in relation to relatively young fossils — some bones belonging to extinct snakes must have been morphologically different, but other ones could be similar or even identical to those of their living relatives. The use of the ophidian vertebral column, which undergoes intraspecific changes to a lesser degree, enables the avoidance of many of the above-mentioned errors.

As I have mentioned above, many students of fossil snakes from Central Europe have ignored vertebrae in their research; moreover, most of them used SZUNYOGHY's (1932) key for identification of cranial bones instead of comparative

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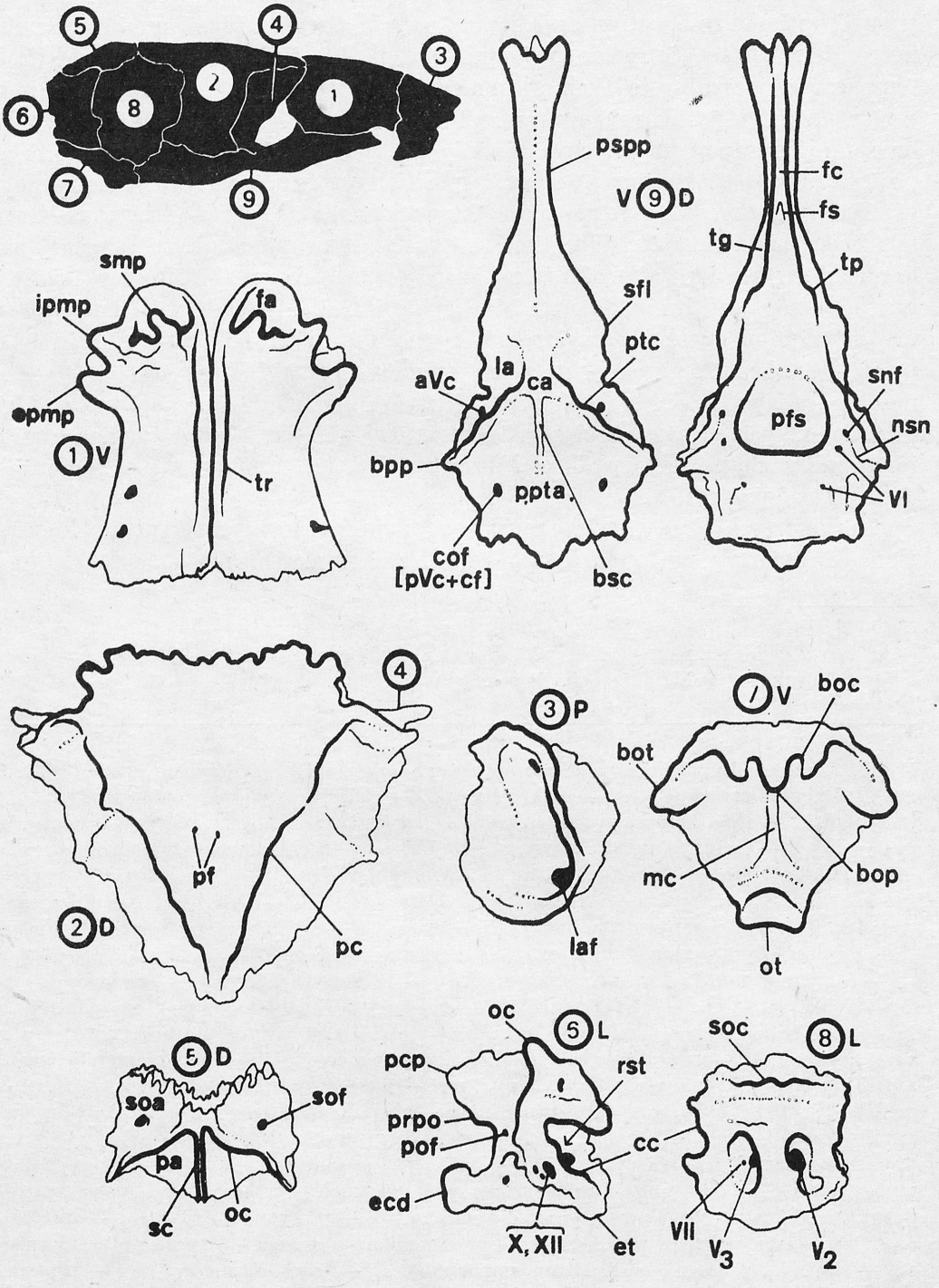
Fig. 2. Anatomical nomenclature of ophidian braincase bones (*Coluber jugularis* ZZSiD 262). 1 — frontals, 2 — parietal, 3 — right prefrontal (lacrimal), 4 — postorbital or postfrontal, 5 — supraoccipital (superior occipital), 6 — right exoccipital (lateral occipital, otoccipital), 7 — basioccipital, 8 — right prootic, 9 — basiparasphenoid = basisphenoid + parasphenoid (sphenoid complex). Abbreviations: aVc — anterior orifice of Vidian canal (anterior carotid foramen), boc — basioccipital crest, bop — basioccipital process, bot — basioccipital tubercle, bpp — basipterygoid process, bsc — basisphenoid crest, ca — central area, cc — circumfenestral crest, cf — cerebral foramen, cof — common foramen, ecd — exoccipital condyle, epmp — external premaxillary process, et — exoccipital tubercle, fa — frontal aperture, fc — frontal crest, fs — frontal step, ipmp — internal premaxillary process, la — lateral area, laf — lacrimal foramen, mc — medial crest, nsn — notch for sympathetic nerve, oc — occipital crest, ot — occipitocondylar tubercle (basioccipital condyle), pa — posterior area, pc — parietal crest, pcp — parotic process (postoccipital process), pf — parietal foramen, pfs — pituitary fossa (fossa hypophyseos), pof — postoccipital foramen, ppta — postpterygoid area, prpo — protuberantia postoccipitalis, pspp — parasphenoid process, ptc — pterygoid crest, pVc — posterior orifice of Vidian canal (posterior carotid foramen), rst — recessus scalae tympani, sc — sagittal crest, sfl — suborbital flange (suborbital process), smp — septomaxillary process, snf — sympathetic nerve foramen, soa — supraoccipital area, soc — supraoccipital crest, sof — supraoccipital foramen, tg — trabecular groove (sulcus trabeculae), tp — trabecular process, tr — trabecular ridge, V_2 — foramen for maxillary branch of trigeminal nerve (anterior prootic foramen), V_3 — foramen for mandibular branch of trigeminal nerve, VI — abducens nerve foramen, VII — facial nerve foramen, X, XII — vagus-hypoglossal nerve foramen; D — dorsal, L — lateral, P — posterior, V — ventral views. Not to scale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materials. This comprehensive publication, no doubt a good piece of work and full of beautiful illustrations showing ophidian cranial bones, seems to be trusted without reservation and in this way is a reason for a number of erroneous descriptions. SZUNYOGHY (supra cit., p. 42) divided cranial bones into four groups according to their presumed diagnostic value *; however, his judgement (except nasals and septomaxillae described in detail) was based only on rather unimportant features, mainly the general shape of the bones. Important diagnostic features, e. g. disposition of nerve foramina or number of teeth together with relation of these elements to other structures, have not been taken into consideration in SZUNYOGHY's paper. It is easy to find doubtful descriptions of snake taxa, based exclusively on the shape of solitary cranial bones and omitting vertebrae (vide infra). I myself was incorrect in my description of squamates from the Pleistocene of KG (SZYNDLAR, 1981, pp. 89—90, Fig. 12), in erecting a new ophidian genus, *Palaeomalpolon borealis*, making a diagnosis of the basis of the shape of a single basiparasphenoid only; present analysis of nerve and carotid foramina indicates that the bone, despite its peculiar shape, belonged to *Natrix natrix*, the commonest snake in KG deposit (vide infra).

In the present study, for the purpose of identification and diagnostic descriptions of fossils, I have used morphological and numerical methods alike. Com-

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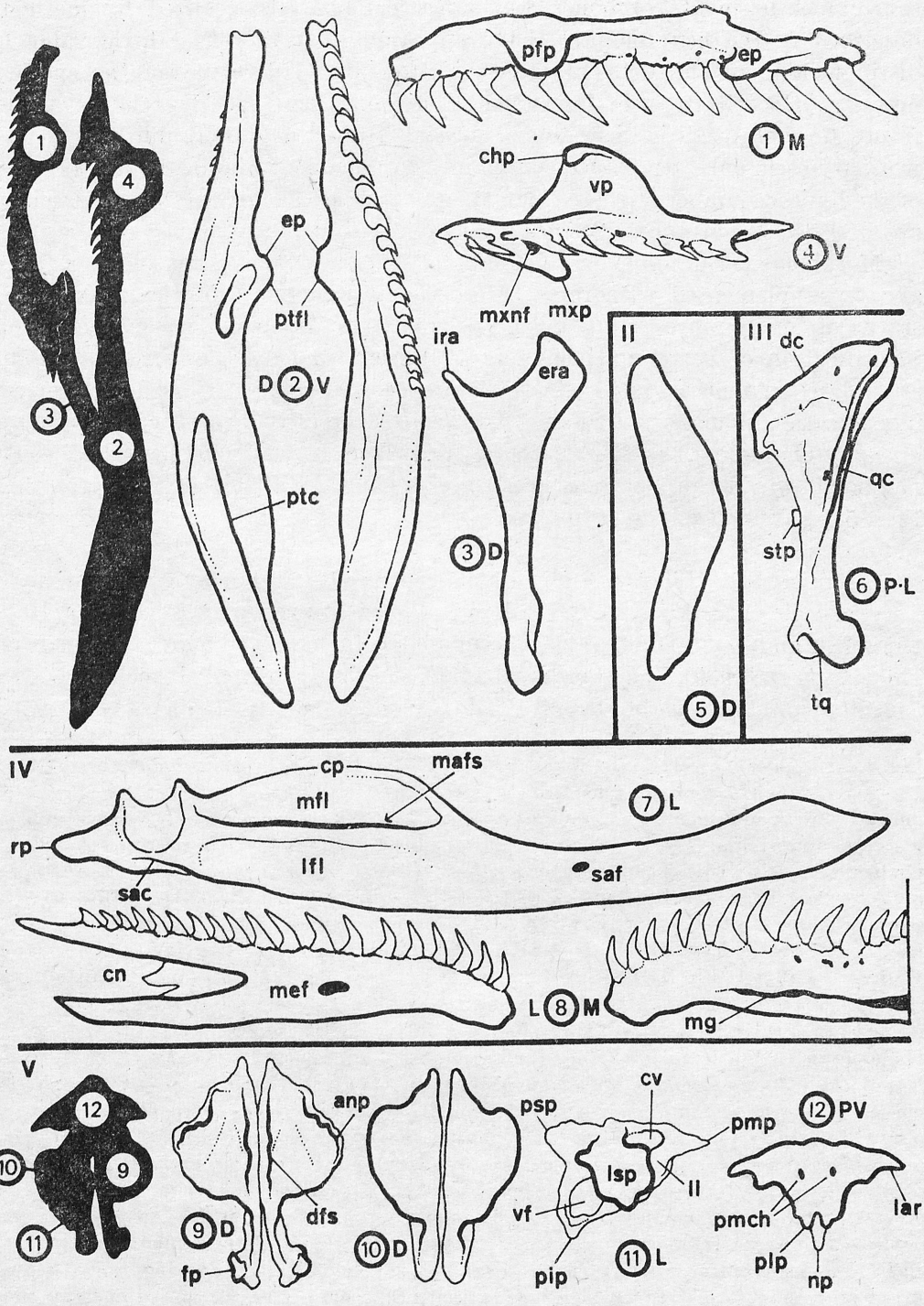
* See also MŁYNARSKI (1961a, p. 7) for critique of SZUNYOGHY's (1932) standpoint to diagnostic value of ophidian cranial bones.

Fig. 3. Anatomical nomenclature of remaining ophidian skull bones (*Coluber jugularis* ZZSiD 262). I. Palatomaxillary Unit: 1 — right maxilla, 2 — right pterygoid (endopterygoid, internal pterygoid), 3 — right ectopterygoid (transverse, transpalatine, external pterygoid, transverse pterygoid), 4 — right palatine; II. Squamosal Unit: 5 — right squamosal (supratemporal); III. Quadrate Unit: 6 — right quadrate; IV. Mandibular Unit: 7 — right compound bone = supraangular + prearticular + articular (composite bone), 8 — right dentary; V. Snout complex: 9 — septomaxillae (intranasals), 10 — nasals, 11 — right vomer (prevomer, ethmoid, turbinal), 12 — premaxilla (intermaxilla). Abbreviations: anp — ascendens nasal process, cn — compound notch, chp — choanal process, cp — coronoid process, cv — cavum vomeris, dc — dorsal crest, dfs — dorsal fossa, ep — ectopterygoid process, era — external ramus, fp — frontal process, ira — internal ramus, lar — lateral arm or process (premaxillary transverse process), lfl — lateral flange (labial flange or process), ll — lamella lateralis anguli anterioris, lsp — lamina spheroidea palatina, mef — mental foramen (dental foramen), mfl — medial flange (lingual flange or process), mafs — mandibular fossa, mg — Meckel's groove, mxnf — maxillary nerve foramen, mxp — maxillary process (lateral process), np — nasal process (medial wing, dorsal process), pfp — prefrontal process, pip — postero-inferior process, plp — palatine process, pmp — premaxillary process, pmch — premaxillary channel, psp — postero-superior process, ptc — pterygoid crest, ptfl — pterygoid flange, qc — quadrate crest, rp — retroarticular process, sac — supraangular crest, saf — supraangular foramen, stp — stapedial process (squama suprastapedialis), tq — trochlea quadrati, vf — vomerine foramen, vp — vomerine process (prevomerine process); D — dorsal, L — lateral, M — medial, PL — postero-lateral, PV — postero-ventral, V — ventral views. Not to scale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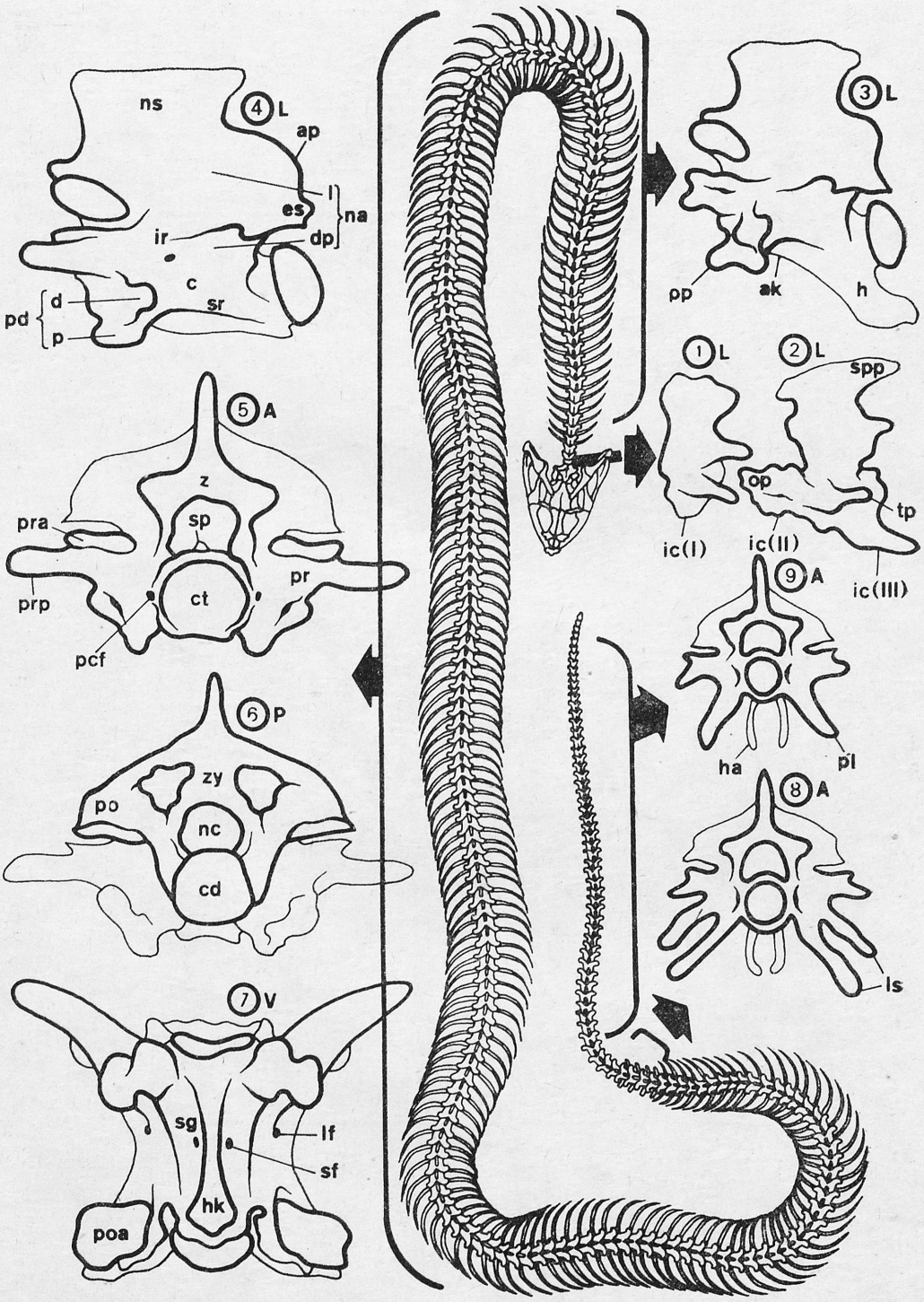
parisons based on morphological characters have been of fundamental importance; measurements of bones and statistical analysis, realized by methods described in the next chapter, have appeared to have rather little value in distinguishing of snake taxa because of the limited diversity of the species; however, they have been instrumental in comparing closely related snakes from different localities with one another. Numerical data published in this work concern only trunk vertebrae; measurements of cranial bones, because of the limited number of these elements and their great intraspecific variability, are of little importance and have been omitted.

Morphological descriptions in Chapter V, if they concern extinct taxa, are always supplemented with remarks on their taxonomic affinities. Taxonomic status of fossils representing living species is not discussed; basic methods of identification of vertebrae belonging to Recent snakes, used in the present study, are summarized in Figs. 5—8. However, it should be stressed that correct identification of snake vertebrae can be realized exclusively on the basis of a set of many characters. All these features, described in detail in Chapter V, could not be shown in the diagrams because of technical difficulties. Owing to this, Figs. 5—8 are not intended to serve as keys for identification of ophidian vertebrae.

Terminology. The anatomical nomenclature is taken from various sources. Terminology of snake vertebrae follows that of AUFFENBERG (1963) and HOFFSTETTER and GASC (1969). Basic terminology for cranial bones is taken from HOFFSTETTER (1939), but in order to adapt the terms to English spelling I have consulted publications of several Anglo-Saxon authors, i. e. FRAZETTA (1959),

Fig. 4. Anatomical nomenclature of ophidian vertebrae (*Malpolon monspessulanus* ZZSiD 244). 1 — atlas, 2 — axis (epistropheus), 3 — cervical vertebra, 4—7 — trunk vertebra (thoracic, dorsal, lumbar, precaudal, presacral vertebra), 8 — cloacal vertebra (sacral, pygal vertebra), 9 — caudal vertebra. Abbreviations: ak — anterior keel, ap — „aliform process" (pterapophysis), c — centrum (pleurocentrum), cd — condyle (vertebral condyle, ball of centrum), ct — cotyle (glenoid cavity, cup of centrum), d — diapophysis, dp — descending part of neural arch, es — epizygapophyseal spine, h — hypapophysis, ha — haemapophysis, hk — haemal keel (carina haemalis), ic (I) — intercentrum I (hypocentrum I), ic (II) — intercentrum II (hypocentrum II), ic (III) — intercentrum III (hypapophysis I), ir — interzygapophyseal ridge (zygapophyseal ridge, lateral ridge, margo lateralis, l — laminae (tectum), lf — lateral foramen (pedicular foramen, nutritive foramen, intervertebral superior foramen), ls — lymphapophysis, na — neural arch (neurocentrum), nc — neural canal (vertebral canal), ns — neural apine (neurapophysis, spinal apophysis), op — odontoid process, p — parapophysis, pcf — paracotylar foramen, pd — paradiapophysis = parapophysis + diapophysis (synapophysis, transverse process), pl — pleurapophysis, po — postzygapophysis (posterior articular process, posterior zygapophysis), poa — postzygapophyseal articular surface, pp — parapophyseal process (transverse inferior apophysis), pr — prezygapophysis (anterior articular process, anterior zygapophysis), pra — prezygapophyseal articular surface, prp — prezygapophyseal process (accessory process), sf — subcentral foramen (intervertebral inferior foramen), sg — subcentral groove (ventral fossa), sp — subneural process (epapophysis), spp — spinal process, sr — subcentral ridge (margo ventralis, margo inferior), tp — transverse process of atlas (pleurapophysis or pleurophysis), z — zygosphene, zy — zygantrum; A — anterior, L — lateral, P — posterior, V — ventral views. Not to scale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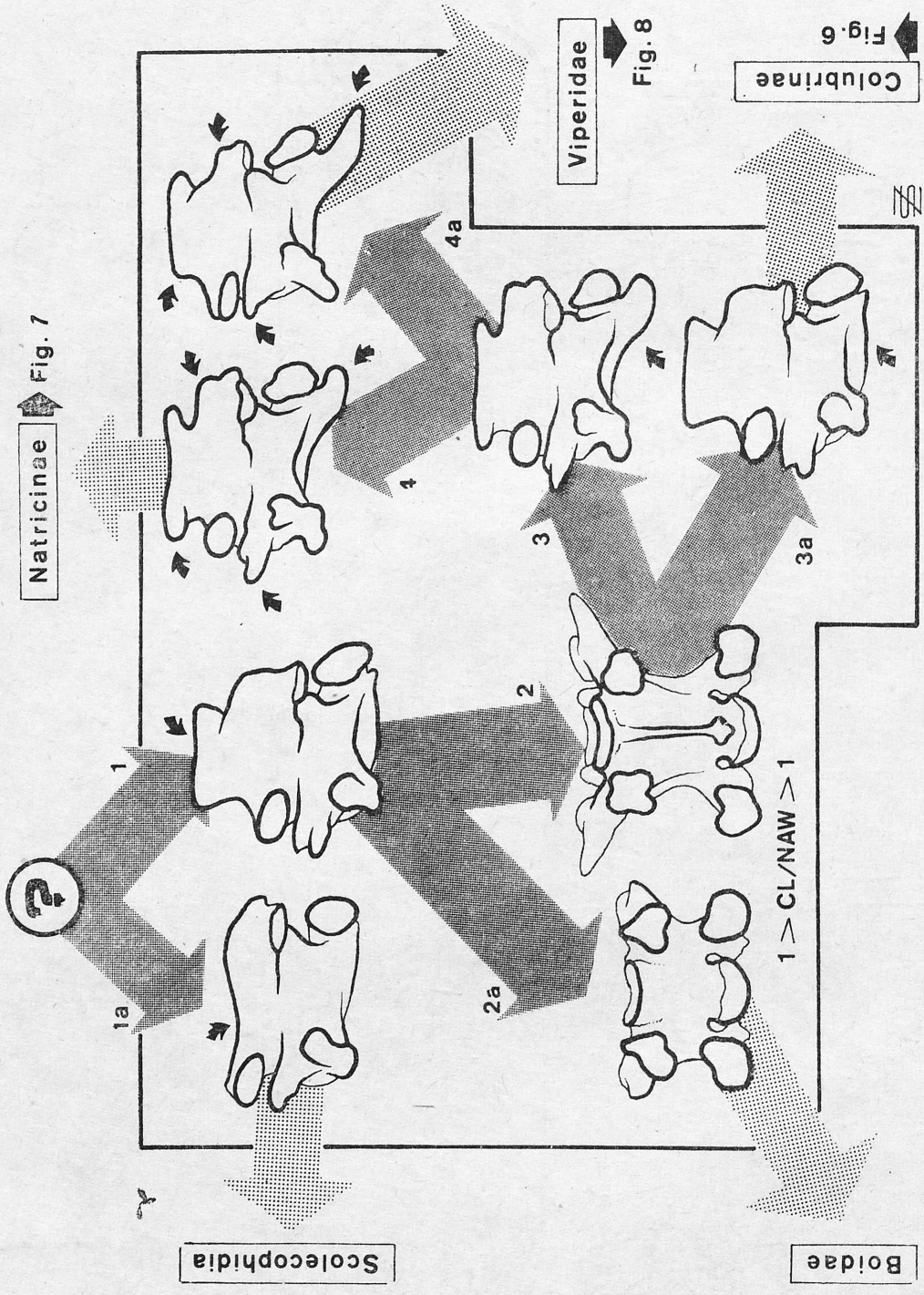
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Fig. 7
Viperidae
Fig. 8
Colubrinae
Fig. 6
Scolecophidia
Boidae
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1a
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ESTES et al. (1970), MARX and RABB (1972), and others. Cranial foramina have been interpreted after UNDERWOOD (1967) and MCDOWELL (1967, 1979). Terminology concerning dentition follows that of SMITH (1952; cf. also EDMUND, 1969). To avoid misunderstanding, I include figures of ophidian bones with terminology used consistently below in the text (Figs. 2—4). Additionally, in parentheses I give synonyms found in the literature.

In this work I subdivide the ophidian vertebral column into four basic regions: (1) cervical vertebrae, (2) trunk vertebrae, (3) cloacal vertebrae, and (4) caudal vertebrae. For the members of the subfamily *Colubrinae* partition of the column into cervical region (hypapophyses present) and trunk region (hypapophyses absent) is obvious; in the case of *Natricinae* and *Viperidae*, which have hypapophyses throughout the precaudal region, the subdivision is somewhat arbitrary. The term anterior trunk vertebrae means here always anteriormost bones of the trunk region, and is not intended as a synonym of cervical vertebrae. The term precaudal vertebrae means cervical and trunk vertebrae jointly.

All measurements are given in millimetres; the black and white line on each figure equals approximately 2 mm. Capital letters used in figures showing snake bones mean views or side. All maps showing distribution of fossil and living snakes in Central Europe are provided with 1000 m contour lines; other symbols are explained in captions.

The systematics used below follows (with small modifications) that of SMITH et al. (1977). Subdivision of the family *Colubridae* into two groups: "*Natricinae*", possessing hypapophyses throughout the precaudal region of the vertebral column, and "*Colubrinae*", with hypapophyses restricted to the cervical region of the column, employing here, is generally accepted by workers on fossil snakes (HOFFSTETTER, 1962, p. 269; RAGE, 1974, p. 294).

IV. MEASUREMENTS AND STATISTICAL METHODS

Biometrical studies of vertebral column of snakes, initiated by JOHNSON (1955), have been used in later studies concerning intracolumnar variation of living forms by several other authors. JOHNSON (supra cit.) also introduced

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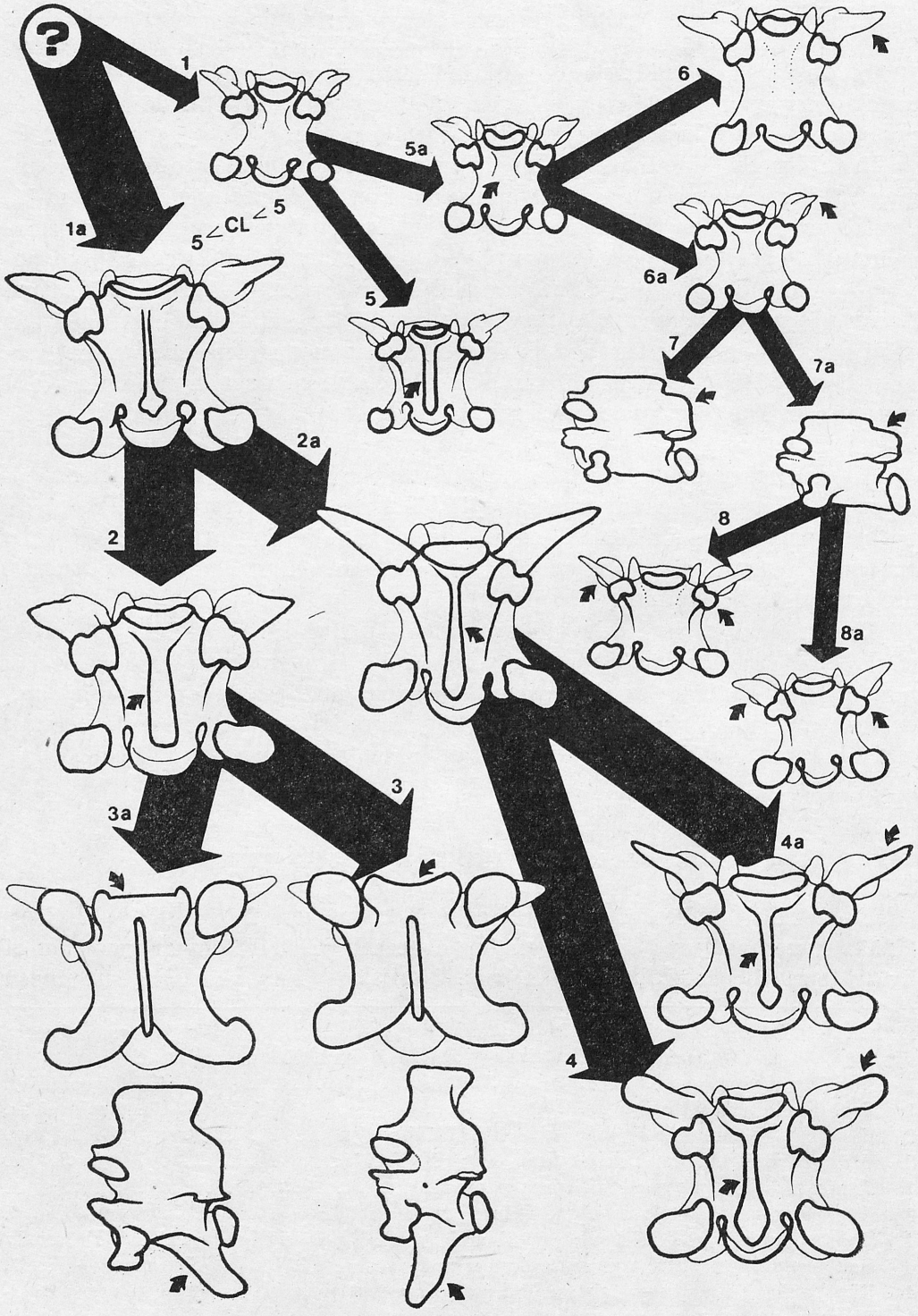
Fig. 5. Pictorial key to (sub) families of living European snakes. Asterisk (*) means absence of members of a given group in Poland. Not to scale

1. Neural spine present . . . . . 2 *(Alethinophidia)*.
1a. Neural spine absent . . . . . (*) *Scolecophidia*: *Typhlopidae*.
2. Vertebral centrum longer than wide (CL/NAW > 1) . . . . . 3.
2a. Vertebral centrum much wider than long (CL/NAW < 1) . . . . . (*) *Boidae*.
3. Trunk vertebrae provided with hypapophysis . . . . . 4.
3a. Hypapophysis of trunk vertebrae reduced to haemal keel. . . . *Colubrinae* → Fig. 6.
4. Hypapophysis sigmoid-shaped; neural arch vaulted posteriorly; neural spine strongly overhanging anteriorly; prezygapophyseal process obtuse . . . . *Natricinae* → Fig. 7.
4a. Hypapophysis usually straight; neural arch depressed posteriorly; neural spine not overhanging anteriorly; prezygapophyseal process acute. . . . . *Viperidae* → Fig. 8.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the use of bivariate ratios of measurements of snake vertebrae employing the data in statistical tests of independence. The use of ratios is plausible in animal taxonomy, because ratio is independent of the absolute size of the original figures; it therefore removes the effect of body size.

AUFFENBERG's (1963) careful study of fossil snakes from Florida was the first work in which measurements and ratios of vertebral elements were used for identification and diagnostic description of extinct ophidians. Based on the ratios, AUFFENBERG (supra cit.) also compared vertebrae of various species of snakes with one another. Unfortunately, these comparisons, based exclusively on numerical data for which basic estimates of sample parametres (i. e. mean and standard deviation) have not been calculated, most likely are only rough estimates and thus of no value from the standpoint of mathematical statistics.

SZYNDLAR (1981) and MEYLAN (1982), using measurements and ratios proposed by AUFFENBERG (1963), attempted identification of Pleistocene snake vertebrae by use of the Student's t-test. Nevertheless, the mode of sampling of snake vertebrae for use in identification and comparisons that has been accepted by all previous authors is not satisfactory; I myself (SZYNDLAR, 1981) simply have chosen the biggest mid-trunk vertebrae. Such a sampling, however, appears to be incorrect; revised methods of sampling snake vertebrae are discussed below.

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Fig. 6. Pictorial key to living European species of the subfamily *Colubrinae*, known as fossils from Poland. Asterisk (*) means absence of given species in Poland; exclamation mark (!) means that the presence of a given species in Poland was improbable. Not to scale.

1. Length of vertebral centrum (CL) never exceeds 5 mm . . . . . 5.
1a. Length of vertebral centrum (CL) of adult specimens at least 5 mm or longer . . . . . 2.
2. Haemal keel flattened . . . . . 3.
2a. Haemal keel not flattened . . . . . 4.
3. Zygosphene concave; hypapophysis of cervical vertebrae directed anteriorly . . . . . (*) *Elaphe quatuorlineata*.
3a. Zygosphene straight; hypapophysis of cervical vertebrae directed posteriorly . . . . . *Coluber viridiflavus*.
4. Prezygapophyseal process (of large specimens) obtuse; haemal keel spatulate . . . . . *Elaphe longissima*.
4a. Prezygapophyseal process acute; haemal keel of other shape . . . . . (*) *Malpolon monspessulanus*, *Elaphe scalaris* (!), *Coluber hippocrepis* (!).
5. Haemal keel well developed . . . . . (*) *Coluber gemonensis*.
5a. Haemal keel absent or weakly defined . . . . . 6.
6. Prezygapophyseal process long; neural spine well developed . . (*) *Coluber najadum*.
6a. Prezygapophyseal process short; neural spine poorly developed . . . . . 7.
7. Neural arch vaulted . . . . . (*) *Macroprotodon cucullatus* (!), *Elaphe situla*.
7a. Neural arch depressed . . . . . 8.
8. Proximal portion of prezygapophysis slender; parapophysis and diapophysis of equal length . . . . . (*) *Coronella girondica* (!).
8a. Proximal portion of prezygapophysis strongly built; parapophysis much longer than diapophysis . . . . . *Coronella austriaca*.

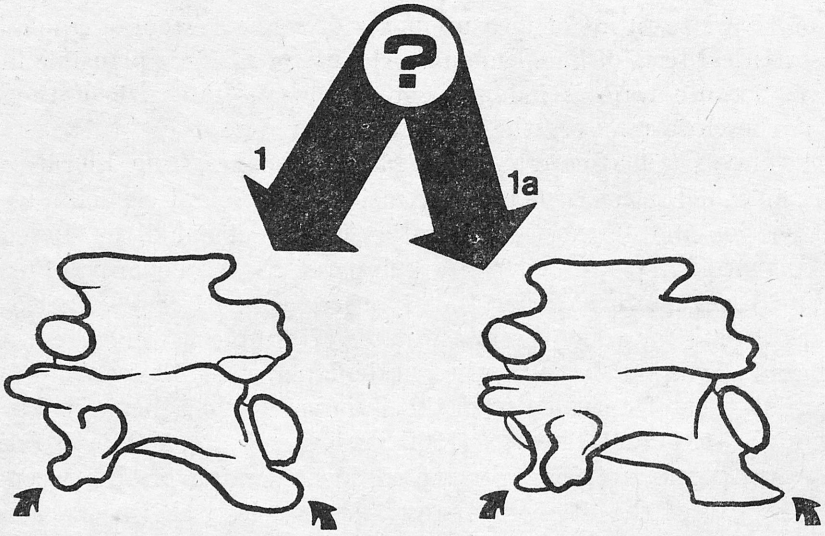

Fig. 7. Pictorial key to living European species of the subfamily *Natricinae*, known as fossils from Poland. Asterisk (*) means absence of given species in Poland; exclamation mark (!) means that the presence of a given species in Poland was improbable. Not to scale

1. Hypapophysis obtused distally; parapophyseal process strongly built . . *Natrix natrix.*
1a. Hypapophysis pointed distally; parapophyseal process slender . . . . . (*) *Natrix tesselata, Natrix maura* (!).

In the present publication I have followed the use of some measurements and ratios given by AUFFENBERG (1963, Figs. 2—4; see Fig. 9 in this paper). Measurements have been applied to mid-trunk vertebrae. Vertebrae from this part of the vertebral column are biggest, therefore their measurement errors are reduced to a minimum; moreover, intracolumnar variation is here small or almost absent. I have omitted for measurements these elements that I have found showing greatest intracolumnar and intraspecific variability, e. g. neural spine and hypapophysis. I have also rejected measuring of small vertebral structures to avoid large measurement errors. For all measurements number of specimens (N) and observed range (OR) has been given, and additionally, for ratios, the mean ($\overline{X}$), standard deviation ($\pm$SD), coefficient of variation, and standard error have been calculated (the two latter parametres are omitted in the text). The samples intended for statistical comparisons have identical CL/NAW mean (vide infra).

The use here of statistical analysis has aimed at comparison of samples representing the same species but originating from different localities as well as samples representing different species. When possible, comparisons of living snakes have been added. Analysis has always concerned PO-PO/NAW, PR-PR/PR-PO, CL/ZW and PR-PR/NAW ratios that I have found to be most

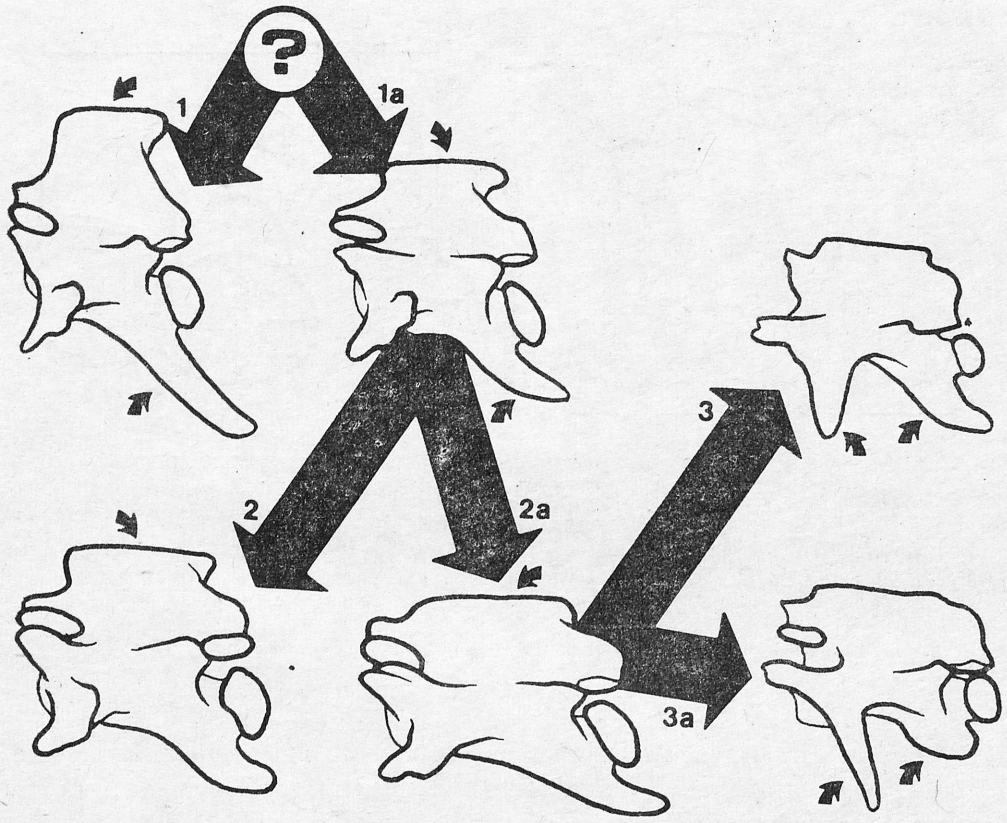

Fig. 8. Pictorial key to living European species of the family *Viperidae*, known as fossils from Poland. Asterisk (*) means absence of given species in Poland; exclamation mark (!) means that the presence of a given species in Poland was improbable. Not to scale.

1. Hypapophysis of cervical vertebrae longer than centrum; neural spine of cervical vertebrae at least as high as long or higher . . . . *Vipera ammodytes*, (*) *Vipera latasti* (!).
1a. Hypapophysis of cervical vertebrae shorter than centrum; neural spine of cervical vertebrae lower than long . . . . . 2.
2. Neural spine of trunk vertebrae well developed (*) *Vipera aspis*, *Vipera seoanei* (!).
2a. Neural spine of trunk vertebrae strongly reduced . . . . . 3.
3. Pleurapophyses and haemapophyses of caudal vertebrae of equal length (*) *Vipera ursinii*.
3a. Pleurapophyses much longer than haemapophyses . . . . . *Vipera berus*.

invariable. To enable the comparison of numerous samples with one another, I have used here one-factor analysis of variance independently for these four ratios, and then new multiple range test (DUNCAN, 1955) to find differences between means. The use of multivariate statistical analysis with ratios as the raw variables would be incorrect and such methods have recently been questioned (cf. ATCHLEY et al., 1976).

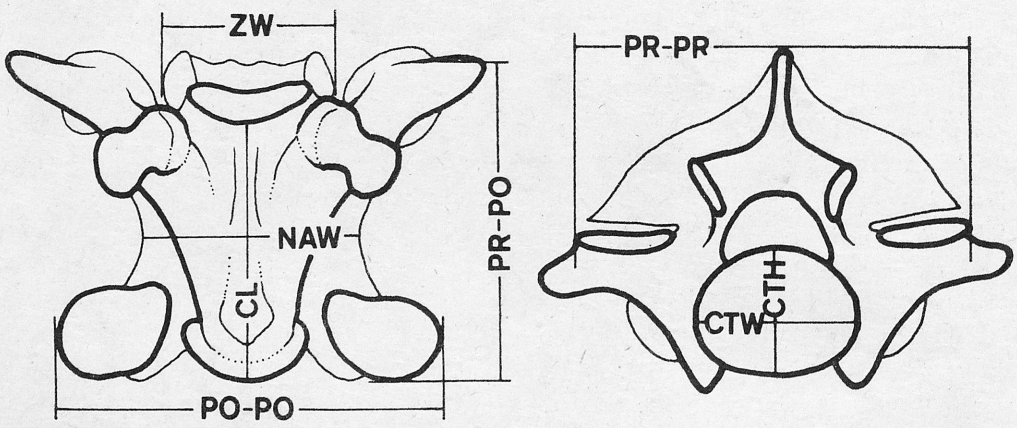

Fig. 9. Measurements of snake vertebrae used in the paper (after AUFFENBERG, 1963). CL — centrum length, CTH — cotyle height, CTW — cotyle width, NAW — centrum width, PO-PO — width between the outer edges of postzygapophyseal articular surfaces, PR-PO — length from the anterior edge of prezygapophyseal articular surface to the posterior edge of postzygapophyseal articular surface, PR-PR — width between the outer edges of prezygapophyseal articular surfaces, ZW — zygosphene width

Sampling of snake vertebrae

It has appeared from my studies on both fossil and comparative Recent materials that sampling of snake vertebrae for statistical purposes without thorough knowledge of allometric changes of ophidian vertebral column can lead to significant errors. The few available studies on allometric variability of snake vertebral column (e. g. AUFFENBERG, 1963; PRANGE and CHRISTMAN, 1976), concerning also other aspects of the problem under discussion, are insufficient for use here. Below follows some observations on the allometry of the snake vertebral column in relation to European colubroids, but presumably also applicable to snakes as a whole.

While with increasing dimensions of a snake body simultaneous growth of each vertebral element occurs, the process proceeds in a highly unsynchronized way. For instance, juvenile specimens of snakes have relatively short centra or low CL/NAW. In older specimens centrum length increases more rapidly than does its width. The increase of the CL/NAW ratio follows probably until the snake reaches average (for given species) dimensions or nearing them. In larger specimens again the rate of lateral centrum growth exceeds its anteroposterior growth and the CL/NAW ratio diminishes. These observations are also equally valid in relation to other vertebral elements and, in consequence, ratios of younger and older (or, although not always quite correctly: smaller and larger) snakes belonging to the same species differ from each other. It is thus easy to determine that statistical comparison of these vertebrae (obviously those taken from the same parts of the vertebral column) will show highly significant differences.

Table III shows an example of ontogenetic distinction: vertebrae of two specimens of *Vipera ammodytes*, an adult and a subadult, both originating from the same site in Bulgaria, have been subjected to statistical comparison. In both cases measurements have been taken from succeeding vertebrae from 66 to 95, including those of largest absolute size in vertebral column of these vipers. All compared ratios show highly significant differences ($p<.01$); it can be seen at first glance even without use of statistical analysis as the extreme values of the compared ratios do not overlap each other. This example should serve as an admonition against too hasty and optimistic use of numerical data for distinguishing of ophidian vertebrae belonging to species that show extreme similarity in vertebral form.

The situation becomes more complicated as frequently specimens having similar body size do not necessarily have equally developed vertebral structures (e. g. *Elaphe longissima* — ZZSiD 20 from Bulgaria and 291 from Poland). Development of vertebrae to equal degree (i. e. of similar ratios) depends rather on age than absolute body size. In other words, assuming that growth of reptiles is subject to the reverse of BERGMANN's rule, adult specimens living in cooler climates will be relatively smaller than specimens of similar age living in warmer climates and will most likely have similar ratios of measurements of their vertebrae in spite of different absolute size.

Table III

Measurements and ratios of trunk vertebrae of two specimens of Recent *Vipera ammodytes* and statistical comparison between them

	ZZSiD 292 (N=30)		ZZSiD 318 (N=30)	
	OR	$\bar{X}\pm SD$	OR	$\bar{X}\pm SD$
PR-PO	5.84—6.27		2.87—3.07	
CL	4.88—5.10		2.25—2.51	
PO-PO	6.23—6.65		3.29—3.47	
NAW	3.06—3.41		1.77—1.90	
ZW	2.92—3.17		1.62—1.76	
CTH	1.96—2.24		1.10—1.23	
CTW	2.27—2.50		1.42—1.57	
PR-PR	6.33—6.66		3.35—3.50	
CL/NAW	1.44—1.63	1.56 ± 0.04	1.21—1.41	1.31 ± 0.06
PO-PO/NAW	1.93—2.07	2.01 ± 0.03	1.79—1.92	1.84 ± 0.03
CTW/CTH	1.07—1.23	1.14 ± 0.04	1.21—1.37	1.27 ± 0.04
ZW/NAW	0.91—0.99	0.95 ± 0.02	0.88—0.97	0.93 ± 0.02
PR-PR/PR-PO	1.03—1.09	1.07 ± 0.02	1.12—1.19	1.16 ± 0.02
CL/ZW	1.57—1.71	1.64 ± 0.03	1.32—1.52	1.41 ± 0.04
PR-PR/NAW	1.91—2.13	2.03 ± 0.04	1.82—1.98	1.88 ± 0.04

ZZSiD 292 (N = 30)		ZZSiD 318 (N = 30)
	PO-PO/NAW: $p<.01$	
	PR-PR/PR-PO: $p<.01$	
	CL/ZW: $p<.01$	
	PR-PR/NAW: $p<.01$	

Table IV

Fossil snakes of Poland and their occurrence in particular localities

	Miocene				Pliocene				Pleistocene																Holocene		
	PR	OP	MA	PO	WI	W II	RKI	RKII	ZB	KD	KA	JZ	KI	ZA	KG	ZY	RZ	WA	NI	ZD	ND	ZS	RA	CI	JO	GI	DS
Boidae																											
Ogmophis europaeus	----	X																									
Colubridae: Colubrinae																											
Colubrinae "A"	X																										
/?/Coluber sp. /=Tamnophis sp./	----	X																									
Zelceophis xenos gen. sp. n.	--------	X																									
Colubrinae "B"	--------	X																									
Colubrinae "C"	--------	X																									
Colubrinae "D"	----------	X																									
Coluber robertmertensi	----------	X																									
Coluber cf. robertmertensi	----------	X																									
Coluber cf. viridiflavus	----------	X																									
Elaphe paralongissima sp. n.	----------	X																									
Elaphe aff. longissima	----------	X							X	-	X	-	X	-	X												
Elaphe longissima	----------	X							X	-	X	-----	X	-	X	-----	X	-	X	-	X	-	X	-	X	-	X
Coronella austriaca	----------	X							X	-	X	-	X	-----	X	-	X	-	X	---------	X						
Colubridae: Natricinae																											
Palaeonatrix silesiaca	----	X																									
Natrix parva n. sp.	--------	X																									
Natrix longivertebrata sp. n.	----------	X																									
Natrix cf. longivertebrata	----------	X	-	X	-----	X																					
Natrix natrix	----------	X	-	X	-----	X	-	X	-	X	-	X	-	X	-----	X	----------	X	-----	X	-	X	-	X			
Viperidae:																											
Viperidae "A"	----	X																									
Viperidae "B"	----------	X																									
Vipera ammodytes	----------	X	-----	X	-	X																					
Vipera berus	----------	X	-	X	-----	X	-	X	-	X	----------	X	-----	X	-----	X	-	X									

Therefore, in sampling vertebrae for statistical comparisons, one must select the bones having neither similar CL nor NAW, but those having equal CL/NAW, a conclusion that I believe to be among the most important results of the statistical study.

The previous inferences concern only ontogenetic and climatic variations; other biologically important kinds of intraspecific variations, e. g. geographical variation, if it exists, remain unknown. Sexual dimorphism is imperceptible in the morphology of the ophidian column (excepting postcloacal vertebrae; cf. KEISER, 1970); analysis of numerical data taken from comparative material at my disposal also has not revealed existence of this variation; the material, however, it too scarce to enable the drawing of firm conclusions.

V. SYSTEMATIC PALEONTOLOGY

Va. MIOCENE AND EARLY PLIOCENE

Suborder *Serpentes* LINNAEUS, 1758
Infraorder *Alethinophidia* HOFFSTETTER, 1955
Superfamily *Booidea* GRAY, 1825
Family *Boidae* GRAY, 1825
Subfamily *Erycinae* BONAPARTE, 1831
Genus *Ogmophis* COPE, 1884

Ogmophis europaeus SZYNDLAR, 1982
(Fig. 10, Table V)

Material. — 19 trunk vertebrae and one fragmentary cervical vertebra from OP.

Description of this Miocene species has been recently published (SZYNDLAR, 1982); below I follow its description in a shortened form.

Centrum of trunk vertebrae usually relatively short (CL/NAW 1.07—1.29), somewhat subtriangular from below, provided with fairly developed subcentral ridges extending from the parapophyses about half-way to the condyle. Haemal keel of the holotype vertebra strongly developed, rounded in shape, uniform in width throughout its length; haemal keel of remaining trunk vertebrae less distinct. Neural arch moderately vaulted. Neural canal narrow, with distinct subneural process. Neural spine low, reaching from the base of the zygosphene to the posterior end of the neural arch, extending more than one-half the greatest length of the neural arch. Anterior margin of the neural spine vertical, its posterior margin unknown. Paradiapophyses well developed, with two poorly defined articular facets. Prezygapophyseal articular facets orbicular in shape. Prezygapophyseal processes underdeveloped, barely visible from above. Zygo-

sphene strongly built, flat in anterior view, and of irregular anterior margin in dorsal view, a little wider than the oval cotyle. Paracotylar foramina lacking. Condyle oblique.

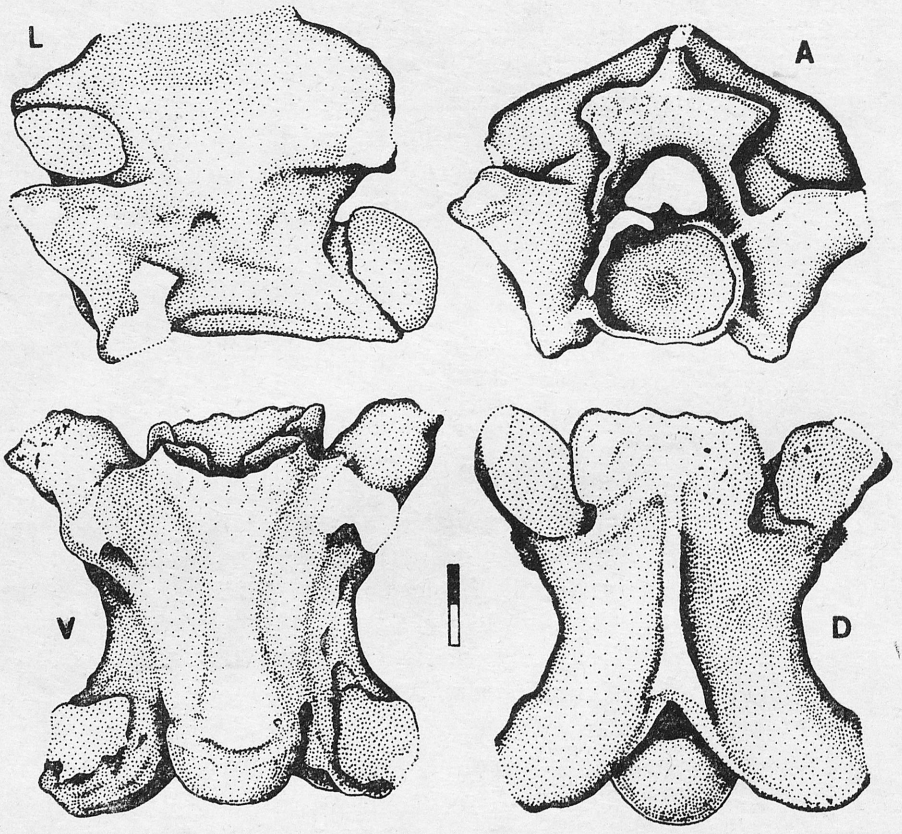

Fig. 10. Holotype trunk vertebra of *Ogmophis europaeus* from OP (ZPUW, OP-86/2) (after SZYNDLAR, 1982). A — anterior, D — dorsal, L — lateral, V — ventral views. Scale equals 2 mm

A fragmentary cervical vertebra consists only of a centrum provided with projected posteriorly hypapophysis, unfortunately broken near its base.

Caudal vertebrae are absent in the material.

Mensuration. With exception of the holotype trunk vertebra, the remaining bones of *Ogmophis europaeus* are poorly preserved and unfit for measurement. Measurements and ratios of the holotype are given in Table V.

Affinities of *Ogmophis europaeus*. Absence of paracotylar foramina and weakly developed prezygapophyseal processes together with small size of vertebrae all indicate that *Ogmophis europaeus* is a characteristic member of the subfamily *Erycinae*. These small boids, known from numerous paleontological records, were widespread in the Tertiary of Europe and North America. Two morphological characters, long neural spine (more than one-half total

Table V

Measurements and ratios of holotype trunk vertebra of *Ogmophis europaeus* from OP (ZPUW, OP 86/2)

PR-PO	9.57	CL/NAW	1.29
CL	8.30	PO-PO/NAW	1.49
PO-PO	9.57	CTW/CTH	1.20
NAW	6.41	ZW/NAW	0.80
ZW	5.11	PR-PR/PR-PO	1.07
CTH	3.31	CL/ZW	1.62
CTW	3.98	PR-PR/NAW	1.60
PR-PR	10.25		

length of centrum) and prominent haemal keel are indicative of close affinities between the erycine from OP and the Holarctic genus *Ogmophis* (cf. HOLMAN, 1979); homologous vertebral structures of European fossil erycines are differently developed (cf. HOFFSTETTER and RAGE, 1972)

Among numerous species of the genus *Ogmophis*, reported from the Tertiary of North America, *O. miocompactus*, described by HOLMAN (1976) from the Middle Miocene of the Rosebud Formation in South Dakota, resembles most closely the OP erycine by having strong haemal keel uniform in width throughout its length, weakly developed prezygapophyseal processes, and similar elongation of the vertebrae (diagnostic characters of *O. europaeus*); however, *O. miocompactus* is much smaller, the length of its centrum does not exceed 3 mm (cf. HOLMAN, 1976, Fig. 1).

Remarks. The description of *Ogmophis europaeus* (SZYNDLAR, 1982) was a first report of this genus from the Old World. According to current views on the dispersal of *Erycinae* (RAGE, 1977), most likely *Ogmophis* invaded Europe in the result of a western migration via the Bering land and Asiatic mainland. In former opinion of HOFFSTETTER and RAGE, 1972 (cf. also UNDERWOOD, 1976), *Erycinae* dispersed in the Early Tertiary from west to east via the North Atlantic.

Erycine remains have been earlier reported from Poland by MŁYNARSKI (1964) from the Pliocene of RK I, although his identification is erroneous as the fossils described above belong instead to colubrine snakes (vide infra: Chapter Vb, p. 60).

Data concerning European erycine snakes reported up to the beginning of the 1970's are summarized by HOFFSTETTER and RAGE (1972). Members of the living European genus *Eryx* are known from the Middle Pliocene: cf. *Eryx* from the Pliocene (MN 15) of Séte and Pliocene (MN 16) of Balaruc-2, France (HOFFSTETTER and RAGE, supra cit.), *Eryx* sp. from the Upper Pliocene of Çalta (MN 15), Turkey (RAGE and ŞEN, 1976), "Erycinae de type moderne" from the Pliocene of Mandriola in Sardinia (PECORINI et al., 1974), and *Eryx* sp. from the Middle Pleistocene of Chios, Greece (SCHNEIDER, 1975). Familial identification by BRUNNER (1957, p. 378, Fig. 17 : 3) of an ophidian caudal

tip ("Wirbelspitze") from the Late Pleistocene of Breitenberghöhle, Germany, as belonging to *Eryx jaculus* is doubtful.

In the opinion of HOFFSTETTER and RAGE (1972), in the Pliocene *Eryx* inhabited a greater part of Europe than to-day; during the Quaternary, because of deterioration of the climate and disappearance of sandy habitats occupied by this snake, its range was reduced to the area of the Balkans.

Superfamily *Colubroidea* OPPEL, 1811
Family *Colubridae* OPPEL, 1811
Subfamily *Colubrinae* OPPEL, 1811

Colubrinae indet. (form "A")
(Fig. 11)

Material. — One fragmentary trunk vertebra from PR.

This vertebral fragment is the only find of a snake in the Miocene deposit of PR; the fossil has been earlier mentioned by MŁYNARSKI (1981, p. 224) as belonging to *Coluber* or *Elaphe* sp.

The vertebra, preserved in very bad state, originates from the middle of the column. The lack of hypapophysis indicates that the bone belonged to a member of the subfamily *Colubrinae*.

Vertebra strongly built, with rather short centrum, somewhat triangular in shape from below. Ventral surface of the centrum flat; subcentral foramina not seen. Haemal keel very distinct in ventral view, cuneate-shaped and flattened, extending posteriorly to the condyle. Subcentral ridges present, but not sharply developed. Neural spine broken, but its remnant indicating a long spine extending from the base of the zygosphene to the posterior end of the neural arch. Zygosphene with very thick roof, slightly convex in anterior view; width of the zygosphene considerably exceeds width of the cotyle. In dorsal view, presumably because of erosion of this portion of the vertebra, the anterior edge of the zygosphene with somewhat irregular shape; in right latero-anterior corner of the zygosphene a small lobe can be seen (left one missing). Dorsal surface of the zygosphene provided with two distinct callosities extending from the anterior edge of the neural spine to postero-lateral corners of the zygosphenal roof. Lateral foramina relatively large. Left parapophysis small, square; right parapophysis and both diapophyses broken off. Right prezygapophyseal articular facet oval; right prezygapophyseal process and left prezygapophysis as a whole missing. Postzygapophyses together with posterior portion of the neural arch also broken. Paracotylar foramina small, but well marked. Condyle oblique, without distinct neck.

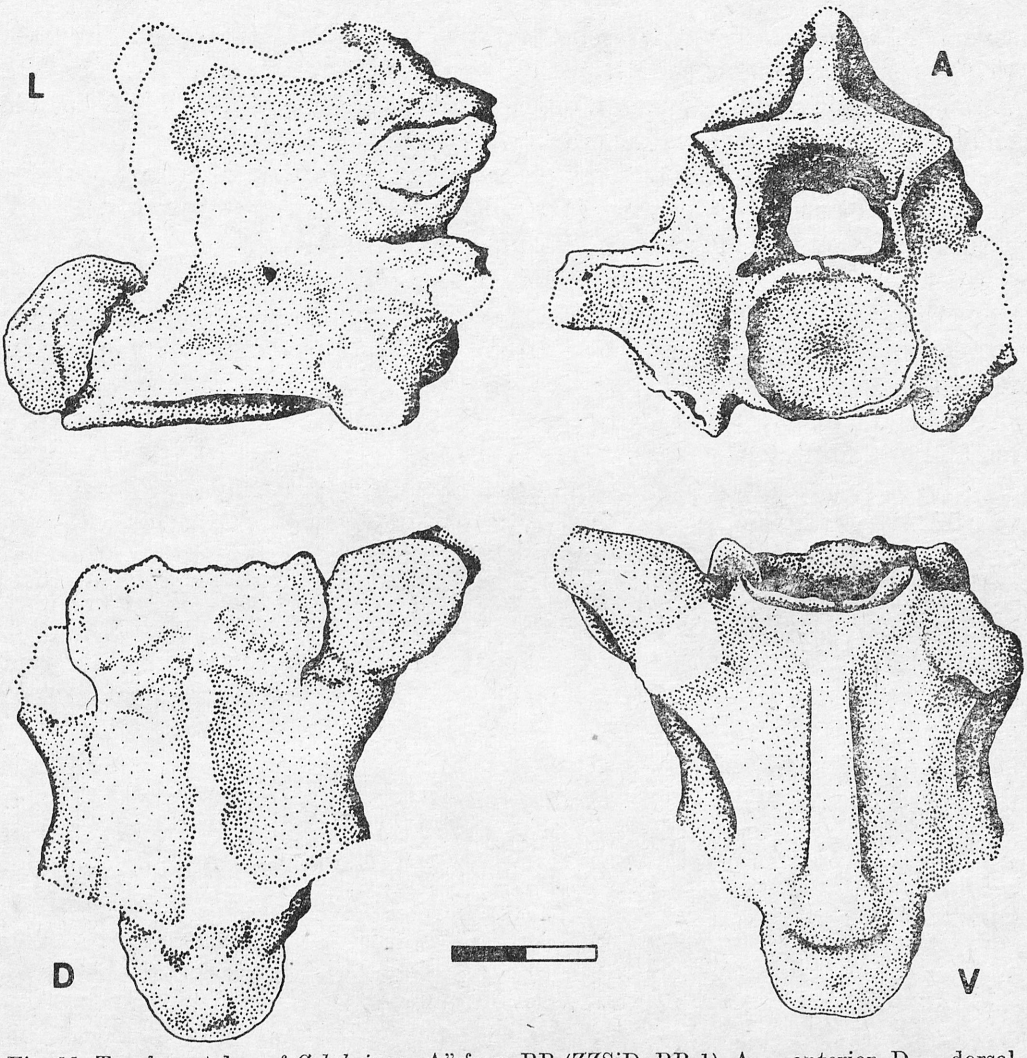

Fig. 11. Trunk vertebra of *Colubrinae* „A" from PR (ZZSiD, PR-1). A — anterior, D — dorsal, L — lateral, V — ventral views. Scale equals 2 mm

Measurements and ratios. CL = 5.27, NAW = 4.25, ZW = 3.64, CTH = 2.17, CTW = 2.48; CL/NAW = 1.24, CTW/CTH = 1.14, ZW/NAW = = 0.86, CL/ZW = 1.45.

Affinities of *Colubrinae* "A". The fossil resembles vertebrae of some larger living members of European genera *Coluber* and *Elaphe* (but not *Malpolon*), but at the same time differs from them by some characteristic features, e. g. its heavy build and presence of a bifid thickening on its zygosphene (presumably muscular insertion). The bone is also dissimilar to those of these Holarctic extinct snakes, vertebrae of which, being correctly described and figured, make comparison possible. *Elaphe nebraskensis* HOLMAN (1964), reported from

several Middle and Upper Miocene localities of North America (cf. HOLMAN, 1979), seems to resemble the PR fossil most of all (HOLMAN, supra cit., Fig. 23). Because of the fragmentary state of the latter form, however, it is not possible identify the snake even to generic level.

Remarks. Below follows some observations concerning Miocene colubrine snakes of Europe; these observations will be also instrumental with reference to other Neogenous snakes from Poland, described below.

Although many fossil snakes referred to *Colubrinae* have been described from the European Miocene, with the exception of *Coluber pouchetii* (de ROCHEBRUNE, 1880, p. 281, pl. 12 : 8) from the Miocene (MN 6) of Sansan (cf. redescription of RAGE, 1981a, pp. 540—541, Fig. 1 B), it appears to be impossible to compare them with Polish fossils. Some of these snakes have been figured and described on the basis of complete skeletons; consequently, morphology of individual vertebrae remains unknown. These snakes include *Coluber owenii* von MEYER from the Miocene (MN 7/8) of Oehningen (von MEYER, 1845, pp. 40—41, pl. 7: Fig. 1; *Elaphe owenii* according to de ROCHEBRUNE, 1880, p. 291) and *Coluber arcuatus* von MEYER from the same locality (von MEYER, 1845, p. 42, pl. 2: Fig. 5; incertae sedis according to de ROCHEBRUNE, 1880, p. 292; cf. also MŁYNARSKI, 1961a, p. 34) as well as *Tropidonotus* (later changed into *Coluber*) *atavus* von MEYER, 1855 (? = *Coluber papyraceus* TROSCHEL in FISCHER, 1858; *Elaphe atavus* after de ROCHEBRUNE, 1880, p. 291) from the Lowermost Miocene (MN 0) of Rott near Bonn (cf. von MEYER, 1860; TROSCHEL, 1861; and MŁYNARSKI, 1961a, pp. 37—38).

Colubrine remains originating from the Uppermost Miocene (MN 13) of Polgárdi were described by BOLKAY (1913) as extinct species belonging to Recent genera: *Zamensis hungaricus* (ibidem: pp. 223—224, pl. 12: Fig. 3) and *Coluber kormosi* (ibidem: p. 224, pl. 12: Figs. 4—8); SZUNYOGHY (1932) has revised BOLKAY's description, recognizing the fossils as members of living species: respectively *Coluber* cf. *najadum* (= *Zamenis* cf. *Dahli*) and *Elaphe longissima* (for further comments see Chapter Vc., p. 100). However, descriptions of these authors, based on cranial bones, disregard vertebrae.

Taxonomic position of other supposed colubrine snakes reported from the European Miocene has been questioned by later students. Some of these fossils, primarily described as belonging to *Colubrinae*, have been recognized as members of other ophidian families and are listed below.

Scaptophis miocenicus de ROCHEBRUNE, described from the Miocene (MN 6) of Sansan (de ROCHEBRUNE, 1880, pp. 279—280, pl. 12: Fig. 7), has been recently recognized as a nomen dubium by RAGE (1981a, p. 541).

Tropidonotus (later *Coluber*) *podolicus* von MEYER (1844) from the Ukrainian Neogene is a nomen dubium as well (Dr. J.—C. RAGE, pers. comm., 1982).

Syntypes of *Coluber steinheimensis* FRAAS (1870, p. 52) (= *Tamnophis pouchetii* de ROCHEBRUNE according to ROGER, 1898, p. 389) from the Miocene (MN 7) of Steinheim contain only a single vertebra belonging to *Colubridae*

(cf. RAGE, 1981a, p. 541), but not to *Colubrinae* (Dr. J.—C. RAGE, pers. comm., 1982).

Several names of ophidian taxa that appeared with neither description nor figure are obviously of no use.

Ophidion antiquus POMEL (1853, p. 128) from the Early Miocene (MN 2) of Langy (St. Gerard), described as belonging to the family *Colubridae*, was later recognized as a boid snake (HOFFSTETTER, 1939, p. 12; HOFFSTETTER and RAGE, 1972, pp. 103—104).

Ophis dubius GOLDFUSS (1831, p. 127, pl. 13: Fig. 8) from the Miocene of Siebengebirge near Bonn was classified as incertae sedis by de ROCHEBRUNE (1880, p. 292).

Coluber elongatus TROSCHEL in FISCHER (1858, p. 32) from the Miocene of Rott (incertae sedis according to MŁYNARSKI, 1961a, p. 34) is not a valid species (KUHN, 1971, p. 21).

Another Miocene snake, indeed belonging to the subfamily *Colubrinae*, has been described from the Miocene (MN 6) of Dévinská Nová Věs (= Neudorf a.d. March) as ? *Malpolon* sp. (WETTSTEIN-WESTERHEIMB, 1955, pp. 813—814), nevertheless, based on the photos of its vertebrae (ibidem: pl. 2: Fig. 4), it is impossible to confirm the determination even to generic level. Ophidian remains, described as belonging to the same genus (*Coelopeltis*?) were earlier reported from the Miocene of Polgárdi by KORMOS (1911, pp. 63 and 187), yet neither BOLKAY (1913) nor SZUNYOGHY (1932), who gave detailed descriptions of the ophidian fauna from this locality, made reference to the presence of *Malpolon* on the Polgárdi deposit. The only true fossil member of this genus is *Malpolon laurenti* (DEPÉRET), described from the Pliocene (MN 15) of Perpignan in the Roussillon Basin (DEPÉRET, 1890, pp. 170—172, pl. 18: Figs. 4—9) *; this snake is closely related or even identical with Recent *Malpolon monspessulanus*.

The only Miocene colubrine snake found in Palearctica outside Europe is that from the Middle Miocene (MN 7) of Beni Mellal in Morocco (RAGE, 1976, p. 61, Fig. 4); in its vertebral form, however, it is extremely different from both living and extinct European snakes.

(?) *Coluber* sp. (= *Tamnophis* sp.)

WEGNER (1913), in his classical description of the Miocene vertebrate fauna from OP, mentioned a solitary fragmentary vertebra of a snake and identified that fossil as *Tamnophis* sp. As WEGNER's monograph contains neither description nor figure of the referred vertebra and the whole material described by this author probably has been mislaid, verification of his determination is impossible

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* A part of the material, diagnosed by DEPÉRET (1890) as belonging to *Malpolon laurenti*, was later redescribed by HOFFSTETTER (1939, pp. 66—67, pl. 2: Fig. 16) as an extinct member of the family *Elapidae, Palaeonaja depereti*.

(SZYNDLAR, 1982). However, most likely WEGNER diagnosed the fossil as a result of the influence of ROGER's (1898, p. 389) description of *Tamnophis pouchetii* from the Bavarian Miocene (cf. WEGNER, 1913, p. 212). *Tamnophis pouchetii*, to which Wegner has referred his find, was described by de ROCHEBRUNE (1880) from the Miocene of Sansan and has been lately redescribed by RAGE (1981a) as *Coluber pouchetii* *.

Zelceophis gen. n.

Type species (by monotypy). — *Zelceophis xenos* sp. n.
Type locality. — Mała Cave (MA) at Zelce Hill near Działoszyn (Northern Kraków—Wieluń Upland in central Southern Poland).
Type horizon. — Upper Miocene (Turolian/Pontian), layer 7+8 (= Early /Middle Pliocene in traditional East European classification).
Name derivation. — From Zelce Hill, a place of situation of Mała Cave, and and from Greek οφις — a snake.
Diagnosis. — As for the type-species.

Zelceophis xenos sp. n.
(Fig. 12)

Holotype. — A trunk vertebra, ZPUW, no. IZ—6/R/1.
Type locality and type horizon. — As for the genus.
Name derivation. — From Greek ξένος — alien.
Diagnosis. — A colubrine snake having a peculiar shape of its vertebral form, differing from other *Colubrinae* by combination of the following features of the trunk vertebrae: (1) very short centrum, wider than long, (2) lack of paracotylar foramina, (3) dinstinct haemal keel of uniform width throughout its length, (4) deeply concave zygosphene, (5) strongly developed prezygapophyseal process, flattened and obtuse-shaped.

Description of the holotype

A medium-sized colubrine vertebra from the middle of the column, somewhat fragmentary. Neural spine, condyle, and right postzygapophyseal portion of the neural arch are missing. In addition, left paradiapophysis as well as prezygapophyseal process on the same side are broken off.

Centrum very short, somewhat cylindrical; although devoid of the condyle, beyond a doubt wider than long (CL/NAW<1). Haemal keel prominent, of almost uniform width throughout its length. Subcentral grooves are especially

* *Tamnophis* de ROCHEBRUNE and North American living snake *Thamnophis* FITZINGER are two different forms. Similarity of their generic names has led some zoologists into error, e. g. ROMER (1956) has classified *Tamnophis* among synonyms of *Thamnophis*, though the snakes represent two different subfamilies, *Colubrinae* and *Natricinae* (cf. also MŁYNARSKI, 1961a, and RAGE, 1981a).

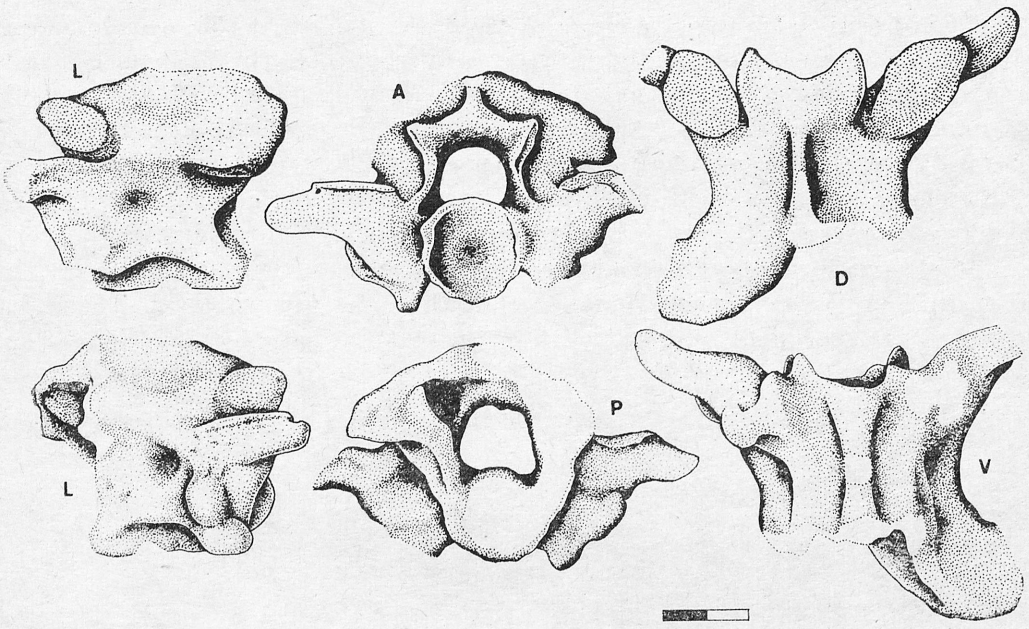

Fig. 12. Holotype trunk vertebra of *Zelceophis xenos* gen. sp. n. from MA (ZPUW, IZ-6/R/1). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

deep between parapophyses and the anterior portion of the haemal keel. Subcentral ridges well developed. Neural arch robust, deeply V-shaped posteriorly, with laminae strongly extended before and after postzygapophyses; in consequence, interzygapophyseal ridges are prominent and postzygapophyseal area of the neural arch is produced into a prominent expansion ("aliform process" *), seen in lateral view. Neural canal somewhat subtriangular from the front, of about the same size as the round cotyle. Neural spine missing, but presumably short, occupying one-half the length of the neural arch. Zygosphene of heavy built, flat in anterior view and strongly concave from above. Postzygapophyseal articular surface (left) large, its distal portion damaged. Prezygapophyseal articular surface elongate, diamond-shaped. Right prezygapophyseal process extremely long, obtuse, widening distally and flattened. Lateral foramina large, located in deep depressions. Right paradiapophysis weakly divided into parapophyseal and diapophyseal portions, the latter structure twice the length of the former and projected forward. The fossae on either side of the cotyle lack foramina.

Measurements and ratios. PR-PO = 6.28, NAW = 4.66, ZW = 3.17, CTH = 2.32, CTW = 2.21, PR-PR = 7.53; CTW/CTH = 0.95, ZW/NAW = = 0.79, PR-PR/PR-PO = 1.20, PR-PR/NAW = 1.62.

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* As used by Thireau (1967) with reference to vertebrae of vipers. Usually the term „aliform process" (= pterapophysis) is restricted to members of the extinct family *Palaeophidae* and means wing-like processes found at posterior portion of the neural arch.

Taxonomic status of *Zelceophis xenos* gen. sp. n. The combination of peculiar characters of the above-described vertebra clearly distinguishes this snake from living European ophidian species as well as from Holarctic fossil forms. Shortening of the centrum length to the degree, observed in *Zelceophis* is rare among *Colubridae*, also a lack of paracotylar formina is rather salient; these characters are typical for *Erycinae*, yet strong development of prezygapophyseal process makes such a reference impossible. Robust built of the vertebra, strong thickness of cotylar margins, and deep, somewhat asymmetrical, concavity of the zygosphene indicate that the bone presumably belonged to a very large specimen. Zygosphenal form suggest the pathologic nature of the vertebra; if so, the surprising absence of paracotylar foramina may also have been caused by pathologic mechanisms.

Colubrinae indet. (form "B")
(Fig. 13, Table VI)

Material. — Two fused trunk vertebrae from MA.

The vertebrae, originating from the middle of the column, are characteristic for colubrine snakes, except that their cylindrical centra are wider than long (CL/NAW<1). In ventral view, haemal keel broad, but weakly developed; in the anterior vertebra the keel is strongly widened just before the cotyle, in the posterior one it is of uniform width throughout its length. Neural arch well vaulted, without epizygapophyseal spines, slightly upswept in the postzygapophyseal area. Neural canal relatively broad and high, somewhat square in outline from the front, slightly narrower than the round cotyle. Upper portions of both neural spines broken off. Zygosphene of the anterior vertebra also missing; zygosphene of the posterior vertebra remains unknown since, because of accretion of both bones, separation from each other is impossible without damage. Pre- and postzygapophyseal articular surfaces obovate. Prezygapophyseal processes slender, moderately developed. Interzygapophyseal ridges weakly developed. Lateral foramina small, hardly seen, without any depressions surrounding them. Paradiapophyses elongate dorso-ventrally, weakly divided into parapophyseal and diapophyseal portions. Paracotylar foramina small, doubled of the right side of the cotyle. Condyle slightly oblique, provided with a short neck.

Mensuration. Table VI contains measurements and ratios of the anterior vertebra.

Affinities of *Colubrinae* "B". The fossils, in their vertebral form, generally resemble European living snakes of the genera *Coluber* and *Elaphe*. Nevertheless, extremely short vertebral centrum together with indistinct and broad haemal keel indicate that the vertebrae belonged to a separate ophidian species

different from other living and extinct colubrines. Yet, since identification of the genus is problematic * and, in the hope of obtaining additional material from MA, I temporarily postpone describing a new species on the basis of these vertebrae.

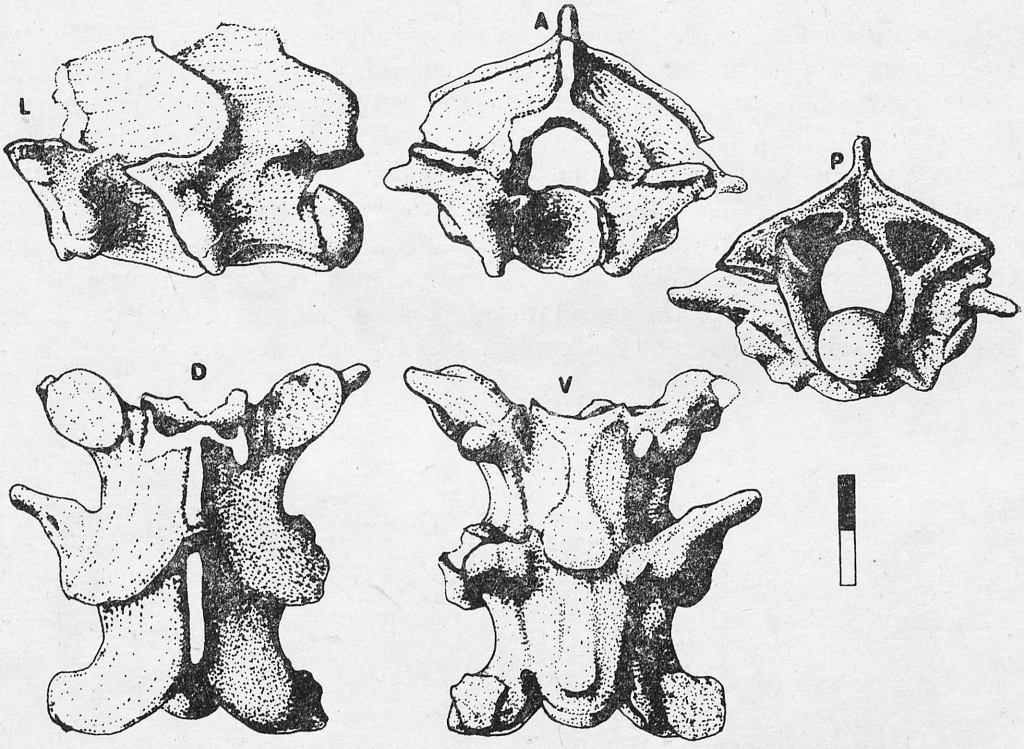

Fig. 13. Trunk vertebrae of *Colubrinae* „B" from MA (ZPUW, IZ-6/R/2). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

Table VI

Measurements and ratios of a trunk vertebra of *Colubrinae* „B" from MA (ZPUW, IZ-6/R/2). (N = 1)

PR-PO	4.33	CL/NAW	0.91
CL	±3.25	PO-PO/NAW	1.56
PO-PO	5.56	CTW/CTH	1.14
NAW	3.57	PR-PR/PR-PO	1.39
CTW	1.90	PR-PR/NAW	1.68
CTH	1.67		
PR-PR	6.01		

* Problems concerning differentiation of vertebrae belonging to genera *Coluber* and *Elaphe* have been discussed by several authors, e. g. Młynarski (1961a), Auffenberg (1963), and Rage (1974). Although usually it is possible to distinguish vertebrae of particular European members of these genera from one another, most likely it is impossible to separate these ge-

Colubrinae indet. (form "C")
(Fig. 14)

Material. — A trunk vertebra from MA.

Judging on the basis of small absolute size of the vertebra (CL = 2.19), large diameter of the neural canal, minute dimensions of zygapophyseal articular facets and other features, the vertebra belonged to a juvenile specimen of a colubrine snake.

Centrum short, somewhat cylindrical, provided with a distinct pair of subcentral ridges, but diminishing posteriorly. Haemal keel oblanceolate in ventral view, arched upward in the middle of the centrum in lateral view. Neural arch short, strongly vaulted. Neural spine lower than long, occupying over one-half of the length of the neural arch, with rounded antero- and postero-dorsal corners. Zygosphene wide, of irregular shape when seen from above. Tiny pre- and post-

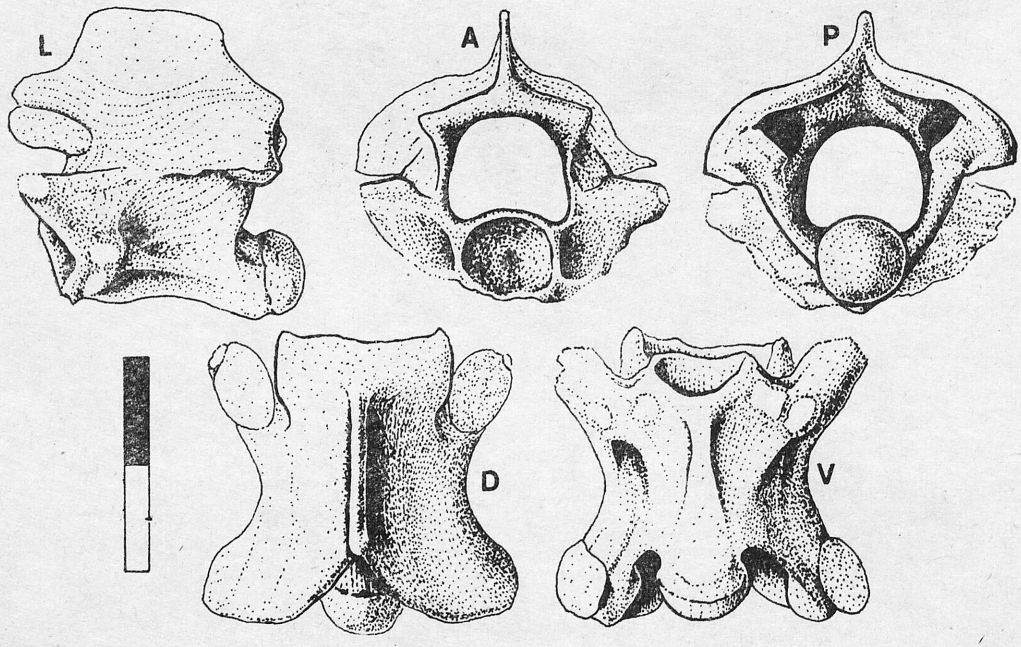

Fig. 14. Trunk vertebra of *Colubrinae* „C" from MA (ZPUW, IZ-6/R/3). A — anterior, D — dorsal L — lateral, P — posterior, V — ventral, views. Scale equals 2 mm

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nera overall based only on vertebral characters. Distinguishing features of *Coluber* and *Elaphe* given by American students of fossil snakes, i. e. presence or absence of epizygapophyseal spines (Auffenberg, 1963, pp. 175 and 180) or, respectively, elongation or shortness of vertebrae (Holman, 1979, p. 206), may be true for Holarctic snakes, are not the case in relation to European species alone. Because of these reasons, determination of generic attachment of fossil species, except forms closely related to Recent species, appears to be always problematic or impossible.

zygapophyseal articular surfaces oval-shaped. Prezygapophyseal processes missing. Paradiapophyses also damaged. Fossae on either side of the cotyle very deep. Condyle small, directed posteriorly, provided with a short neck.

The vertebra has not been identified to generic level.

Colubrinae indet. (form "D")
(Fig. 15)

Material. — 13 fragmentary precaudal vertebrae and 3 caudal vertebrae from PO.

The material consists of strongly damaged vertebral fragments; since no complete vertebra has been preserved, some details of vertebral form remain unknown.

Centrum of rather small (CL<4) trunk vertebrae (Fig. 15: 1—3) is moderately long, distinctly triangular from below, with flat ventral surface. Haemal keel is only moderately produced from the centrum; in lateral view, its posterior portion is downswept in an archwise form. Subcentral foramina prominent, subcentral ridges not sharply developed. Neural arch preserved in fragmentary state in two trunk vertebrae, vaulted and weakly V-shaped posteriorly. Postzygapophyses strongly expanded laterally, provided with elongate articular surfaces, twice as wide as long. Interzygapophyseal ridges sharp and well developed. Lateral foramen large, provided with deep furrow directed anteriorly. Cotyle strongly flattened dorso-ventrally. There is a lack of grooves or depressions between lateral margins of the cotyle and prezygapophyseal rami; paracotylar foramina are situated just next to the lateral limits of the cotyle. Condyle provided with a very long neck, extending far behind the posterior margin of the neural arch. Neural spine, prezygapophyses, zygosphene and paradiapophyses are unknown.

Cervical vertebrae (Fig. 15: 4, 5) have preserved complete neural arch, provided with zygosphene, the latter structure with straight anterior margin when seen from above. Neural spine broken, but presumably long, reaching from the base of the zygosphene to the posterior end of the neural arch. Prezygapophyseal articular surfaces obovate in shape. Paracotylar foramina located in vertical depressions, unlike trunk vertebrae. Hypapophysis, paradiapophyses and prezygapophyseal processes are missing.

A unique caudal vertebra (Fig. 15: 6, 7) is preserved in a better state than precaudal ones. Pleurapophyses and haemapophyses are well developed, the latter broken posteriorly. Neural spine and zygosphene are missing.

Remarks. Although the Early Pliocene colubrine snake from PO has vertebrae similar to the living members of the genera *Coluber* and *Elaphe*, it may be distinguished from both European Recent species and Neogene Holarctic snakes on the basis of the following combination of characters: (1) peculiar form

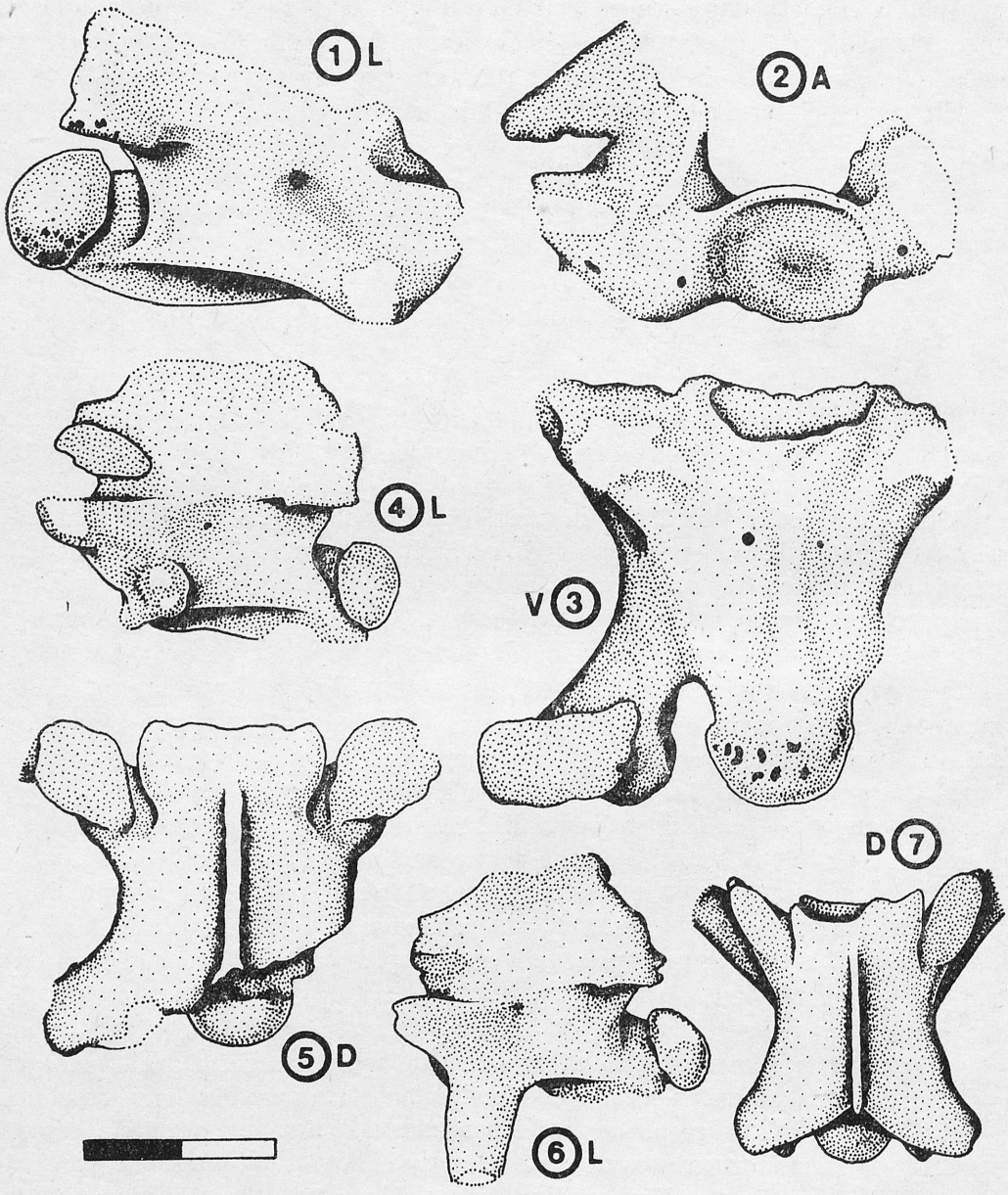

Fig. 15. Vertebrae of *Colubrinae* „D" from PO. 1, 2, 3 — trunk vertebra (ZZSiD, PO-4), 4, 5 — cervical vertebra (ZZSiD, PO-5), 6, 7 — caudal vertebra (ZZSiD, PO-6). A — anterior, D — dorsal, L — lateral, V — ventral views. Scale equals 2 mm

of the posterior portion of the haemal keel, (2) presence of deep furrows connected with lateral foramina, (3) lack of depressions around paracotylar foramina.

Because of fragmentary nature of the trunk vertebrae, however, I have not described a new taxon based on these fossils.

Subfamily *Natricinae* Bonaparte, 1838
Genus *Palaeonatrix* Szyndlar, 1982

Palaeonatrix silesiaca Szyndlar, 1982
(Fig. 16)

Material. — 3 cervical vertebrae, 3 trunk vertebrae, and 2 caudal vertebrae from OP.

This natricine snake, originating from the Miocene of OP, has been recently described by Szyndlar (1982); below I repeat its original description in a shortened form.

Centrum of trunk vertebrae (Fig. 16: 1—5) elongate, provided with a distinct pair of subcentral ridges extending from the parapophyses toward the condyle neck, sharply arched upward posteriorly. Hypapophysis unknown, but presumably short, with strongly developed base, produced into a high, sheet-like anterior keel, reaching cotyle rim in the form of two small tubercles. Neural arch long, weakly vaulted, without epizygapophyseal spines. Neural canal depressed dorso-ventrally, of about the same diameter as the round cotyle. Neural spine very low, not overhanging both anteriorly and posteriorly, occupying one-half of the length of the neural arch. In dorsal view, zygosphene crenate into three distinct lobes, the median lobe greater than the lateral ones; in anterior view, zygosphenal roof is flat. Postzygapophyses damaged in all trunk vertebrae. In dorsal view, prezygapophyses directed antero-laterally; their articular surfaces oval-shaped. Prezygapophyseal processes missing. Interzygapophyseal ridges sharply developed, especially near the postzygapophyseal area. Paradiapophyses, including parapophyseal process, unknown. Foramina on either side of the cotyle. Condyle provided with a distinct neck, projecting behind the posterior margin of the neural arch.

Measurements and ratios of the holotype trunk vertebra: PR-PO = 4.78, NAW = 2.57, PO-PO = 4.23, CTW = 1.48, CTH = 1.42, ZW = 2.55; PO-PO/NAW = 1.65, CTW/CTH = 1.04, ZW/NAW = 0.99. Basic dimensions of another trunk vertebra (with preserved condyle) are: CL = 5.77, NAW = 4.04; CL/NAW = 1.43.

One of the cervical vertebrae (Fig. 16: 6, 7) is the best preserved bone in the material; it has a well vaulted neural arch and strongly developed hypapophysis, with a broad profile, although broken distally. Parapophyses prominent, projected far downwards, triangular in anterior view, provided with distinct processes. Strong development of the above characters is characteristic for cervical vertebrae. Sharply developed subcentral ridges are slightly bowed below the condyle base. Zygosphene barely convex from above. Prezygapophyseal articular facets elongate; prezygapophyseal process missing. The greater part of the neural spine is also broken off. Postzygapophyseal portion of the neural arch unknown.

Caudal vertebrae (Fig. 16: 8, 9), judging on the basis of their elongation,

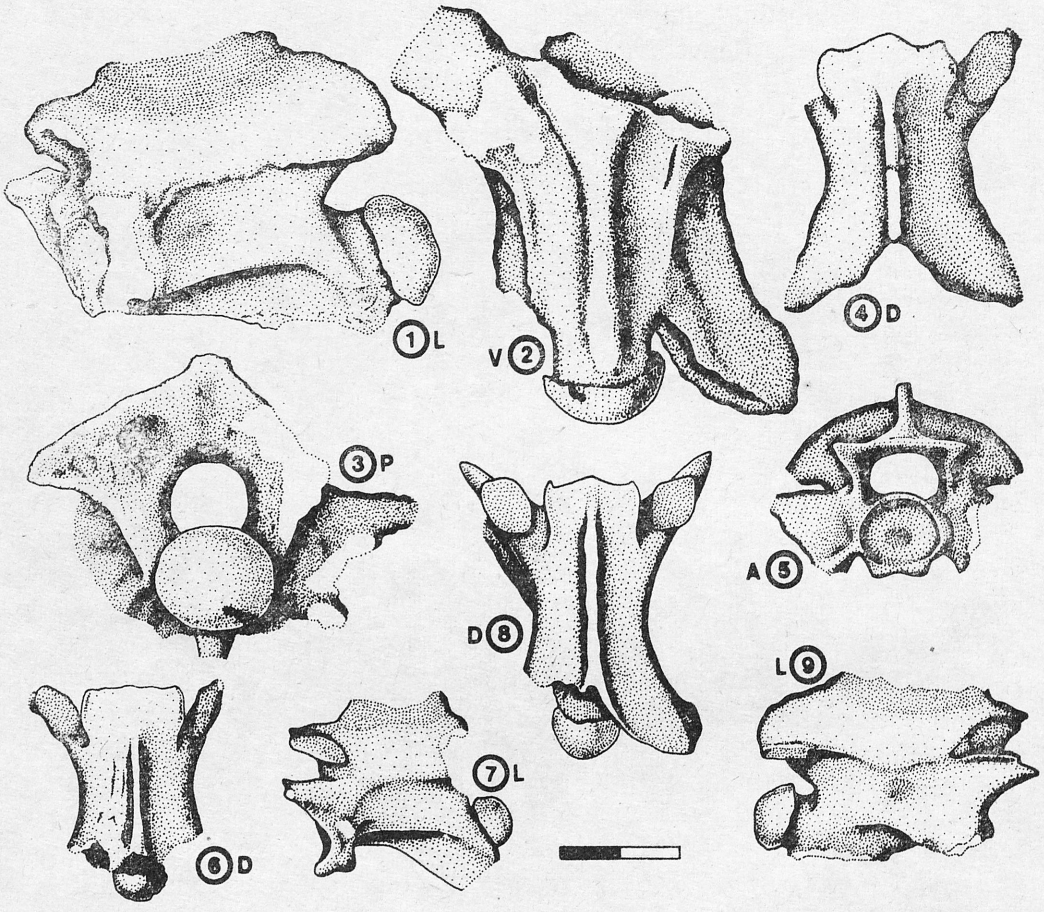

Fig. 16. Vertebrae of *Palaeonatrix silesiaca* from OP (partly after SZYNDLAR, 1982). 1, 2, 3 — trunk vertebra (ZPUW, OP-86/25), 4, 5 — holotype trunk vertebra (ZPUW, OP-86/21), 6, 7 — cervical vertebra (ZPUW, OP-86/24), 8, 9 — caudal vertebra (ZPUW, OP-86/27). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

originate from the posterior region of the tail. Pleurapophyses and haemapophyses strongly developed and presumably long, though missing distally. Prezygapophyseal articular surfaces acuminate-shaped, projected antero-laterally. Zygosphene crenate from above. Neural spine missing.

Affinities of *Palaeonatrix silesiaca*. *Palaeonatrix*, in having hypapophyses on its trunk vertebrae, is a typical member of the subfamily *Natricinae*. Reduction of its neural spine and (presumably) hypapophysis distinguishes the snake from other natricine species known from the Holarctic Neogene except *Neonatrix elongata* HOLMAN (1973), the latter widespread in the North American Miocene (HOLMAN, 1979). *Palaeonatrix*, however, may be easily separated from *Neonatrix* (cf. HOLMAN, supra cit., Fig. 32) in that the former has strongly developed hypapophyseal bases, distinctly bent upward subcentral ridges, and (probably) prominent parapophyses (diagnostic characters of *Palaeonatrix sile-*

siaca). For detailed comparison of *Palaeonatrix* with all *Natricinae* from the Holarctic Miocene see SZYNDLAR, 1982.

Remarks. Only a few finds of natricine snakes have been reported from the Palearctic Miocene, however, in contrast to the fossils referred to *Colubrinae*, discussed above, all these descriptions appear to be correct.

Several snake species from European Miocene, identified as belonging to the living genus *Natrix*, are discussed below (p. 50). In addition, another natricine snake, *Protropidonotus neglectus* SCHLOSSER (1916, pp. 34—35, pl. I: Figs. 2—3), has been described from the Miocene of Eichstätt in South Germany; vertebrae of this snake were reported later by STROMER (1928, pp. 44—45, pl. 3: Fig. 4) and other authors from various sites of the Bavarian Miocene.

Furthermore, a fossil snake identified as a member of the subfamily *Natricinae*, *Mionatrix diatomus* SUN (1961, pls. 1 and 2), has been described from the Miocene of Shanwang in China. This species has been described on the basis of a complete skeleton; unfortunately, morphological form of its individual vertebrae, inexactly figured by SUN (supra cit., text-fig. 1), remains obscure and makes comparisons with other snakes impossible.

Genus *Natrix* LAURENTI, 1768

Natrix parva sp. n.
(Fig. 17, Table VII)

Holotype. — A trunk vertebra, ZPUW, no. IZ-6/R/4.

Referred material. — Four trunk vertebrae, ZPUW, no. IZ-6/R/5-8.

Type locality. — Mała Cave (MA) at Zelce Hill near Działoszyn (Northern Kraków—Wieluń Upland in central Southern Poland).

Type horizon. — Upper Miocene (Turolian/Pontian), layer 7 ±8 (= Early /Middle Pliocene in traditional East European classification).

Name derivation. — From Latin *parva* — small.

Diagnosis. — A typical natricine snake, differing from other members of the genus *Natrix* by combination of the following features: (1) straight hypapophysis, (2) strong narrowing between pre- and postzygapophyses, (3) crenate zygosphene with the lateral lobes projected further anteriorly than the central lobe, (4) strongly elongate prezygapophyseal articular facets, (5) parapophyseal process prominent, of triangular section, (6) very large paracotylar foramina, (7) absence of paired tubercles below the cotyle rim.

Description of the holotype

A somewhat fragmentary mid-trunk vertebra with neural spine, left parapophyseal process and right prezygapophyseal process missing. In dorsal or ventral view, the vertebra is strongly narrowed between pre- and postzygapophyses. Centrum is long and narrow, with a distinct pair of subcentral ridges ex-

tending from parapophyses to the end of the centrum, between the anterior border of the condyle and the base of hypapophysis. These ridges are especially well developed just posterior to parapophyses. Subcentral grooves broad and shallow; anteriorly these grooves form narrow and deep furrows, penetrating between the anterior keel and parapophyseal processes and reaching the cotyle lip. Subcentral foramina minute. Hypapophysis moderately long, more straight than sigmoid-shaped when seen from lateral side, projected ventro-posteriorly. Anterior keel flattened, triangular in ventral view, without any lateral tubercles below the cotyle rim. Neural arch moderately vaulted, without epizygapophyseal spines; its posterior border weakly V-shaped. Neural canal subtriangular from the front, of about the same size as depressed cotyle. Neural spine almost completely missing, but its remnants indicate a spine extending more than one-half the greatest length of the neural arch. Zygosphene slightly convex from the front, crenate from above with lateral lobes developed stronger than the median one. Zygantrum moderately high and wide; zygantral recesses are pierced by a pair of distinct foramina. Foramina are also present on the posterior wall of postzygapophyseal rami: a single foramen on the left ramus and two foramina on the right ramus. Interzygapophyseal ridges weakly developed. Lateral foramina well marked without depressions around them. Postzygapophyseal articular facets small, somewhat subtriangular. Prezygapophyseal articular facet

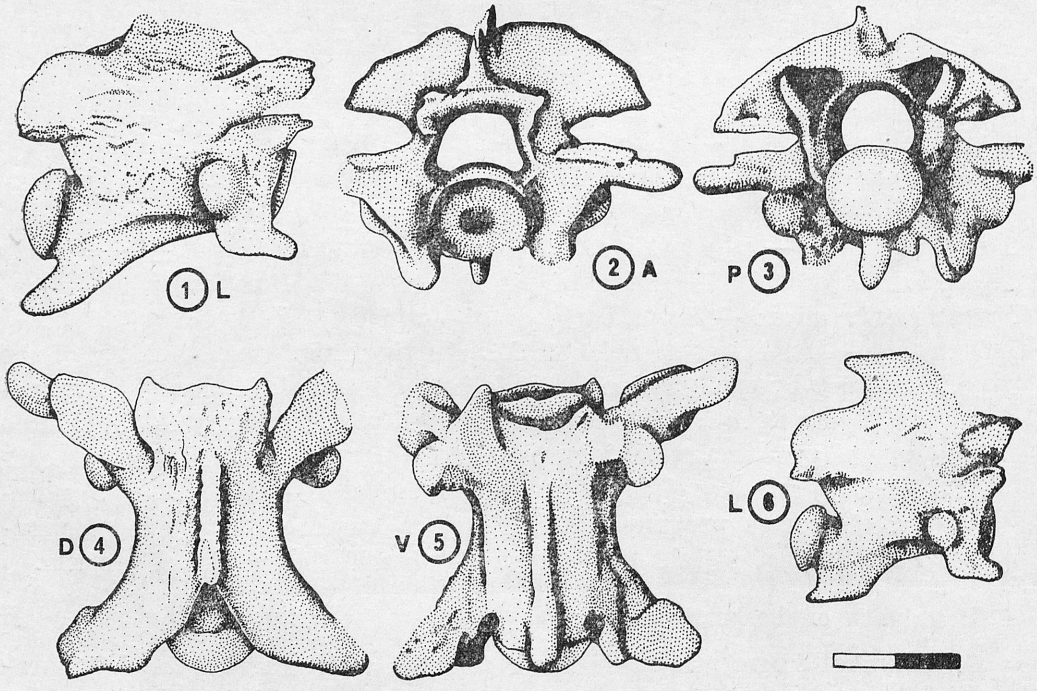

Fig. 17. Vertebrae of *Natrix parva* sp. n. from MA. 1, 2, 3, 4, 5 — holotype trunk vertebra (ZPUW, IZ-6/R/4), 6 — trunk vertebra (ZPUW, IZ-6/R/5). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

strongly elongate, twice longer than wide. Prezygapophyseal process long, slightly flattened dorso-ventrally, obovate in shape. Paradiapophyses well developed, with two articular facets; diapophyses strongly projected laterally. Parapophyseal process (right) well developed, projected forwards, of triangular section, with a flat ventro-medial surface. Paracotylar foramina very large, located in deep depressions on either side of the cotyle. Condyle moderately oblique, oval, without a distinct neck.

Measurements and ratios of the holotype are given in Table VII.

Table VII

Measurements and ratios of holotype trunk vertebra of *Natrix parva* sp. n. from MA (ZPUW, IZ-6/R/4

PR-PO	4.70	CL/NAW	1.73
PR-PO	4.82	PO-PO/NAW	2.22
CL	4.04	CTW/CTH	1.10
PO-PO	5.17	ZW/NAW	0.99
NAW	2.33	PR-PR/PR-PO	1.06
ZW	2.30	CL/ZW	1.76
CTH	1.47	PR-PR/NAW	2.16
CTW	1.61		
PR-PR	5.04		

Description of remaining material

Amongst four trunk vertebrae two are preserved in only fragmentary state, devoid of their posterior portions; two others are almost complete, but with prezygapophyseal processes and neural spines missing. These two latter vertebrae, much smaller than the holotype and of much more vaulted neural arch, originate probably from subadult specimen(s). Postzygapophyseal part of the neural arch is slightly upswept. Hypapophyses of both vertebrae very short and distinctly sigmoid in lateral view; shortness of hypapophyses indicates that the bones represent the posterior section of the column. One vertebra has the posterior portion of its neural spine preserved, provided with prominent overhang; the remnant indicates that neural spine was longer than high. Beyond this, other features are identical with those of the holotype.

Neither cervical nor caudal vertebrae have been found.

Taxonomic status of *Natrix parva* sp. n. *Natrix parva* by its vertebral form resembles closely other members of the living genus *Natrix*, namely the Recent European species *Natrix natrix*, *N. tesselata*, and *N. maura* as well as *N. sansaniensis* (LARTET, 1851, p. 40) from the Middle Miocene (MN 6) of Sansan, France, recently redescribed as a member of the genus *Natrix* by RAGE (1981a, pp. 538 and 540, Fig. 1 A).

In lateral extension of zygapophyses, triangular-shaped parapophyseal processes and elongate prezygapophyseal articular facets *Natrix parva* most resembles *N. tesselata* (ZZSiD 16 and others), but has differently built hypapo-

physis. Hypapophysis of *N. tesselata* (as well as that of *N. maura*, MNCN 824272) has a sharp antero-ventral inflexion, well defined ventral edge and pointed distal tip, unlike *N. parva*. Its hypapophysis, straight rather than sigmoid, together with prezygapophyseal processes not widened distally and reduced central lobe of zygosphenal anterior border, appear to be the most important specific characters of *N. parva*. Prezygapophyseal processes of all three European living species of *Natrix* (large specimens) have strongly widened distal portions in dorsal view. Crenate zygosphene of these species, including fossil *N. sansaniensis*, usually has a well defined central lobe. Thickness for muscular insertion on zygosphenal roof, a specific feature of *N. sansaniensis*, is absent in vertebrae of *N. parva*.

Remarks. *Natrix sansaniensis*, mentioned above, has until now been the only extinct member of the genus *Natrix* described from the Miocene of Europe. Besides this, ophidian remains identified as belonging to living species of the genus, *N. natrix* and *N. tesselata*, have been reported from the Upper Miocene (MN 13) of Polgárdi, Hungary, by BOLKAY (1913, p. 223); his identification has been later confirmed by SZUNYOGHY (1932). Studies of both authors have been restricted to skull bones only: 3 parietals of *N. natrix* and 2 basiparasphenoids plus 2 compounds of *N. tesselata* (cf. SZUNYOGHY, supra cit., pp. 8 and 9; if both authors have indeed examined the same fossil specimens). Unfortunately, the fossils have not been figured and no diagnostic description of them has been given.

Family *Viperidae* LAURENTI, 1768

Viperidae indet. (form "A")
(Fig. 18: 1, 2)

Material. — Two fragmentary vertebrae from OP.

Viperid remains from the Miocene of OP have been recently described by SZYNDLAR (1982). Both fragments are poorly preserved, consisting only of centra provided with bases of hypapophyses. Manner of development of the hypapophyses and presence of subcentral ridges only in the anterior portion of the centra are characteristic for *Viperidae*. Moreover, the smaller fragment is provided with an undamaged left parapophysis including a downward directed parapophyseal process, long and slender in lateral view and broad when seen from anterior view. Judging on the basis of slight posterior inclination of the hypapophyses, both fragments originate from the cervical or anterior trunk region of the column.

Because of the fragmentary state of preservation of the bones it is impossible to determine even their subfamilial attachment. Preserved vertebral structures (long hypapophyses and long parapophyseal process) are of the same morpholo-

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gical pattern as these of some true vipers *(Viperinae)*, e. g. *Vipera ammodytes* (ZZSiD 292 and others), *V. latasti* (MNCN 820971), and *Cerastes vipera* (ZZSiD 280) as well as pit vipers *(Crotalinae)*, e. g. *Agkistrodon piscivorus* (ZZSiD 233).

Remarks. — Vide infra (p. 52).

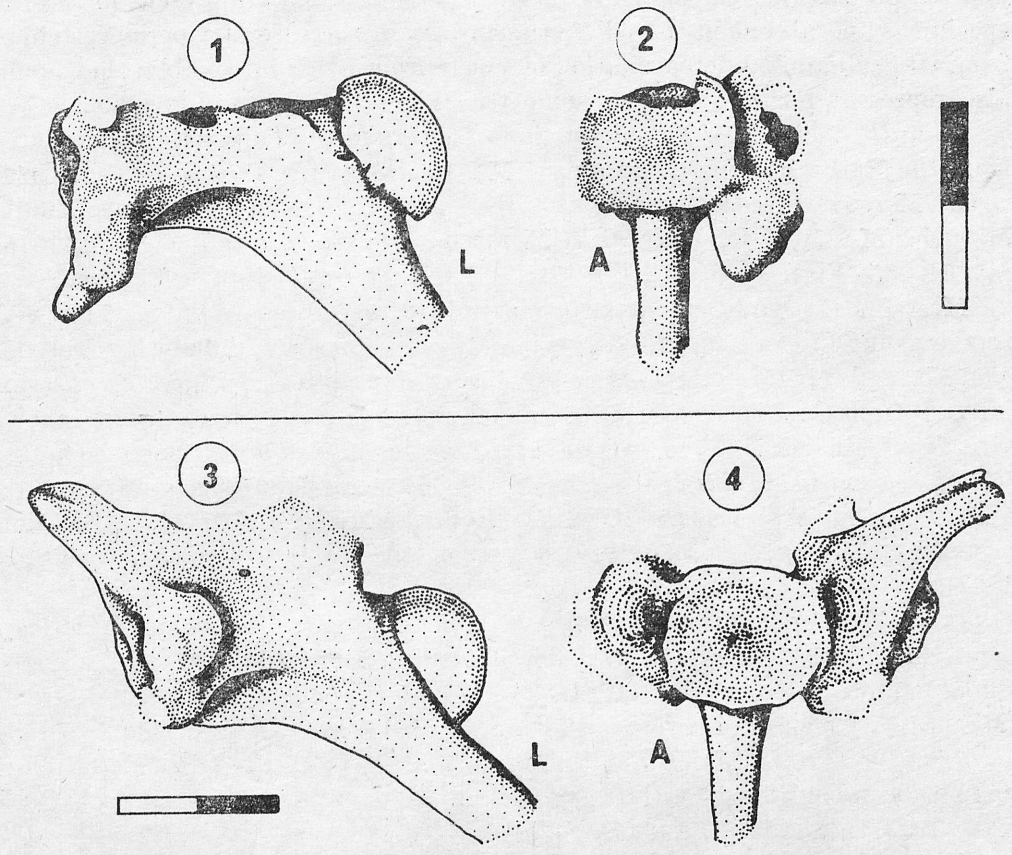


Fig. 18. 1, 2 — precaudal vertebra of *Viperidae* „A" from OP (ZPUW, OP-86/29) (after SZYNDLAR, 1982). 3, 4 — trunk vertebra of *Viperidae* „B" from PO (ZZSiD, PO-2). A — anterior, L — lateral views. Each scale equals 2 mm

Viperidae indet. (form "B")
(Fig. 18: 3, 4)

Material. — Two fragmentary trunk vertebrae from PO.

These fragments, not described earlier, consist only of centra provided with prezygapophyses and proximal portions of hypapophyses. Hypapophyses are slender in lateral view and presumably were of considerable length in living specimens; postero-ventral inclination of the hypapophyses indicates that the vertebrae belonged to the mid-trunk region of the vertebral column. Subcentral ridges developed only in the anterior portion of the centrum. Paradiapophyses

elongate dorso-ventrally in lateral view; parapophyseal processes missing. Prezygapophyseal articular facet elongate; prezygapophyseal process scarcely seen from above.

The remains from PO resemble those from OP; the only difference is the round depressions surrounding the paracotylar foramina, which are present in the PO specimens and absent in the OP specimens. As in the case of viperid vertebrae from OP, subfamilial determination of vipers from PO is impossible; they could also represent forms related to some true vipers and pit vipers alike.

Remarks (Fig. 57). The oldest find of vipers in the Palearctic region dates from the Early Miocene (Aquitanian; MN 1) of Western Europe (RAGE, 1976, p. 65). Moreover, Neogene remains of vipers have been reported from the Middle Miocene (MN 7) of Beni Mellal in Morocco (*Vipera maghrebiana* RAGE, 1976, pp. 64—65, Figs. 7—8, pl.: Fig. 14) and from several sites in Europe.

Most finds, usually composed exclusively of vertebrae, have been referred to the genus *Vipera*, i. e. the only viperid genus presently inhabiting Europe. Von MEYER's (1845, pp. 41—42, pl. 6: Fig. 2) description of *Vipera kargii* (von MEYER) from the Miocene (MN 7/8) of Oehningen is based on a complete skeleton. Two fossil species have been described on the basis of only venomous fangs: *Vipera sansaniensis* LARTET from the Middle Miocene (MN 6) of Sansan (LARTET, 1851) and *Provipera boettgeri* KINKELIN from the Miocene of Morbach-Biebrich (KINKELIN, 1892, 1896; cf. also criticism of the latter description by COPE, 1892).

Twice, fossil remains of vipers have been reported as belonging to African genus *Bitis*: by PIVETEAU (1927, p. 38, pl. 9: Figs. 5—6) from the Spanish Early Pliocene and by KORMOS (1911, pp. 63 and 187) from the Uppermost Miocene (MN 13) of Polgárdi. However, the former find has been later identified as a colubrid snake (cf. MARX and RABB, 1965, p. 182) and the latter description has not been confirmed by the later students of the Polgárdi ophiofauna (BOLKAY, 1913; SZUNYOGHY, 1932).

Vipera gedulyi BOLKAY, described on the basis of numerous cranial bones from Polgárdi (BOLKAY, 1913, pp. 225—226, text-fig. 4, pl. 12: Figs. 9—12), has been suggested by BOLKAY (1920) to be a direct ancestor of Recent *V. ammodytes* and *V. latasti*, having "a very wide distribution in Central-Europe before the Glacial-Periode" (ibidem: p. 12). As a matter of fact, true specific characters of *V. gedulyi*, the snake closely related to *V. ammodytes*, were given later by SZUNYOGHY (1932, pp. 51—52, Fig. 116), who also referred one of the syntype bones (parietal) of *V. gedulyi* as belonging to *V.* cf. ? *ammodytes*; moreover, this author has reported another living species, *V.* cf *aspis*, from the same locality (cf. further comments in the Chapter Vb, p. 84).

Viperidae have also been reported from the Lower Miocene (MN 3) of Lisboa (ANTUNES and RAGE, 1974, p. 56, Fig. 4), Middle Miocene (Sarmatian) of Buzhora in Moldavia (CKHIKVADZE and LUNGU, 1973, p. 84) as well as from the Pliocene of Mandriola in Sardinia (PECORINI et al., 1974, p. 313).

The only European fossil viper referred to the subfamily *Crotalinae* is *Laophis*

crotaloides OWEN from the Greek Miocene (OWEN, 1857, pl. 4: Figs. 2—3). According to HOFFSTETTER (1955, p. 659), however, its reference to pit vipers is not demonstrable. At present, snakes of the subfamily *Crotalinae* (*Agkistrodon* *) reach easternmost parts of Europe; adjoining areas of Central Asia are supposed to be a center of origin and dispersion of these reptiles (BRATTSTROM, 1964)

Vb. MIDDLE/UPPER PLIOCENE

Family *Colubridae* OPPEL, 1811
Subfamily *Colubrinae* OPPEL, 1811
Genus *Coluber* LINNAEUS, 1758

Coluber robertmertensi MŁYNARSKI, 1964
(Figs. 19—21, Table VIII)

Material. — From RK I:

Basioccipital	8
Basiparasphenoid	8
Maxilla (R)	3
Pterygoid (R)	1
——— (L)	2
Ectopterygoid (R)	1
——— (L)	2
Quadrate	11
Compound bone (R)	9
——— (L)	9
Dentary	1
Premaxilla	1
Vertebrae	±12 000

Here follows a redescription of the species *Coluber robertmertensi* described by MŁYNARSKI (1964, pp. 331—332, Figs. 9—12) from the Pliocene of RK I on the basis of four cranial bones. Some other skull remains from the same locality identified as *Coluber* cf. *viridiflavus* (ibidem, pp. 332—334, Figs. 13—16), *Coluber* sp. (p. 334) and *Elaphe* cf. *situla* (partim, p. 334, Fig. 18) are considered here as belonging to *Coluber robertmertensi*. Additionally, a description of numerous vertebrae (approximately a hundred plus a single compound bone from RK I were earlier identified as *Elaphe* sp. by MŁYNARSKI, 1961a, pp. 14—15, pl. V: Figs. 1—6) as well as of a number of previously undescribed skull bones is appended below.

Basioccipital (Fig. 19: 3). 8 well preserved bones, all approximately as wide as long. Basioccipital crest strongly developed, composed of three lobes,

* Or *Gloydius* according to the latest classification of pit vipers (HOGE and ROMANO-HOGE, 1981).

the central lobe (basioccipital process) being usually longer than lateral ones. Basioccipital tubercles distinct, long and acute. Median crest absent. Occipito-condylar tubercle rather distinctly separated.

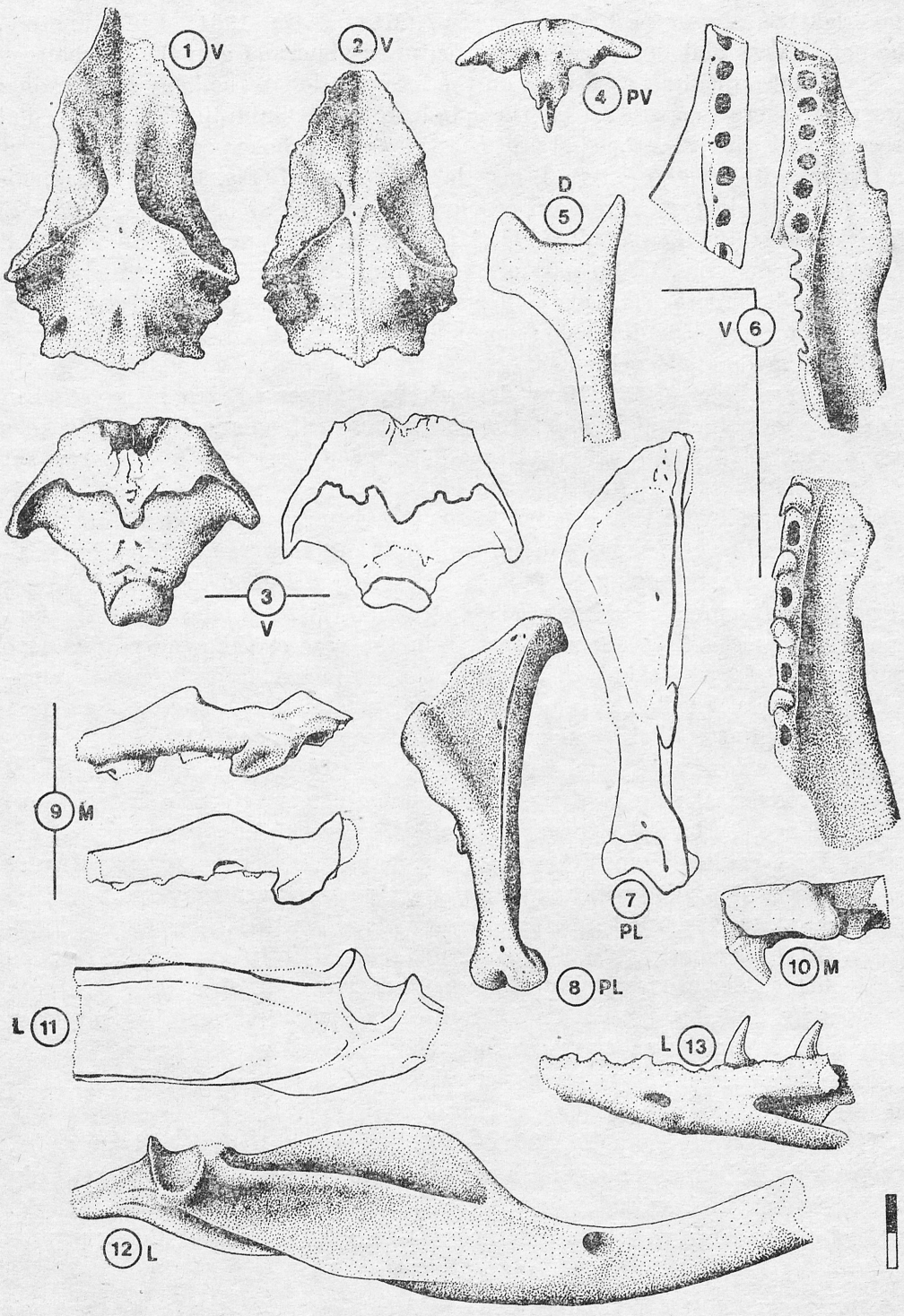
Basiparasphenoid (Fig. 19: 1, 2). 8 bones, previously considered as belonging to four various forms of *Colubridae* (MŁYNARSKI, 1964). One specimen shows pathologic features. Parasphenoid portions of all bones are missing. Basipterygoid process moderately developed. Suborbital flanges distinct, arched ventrally. Basisphenoid crest underdeveloped or absent. Pterygoid crests inclined anteriorly. Foramina of Vidian canal large — posterior orifice (common foramen) provided with a groove reaching lateral margin of the bone; anterior orifice usually covered by pterygoid crest. Additional small foramina (paired) present in postpterygoid area — beyond common foramina or near the mid-line of the bone. On dorsal side, abducens nerve foramina well marked. Foramina for sympathetic nerves, also well seen, are always provided with deep notches that pass outside by basipterygoid process. External orifices of these notches are, partly or entirely, closed dorsally by bony appendices. The biggest bone is a paratype of the species.

Maxilla. Only three maxillary fragments can be referred to *Coluber robertmertensi*. Two posterior parts of right maxillae (Fig. 19: 9) have 6 tooth sockets each. Ectopterygoid process elongate, its distal portion curved ventrally and anteriorly. Dorsal constriction for maxillary ramus of the ectopterygoid present just before ectopterygoid process, forming deep depression. Another maxillary fragment is from the anterior portion of a right bone (Fig. 19: 10) and has preserved prefrontal process. Its anterior margin is square with the bone and its postero-median margin forms a spur projected posteriorly.

Pterygoid (Fig. 19: 6). Only small fragments of several pterygoids are present. Pterygoid flange provided with well developed, spur-like, anteriorly directed ectopterygoid process. A distinct ridge (pterygoid crest) present on the dorsal side of the bone; it extends anteriorly beyond the ectopterygoid process.

Ectopterygoid (Fig. 19: 5). Several anterior fragments are provided with well defined and separated maxillary rami. External ramus broad, internal ramus very narrow and acute. One amongst the bones is the paratype of the species (MŁYNARSKI, 1964).

Fig. 19. Cranial bones of *Coluber robertmertensi* from RK I. 1 — paratype basiparasphenoid (ZZSiD, RK I—4; ex-number used by MŁYNARSKI, 1964: Pt. R. f. 2/63), 2 — basiparasphenoid (ZZSiD, RK I—13; ex no. R. f. 9/63), 3 — basioccipitals (ZZSiD, RK I—5, 6; ex no. R. f. 9/63), 4 — premaxilla (ZZSiD, RK I—58; ex no. R. f. 11/63), 5 — paratype left ectopterygoid (ZZSiD, RK I—3; ex no. Pt. f. 1/63), 6 — pterygoids (ZZSiD, RK I—25, 26, 27), 7 — syntype right quadrate (ZZSiD, RK I—1, ex no. T. R. f. 1/63), 8 — right quadrate (ZZSiD, RK I—30), 9 — right maxillae, posterior fragments (ZZSiD, RK I—22, 23), 10 — right maxilla, anterior fragment (ZZSiD, RK I—24), 11 — syntype left compound bone (ZZSiD, RK I—40), 13 — left dentary (ZZSiD, RK I—57). D — dorsal, L — lateral, M — medial, PL — postero-lateral, PV — postero-ventral, V — ventral views. Scale equals 2 mm


1 V
2 V
4 PV
D
5
V 6
3
V
9 M
7
PL
8 PL
10 M
L 11
L 13
12 L

Quadrate (Fig. 19: 8). Well preserved quadrates are numerous. The largest one (right) is a syntype * of the species (MŁYNARSKI, 1964). Unfortunately, the bone shows undoubted pathologic features: abnormal growths can be seen of the trochlea quadrati as well as on the internal side of the body of the bone; moreover, there is a growth on the quadrate crest "imitating" the stapedial process, while the true stapedial process, which would be expected to be present on the opposite (postero-internal) margin, is broken off (Fig. 19: 7). The remaining quadrates in part have been previously described as belonging to *Coluber* cf. *viridiflavus* and *Elaphe* cf. *situla* (MŁYNARSKI, 1964) or originate from still undescribed material. Distal part of the trunk thin, proximal (dorsal) portion rather broad. On either end of the dorsal margin distinct spurs projected internally are present. Quadrate crest prominent, sharp-edged. Stapedial process usually of moderate development.

Dentary (Fig. 19: 13). Many dentaries are preserved, but all are broken posteriorly and almost all also anteriorly. The bone is long and narrow. Meckel's groove open widely into compound notch, anteriorly reduced to a narrow slit or completely closed. Dental foramen elongate.

Compound bone (Fig. 19: 12). Amongst numerous compound bones several have not been previously described, while others were identified by MŁYNARSKI (1964) as belonging to *Coluber* cf. *viridiflavus* and *Elaphe* cf. *situla*; the posterior fragment of a bone much bigger than the remaining ones is the syntype of the species (Fig. 19: 11). Just as in the case of the syntype quadrate (vide supra), also the choice of the second syntype bone has been rather unlucky because of lacking its anterior portion, medial flange and retroarticular process as well as of high erosion of the preserved fragment. Remaining compound bones are nearly complete. Medial flange distinctly higher than lateral flange; anterodorsal margin of the medial flange usually steep in lateral view. Lateral flange distinctly concave. Supraangular crest sharply developed, extending from cavitas sigmoidea toward supraangular foramen. Retroarticular process long and imperceptibly tapering, slightly curved ventrally and medially.

Premaxilla (Fig. 19: 4). A single premaxilla, described incorrectly by MŁYNARSKI (1964) as belonging to *Elaphe* cf. *situla*, is perfectly preserved. The bone is triangular in dorsal view, with a flattened anterior tip. Lateral arms elongate and strongly tapering, provided with well defined processes on their posterior margins. Paired opening for premaxillary channels well marked on both dorsal and lateral walls. Palatine processes very short. Nasal process slender and flattened laterally, as long as the lateral arms.

Mid-trunk vertebrae (Fig. 20: 6—10). In large specimens centrum short, triangular from below, possessing a well defined cuneate-shape and strongly flattened haemal keel, extending just behind the cotyle to just before the condyle. The keel of the large vertebrae is often ⊥ — shaped in section. Centrum pro-

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* MŁYNARSKI (1964) designated erroneously two holotypes of *Coluber robertmertensi*; these bones, quadrate and compound, are considered here as syntypes.

vided with two not very deep grooves, one on either side of the haemal keel. Neural arch moderately long, with small but (in larger vertebrae) well defined epizygapophyseal spines, the latter structure sometimes missing in small specimens. Neural canal round to subtriangular when seen from the front. Neural spine approximately as high as long or somewhat lower, overhangs posteriorly and mostly also anteriorly. In larger specimens anterior portion of the dorsal edge of neural spine is often thickened; antero-dorsal margin of the spine often rounded. Zygosphene concave from above, in smaller specimens, however, sometimes straight or slightly convex. Postzygapophyseal articular facets mostly rectangular in shape, much wider than long. Prezygapophyseal articular facets oval, in some large specimens rectangular, always distinctly elongate laterally. Prezygapophyseal processes always well developed, acute or acuminate in shape, long and directed laterally in dorsal and anterior views. Because of far lateral projection of postzygapophyses, the narrowing between pre- and postzygapophyses is well marked. Interzygapophyseal ridges prominent, but not overly developed, parallel to the axis of the centrum. Subcentral ridges present, but not strongly developed, extending from the diapophyses toward the condyle, but not reaching it. Paradiapophyses not distinctly divided into two articular facets; in lateral view, parapophyses minimally longer than diapophyses or of the same length, the former projecting below the centrum and somewhat anteriorly. Cotyle rounded, fossae on its either side provided with tiny foramina. Condyle slightly directed upwards.

Measurements: see Table VIII. Dimensions of trunk vertebrae reach CL = 6.77 and NAW = 5.76. CL/NAW ratio for 60 greatest vertebrae is 1.17 on average (1.07—1.29±0.05). Table VIII contains measurements of 36 vertebrae selected from this amount in order to obtain a sample of mean $\bar{x} = 1.15$. Pathologic vertebrae have larger dimensions (vide infra). Total length of biggest snakes must have been at least 220 cm and most likely reached 300 cm *.

Intracolumnar variation. Three axes are present in the material from RK I. One of them, preserved in a perfect state, is provided with odontoid process and intercentra. Neural arch strongly vaulted, widening posteriorly in dorsal view. Neural spine low and long, slightly lowering anteriorly, strongly overhangs anteriorly and posteriorly. Both intercentra robust, the posterior one (3rd intercentrum) curved posteriorly. Transverse processes are broken off.

Cervical vertebrae (Fig. 20: 1—5) are numerous. Centrum shorter than that of trunk vertebrae and neural arch more vaulted. Neural spine also higher, with thickened (occasionally flattened) dorsal portion in some larger specimens. Zygosphene mostly concave. Both portions of paradiapophyses well developed. Diapophyses strongly projected aside; parapophyses provided with processes projecting anteriorly — in few vertebrae also posterior extension of the parapophyses is present. Hypapophysis strongly built, with rounded tip, often wider than the base in lateral view.

* Estimated from the ratio $\frac{\text{greatest vertebra length}}{\text{body total length}}$ derived from Recent colubrine snakes.

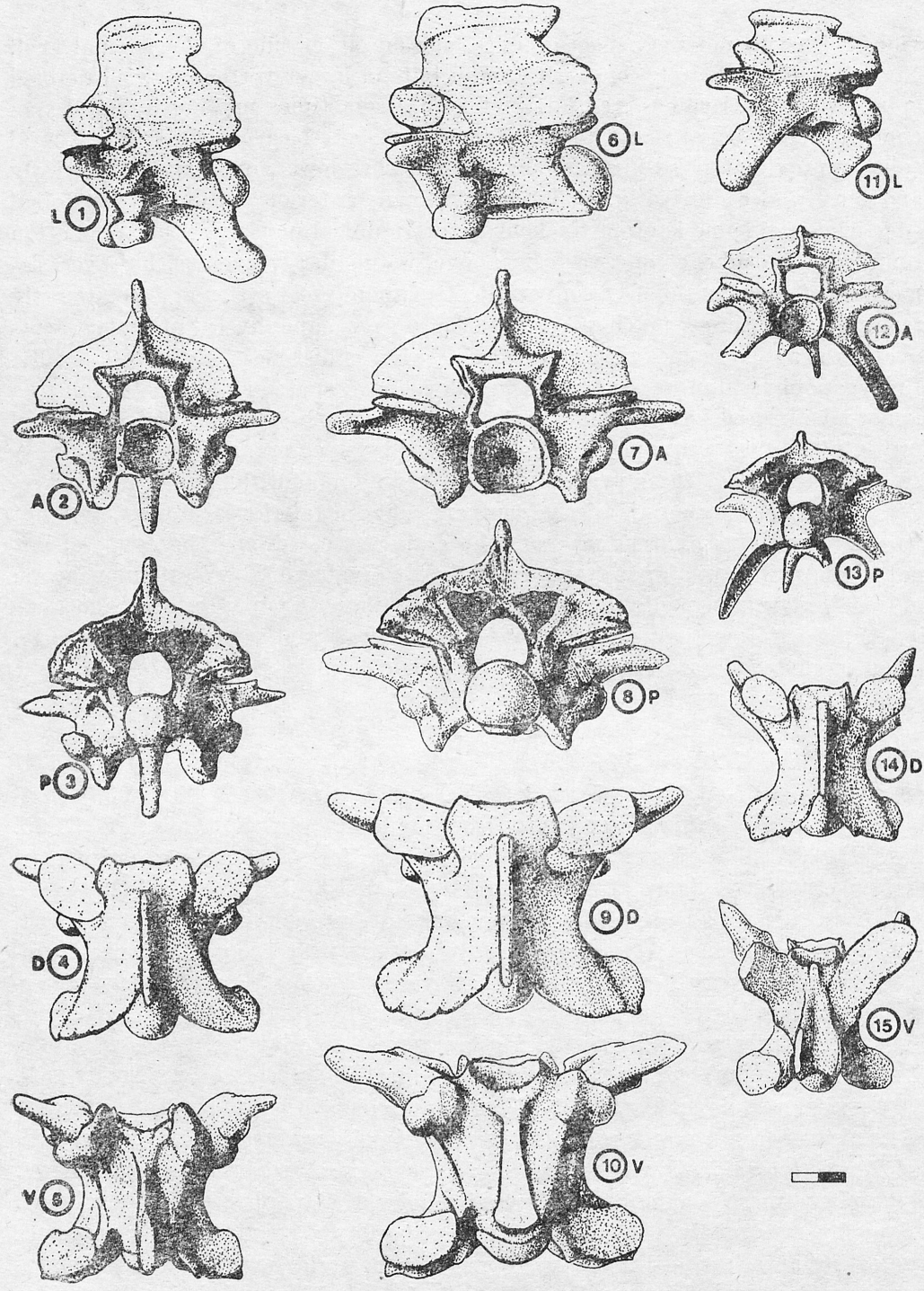


Fig. 20. Vertebrae of *Coluber robertmertensi* from RK I. 1, 2, 3, 4, 5 — cervical vertebra (ZZSiD, RK I—62), 6, 7, 8, 9, 10 — trunk vertebra (ZZSiD, RK I—173), 11, 12, 13, 14, 15 — caudal vertebra (ZZSiD, RK I—2239). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

Table VIII

Measurements and ratios of trunk vertebrae of *Coluber robertmertensi* from RK I (N = 36)

	OR	$\bar{X}\pm SD$
PR-PO	6.94–8.57	
CL	5.49–6.77	
PO-PO	8.40–10.13	
NAW	4.72–5.76	
ZW	3.87–4.85	
CTH	2.49–2.93	
CTW	2.56–3.00	
PR-PR	8.52–10.39	
CL/NAW	1.11–1.20	1.15±0.03
PO-PO/NAW	1.68–1.87	1.77±0.05
CTW/CTH	0.95–1.13	1.04±0.05
ZW/NAW	0.74–0.89	0.82±0.04
PR-PR/PR-PO	1.19–1.40	1.25±0.05
CL/ZW	1.30–1.57	1.41±0.06
PR-PR/NAW	1.72–1.89	1.82±0.05

Mid-trunk vertebrae are most numerous. More than 2 000 of them have been examined, but their total number in the material from RK I is several times higher.

Posterior trunk vertebrae do not differ much from those of the mind-trunk. As in other snakes their neural arch is less vaulted, neural spine very low and parapophyses strongly developed. Haemal keel of variable development, in some vertebrae because of strong flattening the keel has a ⊥ shape when viewed anteriorly.

A single cloacal vertebra is strongly shortened. Its zygosphene is slightly crenate in dorsal view. Posterior notch in neural arch is very deep. Neural spine, occupying less than one-half of the neural arch length, lowers slightly posteriorly. Lymphapophyses broad at the base; their distal portions are broken off. Haemapophyses are missing.

Caudal vertebrae (Fig. 20: 11—15) are also numerous. Anterior caudal vertebrae are relatively short, posterior ones elongate, with centra at least twice longer than wide. Neural spine low and long, often with thickened dorsal edge. In vertebrae of posterior caudal region neural spine extends far forward beyond the zygosphenal base. Zygosphenes of caudal vertebrae are mostly slightly crenate in dorsal view. Pleurapophyses are strongly developed. Their distal portions are very broad and sometimes bear a distinct spur near the base. Well defined haemapophyses project ventro-laterally.

Pathologic vertebrae. Among trunk vertebrae of *Coluber robertmertensi* from RK I there are about thirty strongly deformed large bones (Fig. 21: 1, 2). These vertebrae distinctly exceed in size all others; dimensions of the biggest vertebra are CL — 7.28 and NAW — 6.98. Most likely the vertebrae originate

from a single specimen of an enormous snake, perhaps the same one having pathologic quadrate and compound bone (syntypes, vide supra). There is no obvious explanation of reasons leading to such changes in a snake skeleton, but there is no doubt that the deformations of the bones appeared during the lifetime of the animal. Similar deformations occur, though not to such a degree, also in skeletons of living snakes; it concerns always only large animals.

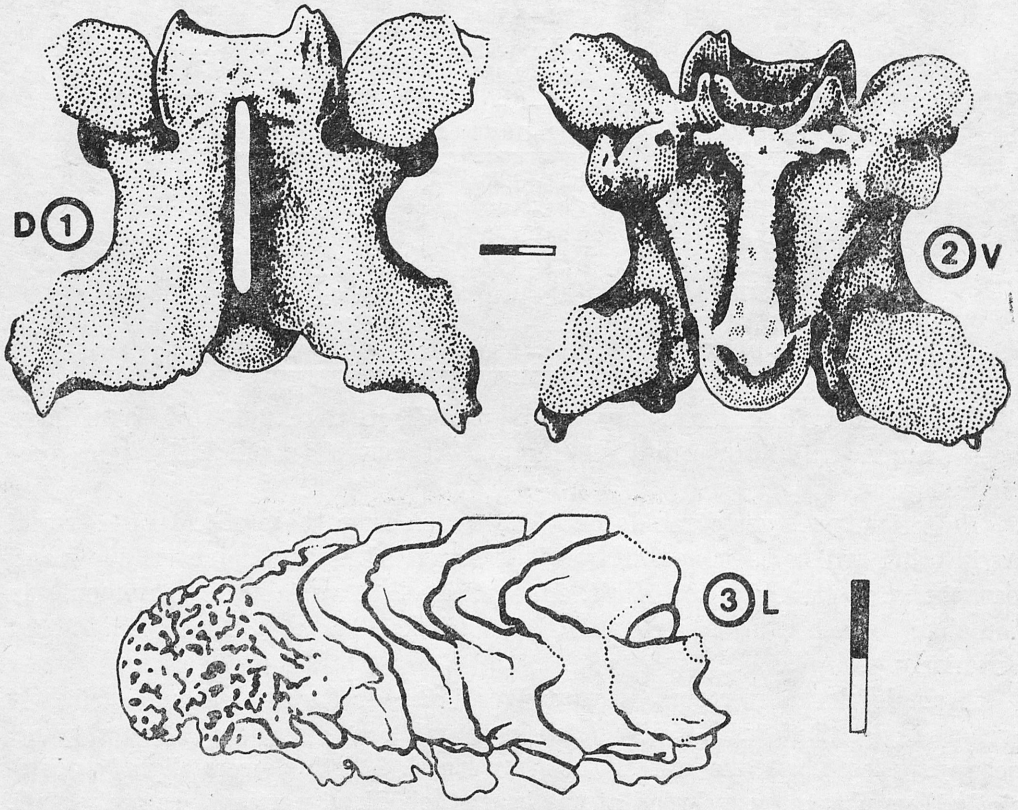


Fig. 21. Vertebrae of *Coluber robertmertensi* from RK I. 1, 2 — pathologic trunk vertebra (ZZSiD, RK I—2277), 3 — fusion of terminal caudal vertebrae (ZZSiD, RK I—2272, ex no. R. f. 6/63). D — dorsal, L — lateral, V— ventral views. Each scale equals 2 mm

The material from RK I contains also a number of fusions of snake vertebrae. Three of them have been described as terminal caudal vertebrae ("Letzte Kaudalwirbel") of erycine snakes by MŁYNARSKI (1964, p. 330, Figs. 19—21). In a later paper MŁYNARSKI (1977, p. 31) denied his previous standpoint and recognized the remains as pathologic elements belonging to a member of the family *Colubridae*. I agree with MŁYNARSKI's (supra cit.) latter standpoint as regards the first of the above-mentioned bony remains (*Eryx* cf. *jaculus* according to MŁYNARSKI, 1964, Fig. 19); presumably it belonged to *Coluber robertmertensi* (here Fig. 21: 3). However, I disagree with his opinion on the pathologic

nature of these structures; it seems that such a phenomenon occurs sometimes among snakes, other than erycines, with normally developed skeleton (e. g. *Elaphe quatuorlineata*, ZZSiD 248, or *Macroprotodon cucullatus*, MNCN 82561). Two remaining specimens (*Eryx* sp. and ? *Eryx* sp. according to MŁYNARSKI, 1964, Figs. 20 and 21) are lost from the ZZSiD collection, but, judging on the basis of MŁYNARSKI's illustrations, surely they did not belong to erycine snakes, the latter fragment probably representing not caudal but rather the trunk vertebral region.

Affinities of *Coluber robertmertensi*. As already pointed out by MŁYNARSKI (1964, p. 332) *Coluber robertmertensi* was a form closely related to *C. viridiflavus*, occurring at present in Western Europe. However, MŁYNARSKI's judgement was based on only four bones, in part of pathologic nature. Here follows a full list of affinities and differences between both snakes based on all above described bones of *C. robertmertensi*. Since I have at my disposal only a single specimen of *Coluber viridiflavus* originating from Yugoslavia (ZZSiD 278), I refer below to description of some features of ten *C. viridiflavus* skeletons kindly provided by Dr. J.—C. RAGE (pers. comm., 1982); for cranial bones SZUNYOGHY's (1932) paper has also been useful. However, one ought to say that some differences between the bones of ZZSiD 278 and those described by SZUNYOGHY on the one hand and French specimens on the other hand have been revealed. The differences may be caused by geographic variation (the former forms belong to the subspecies *carbonarius*, the latter ones probably to nominal subspecies *viridiflavus*); unfortunately, as with other European snakes, the subspecific variability of the *C. viridiflavus* skeleton is unknown.

Basioccipital: similar in both species; lateral processes generally more elongate in *C. viridiflavus*.

Basiparasphenoid: not clearly different; in ZZSiD 278 the bone lacks notches for sympathetic nerves.

Maxilla: prefrontal process of the maxilla of ZZSiD 278 differs from that of *C. robertmertensi* in having a posteriorly curved anterior border and rectangular posterior border, without any spur-like process.

Pterygoid and dentary: fossils are too fragmentary to be compared.

Ectopterygoid: ectopterygoids of *C. robertmertensi* resembles the bones of ZZSiD 278 and that figured by SZUNYOGHY (1932, Fig. 100), but differs from French specimens, which have maxillary rami meeting each other at a more obtuse angle.

Quadrate: more elongated in *C. viridiflavus* and with narrower dorsal end than in *C. robertmertensi*.

Compound bone: *C. viridiflavus* (French specimens and ZZSiD 278) differs from *C. robertmertensi* in absence of distinctly developed supraangular crest, concavity of lateral flange and steep antero-dorsal margin of medial flange. According to SZUNYOGHY (1932, p. 48, Fig. 115), however, all these features are well marked in compounds of *Coluber viridiflavus*.

Premaxilla: more pointed anteriorly in *C. viridiflavus*.

Vertebrae: the most important resemblance between trunk vertebrae of both species is the distinctly flattened haemal keel; degree of flattening seems to be higher in *C. robertmertensi*. Differences between trunk vertebrae of both species, aside from the considerably greater dimensions of *C. robertmertensi*, are rather indistinct. Vertebrae of *C. viridiflavus* have more elongate centra, their prezygapophyseal processes are longer, their neural arch is more vaulted, and they lack thickening of the antero-dorsal margin of the neural spine. Nevertheless, shortness of centra observed in largest vertebrae of *C. robertmertensi* is undoubtedly an effect of their size; centra of smaller specimens are always relatively longer. It appears that the main difference between both forms is inherent in their zygosphene. That of *C. viridiflavus* is wider and never concave in dorsal view; it is always straight or with a slight median tubercle. Statistical comparison between vertebrae of both snakes have been, unfortunately, not possible because of lack of an adequately large specimen of *C. viridiflavus*. As for cervical vertebrae, it seems that the robust, distally widened (in lateral view) hypapophysis is a specific feature of *C. robertmertensi*; *C. viridiflavus* has a slender hypapophysis. Caudal vertebrae of both snakes are practically indistinguishable.

Finally, *C. robertmertensi* was a considerably larger animal than *C. viridiflavus*. Maximal total body length of *C. viridiflavus*, according to various sources, reaches 200 cm, although occurrence of such great snakes is rare.

Resemblance between both snakes is close, so a precise conclusion about the differences between *C. viridiflavus* and *C. robertmertensi* cannot be reached. In this connection I classify *C. robertmertensi* as a form closely related to *C. viridiflavus* or even ancestral to it.

Remarks: vide infra (p. 65).

Coluber cf. *robertmertensi* Młynarski, 1964
(Fig. 22)

Material. — 6 cervical vertebrae, 51 trunk vertebrae and 3 caudal vertebrae from RK II.

The material from RK II, referred earlier by Młynarski (1977, p. 17) to *Coluber* sp., differs to a certain degree from *Coluber robertmertensi* from RK I.

Only several trunk vertebrae are preserved in good state. Basic dimensions of the biggest one are: CL = 5.48, NAW = 5.23, CL/NAW = 1.05. Neural spine overhangs posteriorly, not anteriorly; callosity of its dorsal edge does not occur. Epizygapophyseal spine usually present, although hardly seen. Prezygapophyseal processes long, acuminate in shape. Postzygapophyseal articular facets strongly elongate laterally. Paradiapophyses well developed and divided; parapophyses projected slightly anteriorly. In most vertebrae zygosphene is concave in dorsal view, sometimes with lateral lobes and straight anterior margin, rarely crenate. Haemal keel usually flattened.

Only one cervical vertebra has been suitable for examination. Its neural

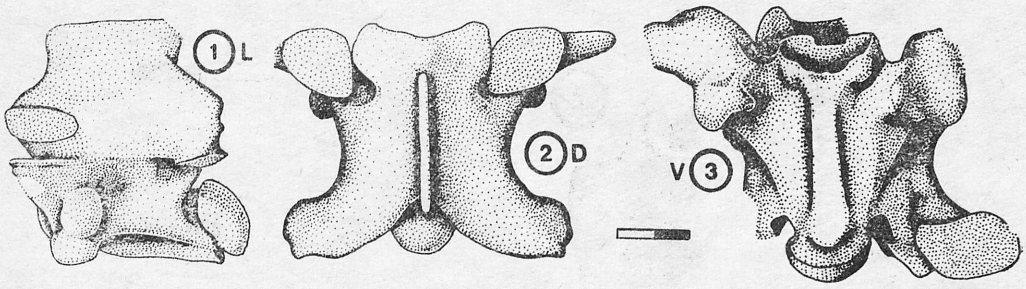


Fig. 22. Vertebrae of *Coluber* cf. *robertmertensi* from RK II. 1, 2 — trunk vertebra (ZZSiD, RK II—7), 3 — trunk vertebra (ZZSiD, RK II—8). D — dorsal, L — lateral, V — ventral views. Scale equals 2 mm

spine does not overhang anteriorly; antero-dorsal margin of the neural spine is not rounded. Its dorsal edge is not thickened. Paradiapophyses developed as in vertebrae from RK I. Hypapophysis distinct, its tip strongly widened in lateral view. Caudal vertebrae strongly damaged.

Affinities. The vertebrae are nearest to those from RK I. The most important differences are absence of callosity of the neural spine and better defined paradiapophyses. Referral of the fossils to *Coluber robertmertensi* is based on presence of concave zygosphene in most vertebrae and robust hypapophysis of cervical vertebrae.

Remarks: vide infra (p. 65).

Coluber cf. *viridiflavus* (LACÉPÉDE, 1789)
(Figs. 23 and 24)

Material. — Two fragments of maxillae, a fragment of a left pterygoid, a left quadrate, a fragment of a right palatine, 5 fragments of dentaries, 20 cervical vertebrae, 522 trunk vertebrae, 27 cloacal and caudal vertebrae from W I.

The colubrine material from W I has been described by MŁYNARSKI (1961a, pp. 10—12, pl. I, II: Figs. 1—5, IV: Figs. 2—5; 1962, pp. 142—144) as *Coluber* cf. *viridiflavus* or *Colubrinae* indet. Since cranial bones and vertebrae from this locality resemble more those of *Coluber viridiflavus* than of *C. robertmertensi*, I concur here with MŁYNARSKI's (1961a) determination. It should be mentioned, however, that the following observations, based in fact on scarce material, may be modified by more complete remains.

Cranial bones. Tiny anterior fragment of a right palatine (Fig. 23: 3) has well preserved, posteriorly projecting, maxillary process and vomerine process. Strongly posteriorly inclined anterior border of the vomerine process is a characteristic feature of *Coluber viridiflavus*. Quadrate (Fig. 23: 1), being slender and with moderately widened dorsal part, does not differ from these of living *C. viridiflavus*. The remaining cranial bones are too fragmentary to be correctly compared, but preserved fragments differ in nothing from bones

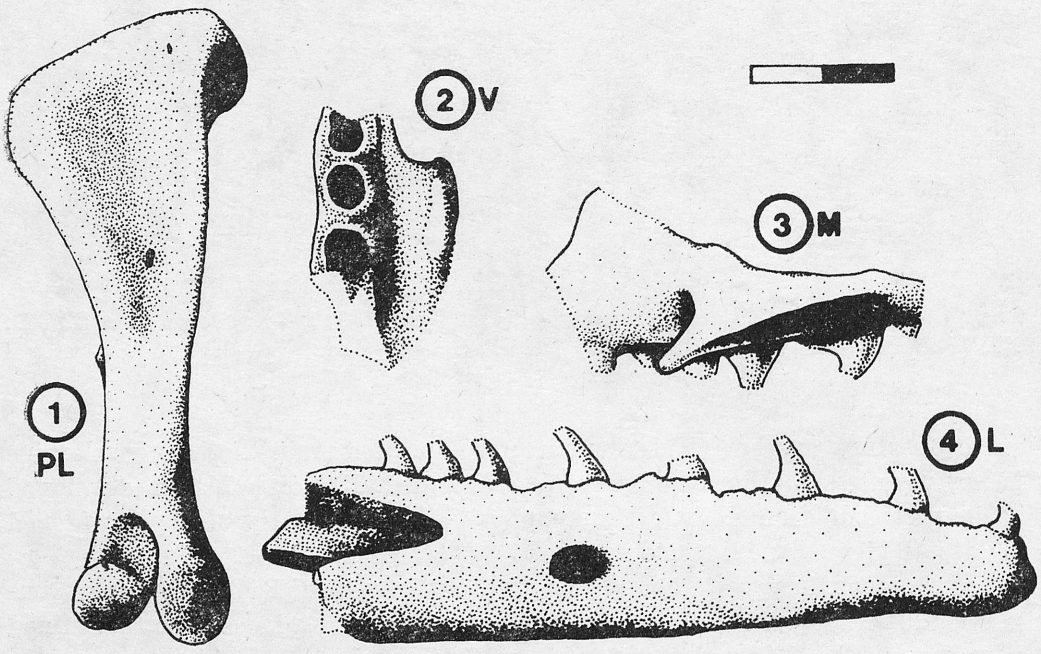


Fig. 23. Cranial bones of *Coluber* cf. *viridiflavus* from W I. 1 — right quadrate (ZZSiD, W I—1), 2 — left pterygoid, anterior fragment (ZZSiD, W I—2), 3 — left palatine (ZZSiD, W I—4), 4 — right dentary (ZZSiD, W I—5). L — lateral, M — medial, PL — postero-lateral, V — ventral views. Scale equals 2 mm

of *C. viridiflavus*. Three dentary fragments from W I, identified as belonging to vipers by Młynarski (1961a, pl. II: Figs. 6—10), have not been found in the ZZSiD collection, but they represent not *Viperidae* but *Colubridae*, presumably the form described above.

Vertebrae (Fig. 24). Only a few vertebrae are well preserved. Basic dimensions of the biggest (fragmentary) vertebra are CL = 5.80 and NAW = 5.50, CL/NAW = 1.05; in remaining larger vertebrae CL/NAW 1.20. Neural spine overhangs posteriorly, rarely anteriorly, no thickness is present on its dorsal edge. Epizygapophyseal spine scarcely seen. Prezygapophyseal processes moderately long, acuminate. Postzygapophyseal articular facets strongly elongate laterally. Paradiapophyses well divided into two separate articular facets. Zygosphene usually straight in dorsal view, sometimes with small median tubercle or slightly convex, but rarely concave. Haemal keel usually flattened, though to a slighter degree than in vertebrae from RK I and RK II. Only one cervical vertebrae has well preserved hypapophysis; it is long and slender. A number of cloacal and caudal vertebrae are preserved rather poorly. Lympapophyses and pleurapophyses relatively broad (their distal portions are broken off). In some cases a spur-like extension is present on the posterior margin of the pleurapophyses. The vertebrae from W I essentially do not differ from those of Recent *Coluber viridiflavus*; a lack of concavity in zygosphene and shape of

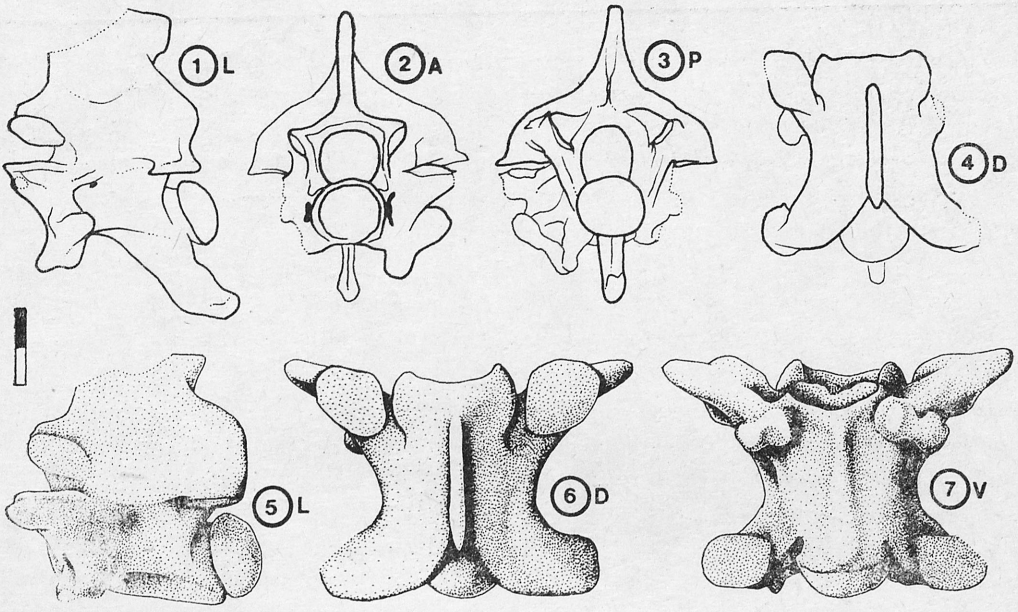
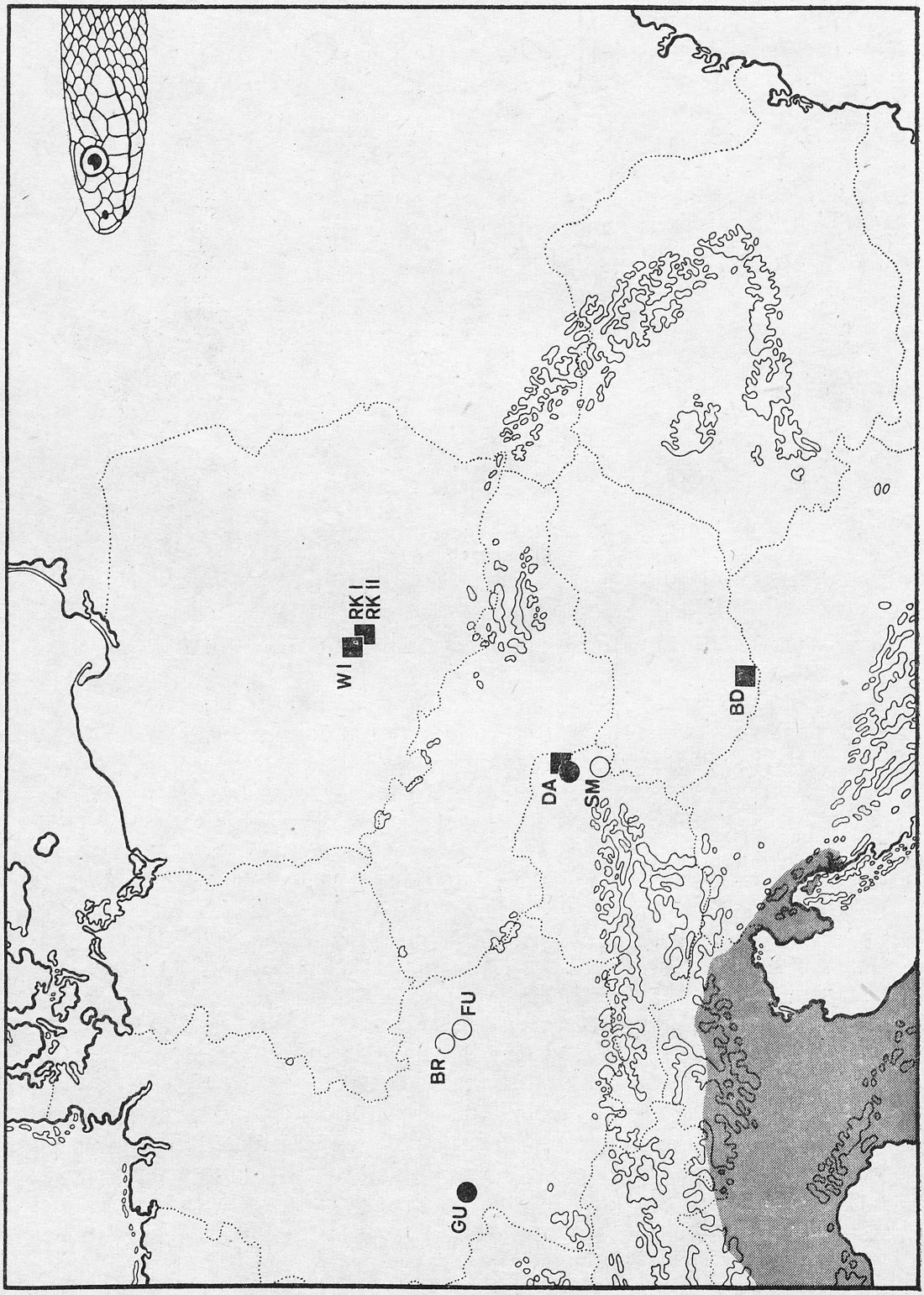


Fig. 24. Vertebrae of *Coluber* cf. *viridiflavus* from W I. 1, 2, 3, 4 — cervical vertebra (ZZSiD, W I—23), 5, 6, 7 — trunk vertebra (ZZSiD, W I—28). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

hypapophysis differentiates them from vertebrae of *C. robertmertensi* from RK I and RK II.

Remarks (Fig. 25). Fossil finds of *Coluber viridiflavus* have been reported from numerous Plio- and Pleistocene localities of Europe, especially from its central part. Pliocene records (unfortunately neither described nor figured) originate from two localities: Deutsch Altenburg-20, Austria (MAIS and RABEDER, 1977, p. 85), and Beremend, Hungary (SZUNYOGHY, 1932, p. 9). These fossils, therefore, are younger than *Coluber* cf. *viridiflavus* from W I (MN 15) and of similar age as its close relative, *C. robertmertensi*, from RK I and RK II (MN 16).

Pleistocene remains of *C. viridiflavus* are known from the following sites: Gundersheim, Germany (HELLER, 1936, p. 143), Breitenberghöhle, Germany (BRUNNER, 1958, p. 512, Fig. 11: 4), Deutsch Altenburg-2, 4, Austria (RABEDER, 1974, p. 148), and St. Margarethen, Austria (RABEDER, 1977a, pp. 86—91, pl. 1: Figs. 1, 5, 7, 8, 10, pl. 2: Figs. 15, 16, 20, 22; 1977b, p. 117). An extinct colubrid species, *Coluber freybergi* BRUNNER (1954), described from the Eemian (Riss/Würm) of Fuchsloch, Germany, has been diagnosed as closely related to *C. viridiflavus*. However, cursory description based on only two bones, a palatine and a maxilla, together with inadequate figures (BRUNNER, supra cit., p. 108, Fig. 18: 1, 2) are not convincing; in addition, occurrence of an extinct ophidian species in the Upper Pleistocene is not very probable. The remains presumably belonged to a living species, perhaps *C. viridiflavus*.


WI
RK I
RK II
BD
DA
SM
BR
FU
GU

Present distribution of *C. viridiflavus* is restricted to France and Italy, including adjacent territories. Fossil records of this snake, originating from sites lying outside its present range, demonstrate that in the past *C. viridiflavus* covered an immense area of Europe.

Fossil remains of this species have also been reported from the Pleistocene of continental Italy (Del Campana, 1911, pl. 24), Sicily (Kotsakis, 1977, pp. 219—221, Fig. 3), and Sardinia (Kotsakis, 1980, p. 152); however, these records, originating from territories inhabiting by *C. viridiflavus* to-day, are of less importance for paleozoogeographical considerations (vide infra: Chapters VI and VII).

Genus *Elaphe* Fitzinger in Wagler, 1833

Elaphe paralongissima sp. n.
(Fig. 26, Tables IX and X)

Holotype. — A mid-trunk vertebra, ZPPAN, no. R III/11

Referred material. — Over 350 vertebrae, ZPPAN.

Type locality. — Węże II (W II) at Zelce Hill near Działoszyn (Northern Kraków—Wieluń Upland in central Southern Poland).

Type horizon. — Upper Pliocene, MN biozone presumably 16.

Name derivation. — Latin *para* and *longissima* — closely related to a living snake species, *Elaphe longissima*.

Diagnosis. — A typical member of *Colubrinae* with strongly built trunk vertebrae resembling most those of Recent *Elaphe longissima*. The vertebrae are characterized by combination of the following features: (1) prominent haemal keel, cuneate-shaped and strongly flattened, provided with paired tubercles below the lower lip of the cotyle, (2) strongly developed, interzygapophyseal ridges, (3) well developed, flattened or obtuse prezygapophyseal process, (4) zygosphene with anterior margin concave or straight, (5) parapophyses twice longer than diapophyses in lateral view.

Description of the holotype (Fig. 26: 1—5)

A strongly built mid-trunk vertebra, somewhat fragmentary. The posterodorsal portion of the neural spine is broken off and the right prezygapophyseal process is missing. Distal portions of postzygapophyseal articular facets, left diapophysis and left lateral lobe of the zygosphene are slightly damaged. Cen-

Fig. 25. Past and present Central European distribution of *Coluber viridiflavus* and its relatives. Abbreviations of Polish localities: see Fig. 1. Abbreviations of foreign localities: BD — Beremend, BR — Breitenberghöhle, DA — Deutsch Altenburg-2, 4 and 20, FU — Fuchsloch, GU — Gundersheim, SM — St. Margarethen. The area of Recent distribution of *Coluber viridiflavus* is dotted (after Bruno and Maugeri, 1977). For further comments see p. 65.

trum short, plane, triangular from below. Cuneate-shaped haemal keel prominent, strongly flattened, extending from the lip of the cotyle posteriorly onto the neck of the condyle, where it ends in a rather obtuse point. Anteriorly, below the lip of the cotyle, the keel is accompanied by a pair of small tubercles situated near the parapophyses. Subcentral ridges well developed, extending from the posterior margin of parapophyses to the base of the cotyle. Subcentral grooves weakly marked, subcentral foramina not seen. Neural arch short, vaulted, with slightly upswept postzygapophyseal portion. Laminae of the neural arch extend far laterally between pre- and postzygapophyses. Neural canal subtriangular from the front, much narrower than large round cotyle. In anterior view, neural canal produces paired sinuses that lead out of its latero-ventral corners. Neural spine as high as long, thicker on the upper edge, slightly overhanging anteriorly, postero-dorsal portion of the neural spine is missing. Zygosphene strongly built, its anterior edge is flat in anterior view. In dorsal view, zygosphene is slightly concave, provided with tiny lateral lobes (left lobe damaged). Zygantrum wide and moderately high. Both pre- and postzygapophyseal articular facets large, elongate, rectangular-shaped; distal portions of right prezygapophyses and both postzygapophyses damaged. In anterior view, prezygapophyses slightly tilted upward. Left prezygapophyseal process prominent but not too long, flattened and obtuse; right process missing. Interzygapophyseal ridges sharp and well developed, parallel to the axis of the centrum. Lateral foramina large, covered dorsally by extensions of interzygapophyseal ridges. Paradiapophyses rather small; in lateral view, parapophyses, rectangular-shaped, twice longer than diapophyses. Parapophyses shifted anterior to diapophyses. Paracotylar foramina small. Condyle rounded, slightly oblique, without a distinct neck.

Measurements and ratios of the holotype are given in the Table IX.

Table IX

Measurements and ratios of holotype trunk vertebra of *Elaphe paralongissima* sp. n. from W II (ZPPAN, RIII/11)

PR-PO (L)	7.39	CL/NAW	1.13
CL	5.89	PO-PO/NAW	1.54
PO-PO	8.01	CTW/CTH	1.05
NAW	5.20	ZW/NAW	0.80
ZW	4.15	PR-PR/PR-PO	1.19
CTH	3.31	CL/ZW	1.42
CTW	2.96	PR-PR/NAW	1.70
PR-PR	8.83		

Description of remaining material

Cervical vertebrae are very few amongst the material and all are poorly preserved (Fig. 26: 7, 8). Centrum is shorter and neural arch more vaulted than in trunk vertebrae. Neural spine, present in a single specimen, is not higher

than that of trunk vertebrae; its anterior edge is vertical and postero-dorsal portion is missing. Fragmentary hypapophysis, preserved in another vertebra, consists only of a thick base, directed downwards. Parapophyses slightly longer than diapophyses in lateral view; parapophyseal process small, projected forward. Prezygapophyseal process short, obtuse. Zygosphene distinctly crenate in dorsal view.

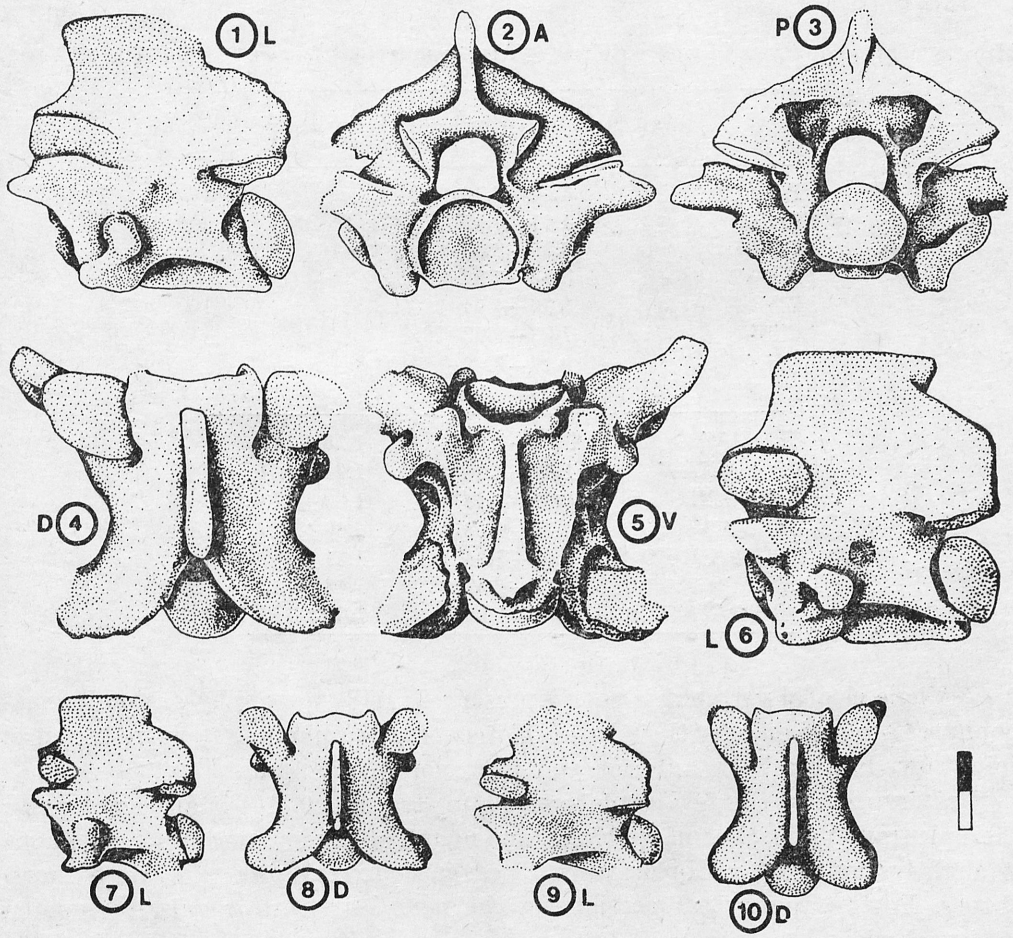


Fig. 26. Vertebrae of *Elaphe paralongissima* sp. n. from W II. 1, 2, 3, 4, 5 — holotype trunk vertebra (ZPPAN, R III/11), 6 — trunk vertebra (ZPPAN, R III/12), 7, 8 — cervical vertebra (ZPPAN, R III/13), 9, 10 — caudal vertebra (ZPPAN, R III/14). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

Trunk vertebrae (Fig. 26: 6), composing a majority of the material, are always strongly built, regardless of their size. All vertebrae are more or less damaged. Haemal keel almost always cuneate-shaped and strongly flattened, rarely lanceolate and not flattened; often the keel is strongly expanded downwards, when seen from the side. Neural spine, if present, is about as high as

long, with vertical anterior edge, and overhanging posteriorly. Zygosphene, in dorsal view, is straight or slightly concave; the former pattern is more frequent among the fossils. Subcentral ridges weakly developed. Prezygapophyseal processes, if preserved, are moderately long and always flattened and obtuse. Otherwise, trunk vertebrae do not differ from the holotype. Measurements and ratios of a sample, consisting of 27 trunk vertebrae, are given in Table X.

Table X

Measurements and ratios of trunk vertebrae of *Elaphe paralongissima* sp. n. from W II (N = 27)

	OR	$\bar{X} \pm SD$
PR-PO	5.52–7.79	
CL	4.61–6.48	
PO-PO	6.30–8.35	
NAW	3.82–5.85	
ZW	3.13–4.54	
CTH	1.93–3.03	
CTW	2.27–3.09	
PR-PR	6.36–9.66	
CL/NAW	1.08–1.23	1.15±0.04
PO-PO/NAW	1.49–1.94	1.64±0.10
CTW/CTH	0.91–1.18	1.09±0.06
ZW/NAW	0.71–0.88	0.80±0.04
PR-PR/PR-PO	1.09–1.34	1.21±0.06
CL/ZW	1.31–1.57	1.43±0.08
PR-PR/NAW	1.51–1.85	1.68±0.08

A single cloacal vertebra is poorly preserved; its lympapophyses and haemapophyses are broken near their bases. Moreover, zygosphene is damaged. Neural spine low, lacking both anterior and posterior overhangs.

Preservation of the few caudal vertebrae (Fig. 26: 9, 10) is also very poor; their pleurapophyses, haemapophyses, and neural spines are missing. Zygosphene is slightly concave in dorsal view. Prezygapophyseal processes very short, obtuse. Postzygapophyseal portions of the neural arch are regularly rounded in dorsal view.

Taxonomic status of *Elaphe paralongissima* sp. n. The species has vertebrae similar to the living *Elaphe longissima*, most of its diagnostic characters are identically developed in both species, and contrary to other large species of European *Colubrinae*, including *Elaphe* aff. *longissima* described below (Chapter Vc, p. 97). The most important specific character of *E. paralongissima* is strong flattening of its haemal keel, a feature very rarely observed in *E. longissima* (vide infra: Chapter Vc, p. 93). Among large species of European *Colubrinae* a flattened haemal keel is present only in trunk vertebrae of *Coluber viridiflavus* (ZZSiD 278) (including its fossil relative, *C. robertmertensi*, pre-

viously described) and *Elaphe quatuorlineata* (ZZSiD 231, 248, 316). Apart from other features, however, both *Elaphe longissima* and *E. paralongissima* may be easily separated from these snake on the basis of obtuse-shaped and flattened prezygapophyseal processes, the feature unparalleled with other large colubrines from Europe (though found in some extra-European *Elaphe* species, e. g. North American *E. guttata*, ZZSiD 352). Prezygapophyseal processes of *Coluber viridiflavus* and *Elaphe quatuorlineata*, long in the former and extremely short in the latter, are always pointed distally; moreover, the latter species, as the only European snake, has its cervical vertebrae provided with anteriorly directed hypapophyses (cf. also Fig. 6).

A straight zygosphene, most frequent among trunk vertebrae of *Elaphe paralongissima*, is often observed in large specimens of *E. longissima* (vide infra). Zygosphenal form of smaller specimens is unknown, but judging on the basis of vertebrae from the cervical region of *Elaphe paralongissima*, one can suppose that anterior margin of the zygosphene was crenate, since this is characteristic for *E. longissima*. Paradiapophyses of both species show a similar morphological pattern. Paired tubercles below the cotyle rim (usually observed in natricines but not colubrines) appear to be a distinct character of *E. paralongissima*.

Statistical comparison of trunk vertebrae of *Elaphe paralongissima* with those of *E. longissima* and *E.* aff. *longissima* (Table XVI) indicates that differences between both species are unequivocally higher than differences within the latter group. In 5 to 7 cases — *E. paralongissima* vs. *E. longissima* and *E.* aff. *longissima* — significant ($p<.05$) or highly significant differences ($p<.01$) can be observed for at least 3 to 4 compared ratios.

Elaphe paralongissima seems to be a closely related or ancestral form to the living species, *E. longissima*. Nevertheless, although *E. longissima* has been reported from several Upper Miocene and Pliocene sites of Central Europe (for detailed data see Chapter Vc, p. 100), unfortunately, comparison between these fossils and *E. paralongissima* from W II is impossible, as all these records, have been based exclusively on cranial bones.

Subfamily *Natricinae* Bonaparte, 1838
Genus *Natrix* Laurenti, 1768

Natrix longivertebrata sp. n.
(Figs. 27—29, Tables XI and XII)

Only a few cranial bones from among these referred here as a new species were earlier described by Młynarski (1964, p. 334) as belonging to *Elaphe* cf. *situla*. Most of skull bones and all vertebrae originate from unstudied material from RK I.

Holotype. — A mid-trunk vertebra, ZZSiD, np. RK I—10000.

Referred material. — From RK I (ZZSiD, no. RK I—10001—10635):

Basioccipital	2
Basiparasphenoid	11
Maxilla (L)	5
Pterygoid (R)	2
Ectopterygoid (R)	1
Quadrate (R)	1
Compound bone (R)	3
——————— (L)	4
Cervical vertebra	1
Trunk vertebrae	597
Caudal vertebrae	6

Type locality. — Rębielice Królewskie I (RK I) near Kłobuck, Kraków—Wieluń Upland, central Southern Poland.

Type horizon. — Upper Pliocene (MN 16).

Name derivation. — From Latin *longivertebrata* — having long vertebrae, to stress extreme elongation of vertebrae of this snake.

Diagnosis. — A typical natricine snake with its trunk vertebrae resembling those of European members of the genus *Natrix*, in particular *N. natrix*, but distinguished by the following characters: (1) great elongation of vertebral centra: CL/NAW ratio exceeding value 1.90 on average it adult specimens; (2) very low neural spine with prominent anterior overhang and dorsal edge sloping distinctly posteriorly; (3) neural arch depressed dorsoventrally; (4) hypapophysis sigmoid-shaped with very long ventral edge; (5) parapophyseal process strongly developed, projected anteriorly far outside the lower lip of cotyle; (6) extremely strong development of subcentral ridges. Caudal vertebrae are characterized by long and thin pleurapophyses, projected forward. Amongst skull bones, two possess specific features: (1) basioccipital, provided with a bony collar separating basioccipital tubercle from the remaining portion of the bone, besides, with underdeveloped basioccipital process, then unlike other species of the genus *Natrix*; and (2) compound bone similar to that of *Natrix natrix*, but provided with large foramen below posterior end of the lateral flange of mandibular fossa.

Description of the holotype (Fig. 29: 6—10)

A medium-sized natricine vertebra from the middle of the column, preserved in a perfect state, except right parapophyseal process being missing. Centrum is elongate and narrow, provided with a distinct pair of subcentral ridges. Under anterior portion of the centrum subcentral ridges form sharply developed crests continued anteriorly by parapophyseal processes; subcentral ridges diminish posteriorly before reaching the base of the condyle. In lateral view, subcentral ridges are moderately bowed dorsally. There are deep subcentral grooves on

either side of the anterior keel; anteriorly these grooves have a form of narrow furrows, reaching latero-ventral margins of the cotyle. Subcentral foramina minute, hardly visible. Hypapophysis sigmoid, longer than high in lateral view. Its ventral edge, parallel to the main axis of the centrum, flattened and distinctly expanded laterally. Pointed distal tip directed posteriorly, projecting somewhat beyond the posterior edge of the cotyle. Anterior keel flattened, triangular in ventral view, producing two small tubercles below the cotyle rim. Neural arch elongate, somewhat depressed, without epizygapophyseal spines. Interzygapophyseal ridge sharp and well developed. Neural canal slightly depressed, somewhat square in outline from the front and about the same size as the cotyle. In anterior view, there are distinct sinuses in latero-ventral corners of the neural canal. Neural spine very low, occupying two-thirds of the length of the neural arch; upper edge of the neural spine slopes posteriorly in lateral view. Neural spine distinctly overhangs both anteriorly and posteriorly; the anterior overhang is stronger defined than the posterior one. Lateral foramina well marked; there is no depression around these openings. Zygosphene narrow, crenate in dorsal view; in anterior view the zygosphenal roof is arched upward. Upper edge of its articular surfaces projected above the level of the lip of the zygosphene. Zygantrum wide and low. There is a foramen on the posterior wall of the right postzygapophyseal ramus, outside zygantral articular recess; on the left ramus such a foramen is absent. Postzygapophyseal articular surfaces small, irregular. Prezygapophyseal processes prominent, flattened dorsoventrally with strongly widened tips in dorsal view. Paradiapophyses auriculiform, weakly divided into parapophyseal and diapophyseal portions. Left parapophyseal process well developed, acute rather than obtuse in shape, strongly projected forwards far anterior to the lower lip of the cotyle. Right parapophyseal process broken off at its base. Cotyle rounded, slightly wider than high. Paracotylar foramina located in deep depressions on either side of the cotyle. Condyle distinctly separated from the centrum by a neck.

Measurements and ratios of the holotype are given in Table XI.

Table XI

Measurements and ratios of holotype trunk vertebra of *Natrix longivertebrata* sp. n. from RK I (ZZSiD, RK I—10000)

PR-PO (R)	5.82	CL/NAW	1.78
PR-PO (L)	5.72	PO-PO/NAW	1.83
CL	4.77	CTW/CTH	1.15
PO-PO	4.90	ZW/NAW	0.85
NAW	2.68	PR-PR/PR-PO	0.90
ZW	2.29	CL/ZW	2.08
CTW	1.74	PR-PR/NAW	1.93
CTH	1.51		
PR-PR	5.18		

Description of remaining material

Basioccipital (Fig. 27: 6). Two completely preserved bones; somewhat differing from each other: one bone is considerable wider than long, the second one as wide as long. Lateral lobes of basioccipital crests well developed. Basioccipital tubercles not distinct. Occipitocondylar tubercle separated from the remaining portion of the bone by a thick bony collar, in one bone the collar is divided medially into two parts.

Basiparasphenoid (Fig. 27: 1—5 and Fig. 28). 11 bones altogether, two among them completely preserved, the remaining ones with parasphenoid processes missing. The bones show three different morphological patterns, but similar disposition of nerve and carotid foramina probably indicates that they represent

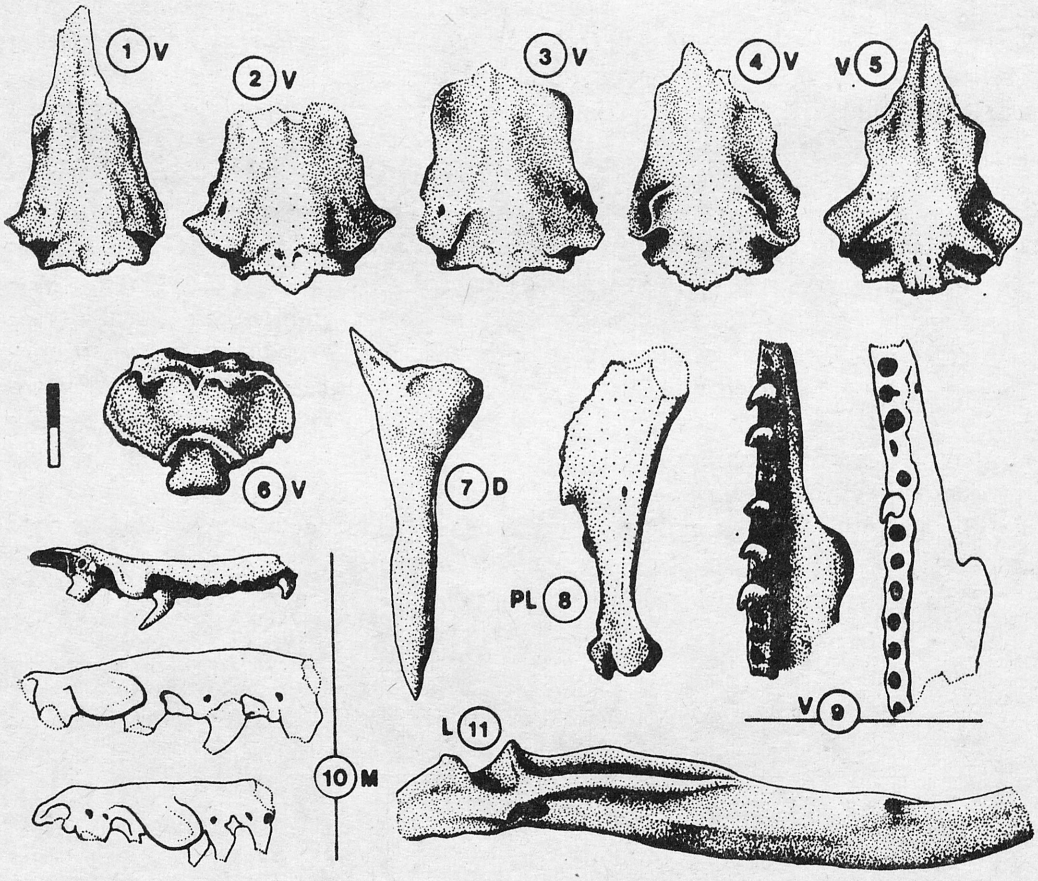


Fig. 27. Cranial bones of *Natrix longivertebrata* sp. n. from RK I. 1, 2, 3, 4, 5 — basiparasphenoids (ZZSiD, RK I—10003—10007), 6 — basioccipital (ZZSiD, RK I—10001), 7 — right ectopterygoid (ZZSiD, RK I—10021), 8 — right quadrate (ZZSiD, RK I—10022), 9 — left pterygoids, anterior fragments (ZZSiD, RK I—10019 and 10020), 10 — left maxillae, posterior ragments (ZZSiD, RK I—10014—10016), 11 — right compound bone (ZZSiD, RK I—10026). D — dorsal, L — lateral, M — medial, PL — postero-lateral, V — ventral views, Scale equals 2 mm

the same snake species. One bone (Fig. 27: 5) was described by MŁYNARSKI (1964, p. 334; ibidem not figured) as belonging to *Elaphe* cf. *situla*. However, very short Vidian canal indicates that the bone belonged to a natricine snake (cf. UNDERWOOD, 1967, p. 118); moreover, other features of basiparasphenoid of *Elaphe situla* (ZZSiD 349) are completely different from those in the fossil. All bones are relatively short, with prominent (in some specimens broken off) basipterygoid processes. Pterygoid crest situated near the posterior border of the bone, strongly inclined backward. Basisphenoid crest absent. Two bones (Fig. 27: 4 and 5) have their pterygoid crests provided with distinct tubercular processes, in both cases differently developed. One basiparasphenoid (Fig. 27: 5) has prominent suborbital flanges; these flanges are moderately developed in other bones. Posterior orifice of Vidian canal is located near the posterior border of the bone, covered by posterior extension of the pterygoid crest. In two bones cerebral foramen is distinctly separated from the posterior orifice of Vidian canal (Fig. 28: 4). One bone is provided with distinct furrows between the pterygoid crests and posterior Vidian foramina (Fig. 28: 2). Anterior orifice of Vidian canal is located immediately before the pterygoid crest and never accompanied by pterygoid nerve foramen. On dorsal side of the bone, anterior foramina for abducens nerves and foramina for sympathetic nerves are located together in depressions situated laterally to pituitary fossa. Notches for sympathetic nerves are covered dorsally by entirely or partially closed bony appendices. Posterior foramina for abducens nerve lie behind postero-lateral corners of pituitary fossa. Trabecular processes weakly developed.

Maxilla (Fig. 27: 10). All 5 fragments are from left maxillae and are missing their anterior halves. The best preserved (largest) fragment is broken across the posterior margin of prefrontal process or at the level of 12th tooth from behind. Ectopterygoid process preserved in all maxillary fragments, is directed antero-ventrally and of somewhat "scraw-like" form. Maxilla is opisthomegadontic; the last three teeth, though broken, are much larger at their base than teeth anterior to them. It is impossible to ascertain whether the teeth either become gradually larger posteriorly or whether the last teeth are abruptly enlarged. Dorsal constriction for maxillary ramus of the pterygoid is not marked.

Pterygoid (Fig. 27: 9). Two anterior fragments are broken immediately posterior to their pterygoid flange. The preserved portions of the toothed-ramus are straight, teeth are present in one fragment and are small, slightly hooked backward and of equal size. Ectopterygoid process distinctly developed.

Ectopterygoid (Fig. 27: 7). A single complete bone. Posterior portion of the bone is flattened dorso-ventrally and pointed posteriorly. External and internal rami of the maxillary articulation are weakly separated from each other, internal ramus is tapering and strongly pointed. The ectopterygoid under discussion was earlier classified by MŁYNARSKI (1964, p. 334, Fig. 17) as belonging to *Elaphe* cf. *situla*. MŁYNARSKI's determination, however, based on SZUNYOGHY's (1932) key, is wrong as the ectopterygoid of *E. situla* (e. g. ZZSiD 349) is differently developed in the fossil, besides, presumably the fossil is too large.

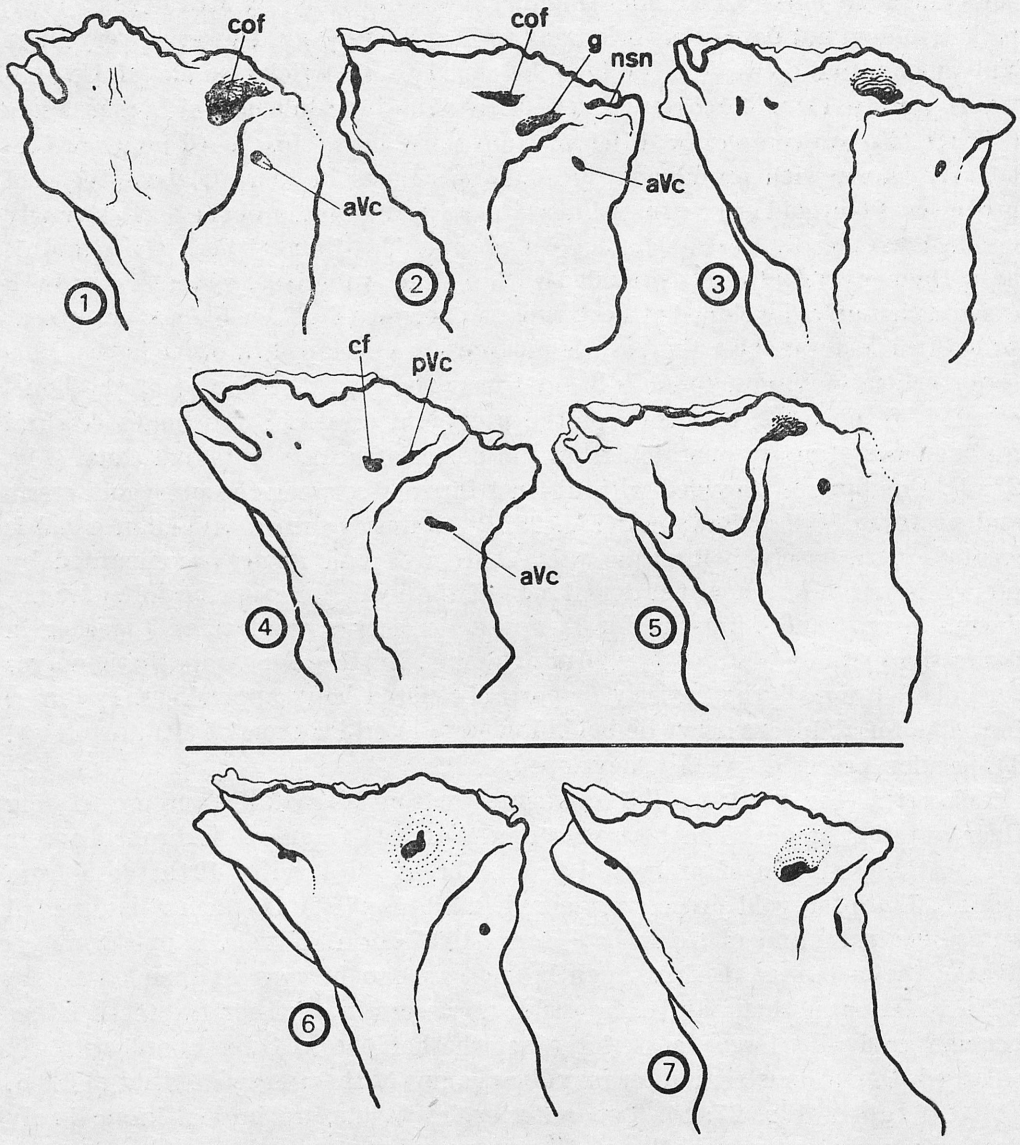


Fig. 28. Patterns of disposition of foramina in postero-ventral basisphenoid area of *Natrix longivertebrata* sp. n. from RK I (1, 2, 3, 4, 5), Recent *Natrix tesselata* ZZSiD 16 (6), and Recent *Natrix maura* MNCN 824272 (7). Abbreviations: aVc — anterior orifice of Vidian canal (for palatine branch of facial nerve (VII)), cf — cerebral foramen (for palatine branch of facial nerve (VII)), cof — common foramen (for cerebral artery and facial nerve: cf + pVc), g — groove, nsn — notch for sympathetic nerve, pVc — posterior orifice of Vidian canal (for cerebral branch of internal carotid artery). Not to scale

Compound bone (Fig. 27: 11). 7 both and right bones altogether. Medial flange of mandibular fossa is not much higher than the lateral flange. Lateral flange is provided with a groove located near its dorsal border. There is a large foramen on lateral wall of the bone, below posterior end of mandibular fossa.

Two bones are additionally provided with smaller foramina situated also on the lateral wall of the bone below the posterior margin of cavitas sigmoidea. Retroarticular process very high in lateral view; its tip, if present, is curved medially. Supraangular foramen located far from the anterior end of mandibular fossa.

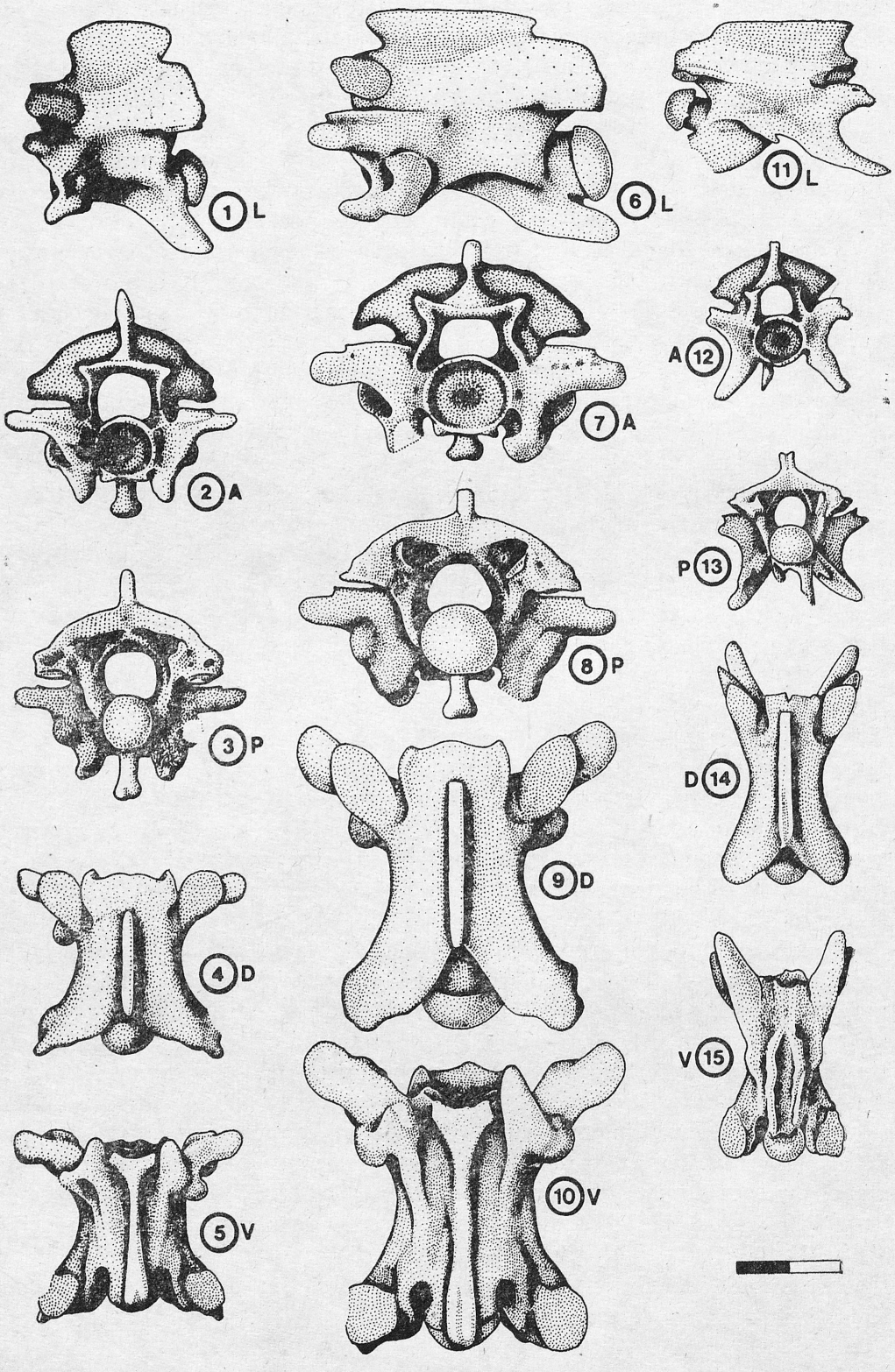
Quadrate (Fig. 27: 8). A single almost completely preserved bone. Distal portion of the bone is slender, provided with relatively large stapedial process. Proximal (dorsal) portion of the bone elongate ventro-posteriorly. Antero-lateral margin slightly concave; quadrate crest absent.

Vertebrae. About six hundred vertebrae belonging to *Natrix longivertebrata* have been selected from among snake remains from RK I; however, the remaining material contains several thousand vertebrae as well, mixed with vertebrae od *Coluber robertmertensi*.

Only a single vertebra representing the anteriormost portion of the column in present in the material; two other bones originate from the posterior cervical region or anterior trunk region. No axis is present in the material.

The anterior cervical vertebra (Fig. 29: 1—5) has a short, somewhat cylindrical centrum, provided with strongly developed subcentral ridges and deep grooves on either side of the anterior keel. Hypapophysis long, projected downward; short ventral surface of the hypapophysis flattened and expanded laterally. Neural arch distinctly vaulted. Neural canal relatively broad and high, slightly wider than the round cotyle. Interzygapophyseal ridges prominent, parallel to the main axis of the centrum. Neural spine much higher than that of mid-trunk vertebrae; its upper edge distinctly slopes posteriorly. In lateral view, anterior border of the neural spine is straight and antero-dorsal margin is rounded; posterior border of the neural spine strongly overhangs posteriorly. Lateral foramina large. Zygosphene crenate from above and distinctly convex from the front. Prezygapophyseal processes flattened and obtuse-shaped, but narrower than those in trunk vertebrae. Parapophyseal articular facets well separated. Parapophyseal processes slender and acute, projected strongly below and anterior to the lower lip of the cotyle. Paracotylar foramina located in deep fossae on either side of the cotyle.

Trunk vertebrae generally resemble the holotype, but for the most part have longer centra. Subcentral ridges and grooves, although prominent, are never developed as strongly as those of the holotype vertebra. Hypapophyses are missing in most bones; if present, they have usually more slender and longer tips and their ventral surface — except a single case — is never flattened. Anterior keel triangular in ventral view and always provided with two lateral tubercles at the lower lip of the cotyle. Parapophyseal processes always strongly developed, extending far forwards. Prezygapophyseal processes always flattened and obtuse, sometimes strongly widened distally in dorsal view. Most vertebrae lack their neural spines. If present, neural spine is always low, overhanging distinctly anteriorly, with the upper edge sloping posteriorly. Neural spine of the two anterior trunk vertebrae (mentioned above) is somewhat higher than in farther vertebrae in the column.


1 L
6 L
11 L
A 12
2 A
7 A
P 13
8 P
3 P
D 14
9 D
4 D
V 15
10 V
5 V

Measurements and ratios of 27 mid-trunk vertebrae selected from among largest and best preserved bones are given in Table XII. The most striking quantitative feature is great elongation of vertebral centra; value of CL/NAW ratio of the sample is 1.92 on average (range 1.76—2.22), but can reach (in a damaged vertebra) even 2.30.

Table XII

Measurements and ratios of trunk vertebrae of *Natrix longivertebrata* sp. n. from RK I (N = 27)

	OR	$\bar{X} \pm SD$
PR-PO	5.08—6.75	
CL	4.27—5.58	
PO-PO	4.48—6.07	
CW	2.26—2.97	
ZW	2.00—2.74	
CTH	1.40—1.82	
CTW	1.60—2.12	
PR-PR	4.56—6.00	
CL/NAW	1.76—2.22	1.92±0.12
PO-PO/NAW	1.83—2.31	2.03±0.11
CTW/CTH	0.99—1.17	1.12±0.06
ZW/NAW	0.80—1.02	0.92±0.06
PR-PR/PR-PO	0.84—1.04	0.93±0.05
CL/ZW	1.86—2.59	2.08±0.17
PR-PR/NAW	1.93—2.45	2.11±0.13

Posterior trunk vertebrae do not differ morphologically from mid-trunk ones, but have shorter centra.

Cloacal vertebrae of *Natrix longivertebrata* remain unknown. Caudal vertebrae (Fig. 29: 11—15) have elongated centra (especially in posterior caudal region), provided with long and slender pleurapophyses and haemapophyses. Pleurapophyses of anterior caudal vertebrae are projected antero-ventrally in lateral view and antero-laterally in ventral view; pleurapophyses of posterior caudal vertebrae very thin and tapering, projecting nearly anterior in both lateral and ventral views. Haemapophyses are poorly preserved in all vertebrae, but preserved remnants indicate their postero-ventral projection. Neural arch elongate and slightly down-swept in postzygapophyseal area. Neural canal

Fig. 29. Vertebrae of *Natrix longivertebrata* sp. n. from RK I. 1, 2, 3, 4, 5 — cervical vertebra (ZZSiD, RK I—10030), 6, 7, 8, 9, 10 — holotype trunk vertebra (ZZSiD, RK I—10000), 11, 12, 13, 14, 15 — caudal vertebra (ZZSiD, RK I—10629). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

subtriangular from the front. Neural spine long and low, strongly flattened on its dorsal edge; the dorsal edge distinctly slopes posteriorly. In lateral view, neural spine overhangs anteriorly; posterior edge of the neural spine vertical in anterior vertebrae and distinctly inclined anteriorly in posterior vertebrae. Zygosphene narrow, convex from the front and concave from above. Zygapophyseal articular facets small, round or oval in shape. Prezygapophyseal processes short, acuminate, directed forward in dorsal view. Cotyle small, rounded.

Taxonomic status of *Natrix longivertebrata* sp. n. Comparison of the natricine from RK I with other European snakes of the genus *Natrix* (including fossil species) indicates separate morphological character of the former form. Three natricine species presently inhabiting Europe, i. e. *Natrix natrix*, *N. tesselata* and *N. maura*, as well as two fossil species, *N. sansaniensis* from the Miocene of Sansan (cf. Chapter Va, p. 49) and the form described here, *N. parva* sp. n. (cf. Chapter Va, p. 47) all possess similarly developed main vertebral structures, unlike *N. longivertebrata*. Vertebrae of these five formerly mentioned species have vaulted neural arch and rather well developed neural spine, while *N. longivertebrata* has its neural arch depressed and neural spine very low. The remaining diagnostic characters of its vertebrae resemble these of other species of the genus *Natrix*, but are much stronger defined. A number of elongate trunk vertebrae belonging to *N. natrix* from some localities of the Polish Early Pleistocene, somewhat resemble those of *N. longivertebrata*. Unfortunately, the majority of these vertebrae lacks their neural spines and hypapophyses and their neural arch is usually more vaulted than in *N. longivertebrata*; the neural spine, if present, is also distinctly higher. Different development of the neural arch and neural spine of *N. longivertebrata*, both characters seeming to be of highest taxonomic importance, can raise doubts towards generic classification of this snake. However, close similarity can be observed between skull bones of *N. longivertebrata* and of *N. natrix*. Quadrate and compound bones are practically identical in both species with exception of a peculiar posterior foramen present in the latter fossil. Besides, disposition of main foramina of basiparasphenoids in both species is similar especially in bones of fossil *N. natrix* from Middle Pleistocene localities, i. e. a single basiparasphenoid from ZA and several from among numerous basiparasphenoids from KG (cf. Fig. 48). Basioccipital differs from those of other European snakes of the genus *Natrix*; to a certain degree also ectopterygoid shows specific characters. Pterygoids and maxillae are preserved only in fragmentary state; maxillae, as is characteristic for most natricine snakes, have enlarged posterior teeth (cf. e. g. MALNATE, 1960, p. 43).

Remarks. Fossil remains of *Natrix* species, reported from several Pliocene localities of Central Europe, have been identified exclusively as belonging to the living species, *N. natrix* and *N. tesselata* (for detailed data see Chapter Vc, p. 119).

Natrix cf. *longivertebrata* sp. n.
(Fig. 30)

Material. — About 250 trunk and caudal vertebrae found in three localities: W I (100 vertebrae), W II (78 vertebrae), and RK II (59 vertebrae).

Natricine remains from W I and RK II have been mentioned in MŁYNARSKI's papers as follows:

W I: *Natricinae* indet. — MŁYNARSKI, 1961a, pp. 12—13; 1962, p. 181;

RK II: *Natrix* cf. *natrix* (L.) — MŁYNARSKI, 1977, p. 17.

The material from W II has not been previously described. Vertebrae from all three localities usually are poorly preserved. Almost all bones lack their neural spine; this structure is preserved, but only in fragmentary state, on one trunk vertebra from RK II and two others from W I. The only vertebra provided with completely preserved neural spine (W I) is from postero-cervical or antero-trunk region of the column. All vertebrae from W II are missing every protruding structure. Trunk vertebrae from these three localities generally resemble those of *Natrix longivertebrata* from RK I, but differ from them by having much vaulted and upswept posteriorly neural arch and absence of subcentral grooves. The neural spine is present in fragmentary state in a few bones and seems to be somewhat higher than in the vertebrae from RK I; posterior sloping of the dorsal edge of the neural spine is well seen in these bones. Moreover, paradiapophyses are usually stronger built than in the vertebrae from RK I; parapophyseal

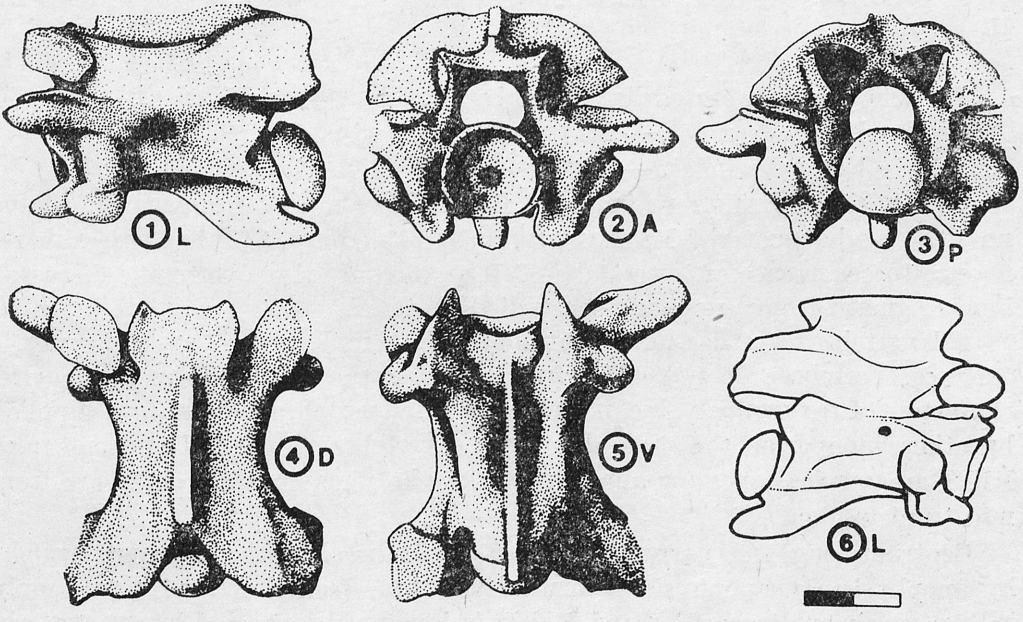


Fig. 30. *Natrix* cf. *longivertebrata* from W I. 1, 2, 3, 4, 5 — trunk vertebra (ZZSiD, W I—601), 6 — trunk vertebra (ZZSiD, W I—600). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

processes, for the most part, are sharply pointed. The hypapophysis, distinctly sigmoid-shaped, has usually shorter ventral edge than in the vertebrae from RK I.

Trunk vertebrae from W I are somewhat shorter than those from RK I; dimensions of 15 biggest vertebrae are: CL 3.62—5.62, CL/NAW 1.68—2.09, $\bar{X} = 1.81 \pm 0.12$. Strong damage of vertebrae from W II and small size of vertebrae from RK II both make impossible good sampling for measurements; the biggest vertebra from RK II measures CL = 5.37, NAW = 2.70, CL/NAW = = 2.00, and from W II respectively CL = 5.55, NAW = 2.82, CL = 1.97.

Several caudal vertebrae, present in all three localities, resemble those of *Natrix longivertebrata*; however, all but one lack their pleurapophyses and haemapophyses. A single vertebra from RK II has completely preserved left pleurapophysis; this structure, as is characteristic for the species, is thin and long and projects forward.

Family *Viperidae* LAURENTI, 1768
Subfamily *Viperinae* LAURENTI, 1768
Genus *Vipera* LAURENTI, 1768

Vipera ammodytes (LINNAEUS, 1758)
(Figs. 31 and 32)

Material. — 15 vertebrae from W I, 3 vertebrae from RK I, and 15 vertebrae from RK II.

Pliocene vipers were earlier listed by MŁYNARSKI as follows:
W I: *Viperidae* indet. — MŁYNARSKI, 1961a, p. 13; 1962, p. 179.
RK I: *Viperidae* indet. — MŁYNARSKI, 1964, p. 343.

So far, the viperine remains from RK II have not been described. I have no idea on what material MŁYNARSKI (1964, Table on p. 343) has based his reference to occurrence of *Viperidae* in RK I; the only three vertebrae discussed here originate from previously unstudied material.

All vertebrae are damaged, but most of them have preserved diagnostic features. Vertebrae do not differ from these of the living *Vipera ammodytes*; characters of taxonomic value, if lacking in some vertebrae, are always supplied by other bones from the same site. Several vertebrae from W I and one from RK I are cervical ones (or anterior-trunk), the remaining vertebrae are from mid-trunk region.

Centrum long and narrow, somewhat cylindrical, with long and straight hypapophysis. Hypapophysis of cervical vertebrae (completely preserved only in two specimens from W I and RK I) is longer and directed less posteriorly than that of trunk vertebrae. Presence of subcentral grooves and ridges, both elements strongly developed, is restricted to only anterior portion of vertebrae.

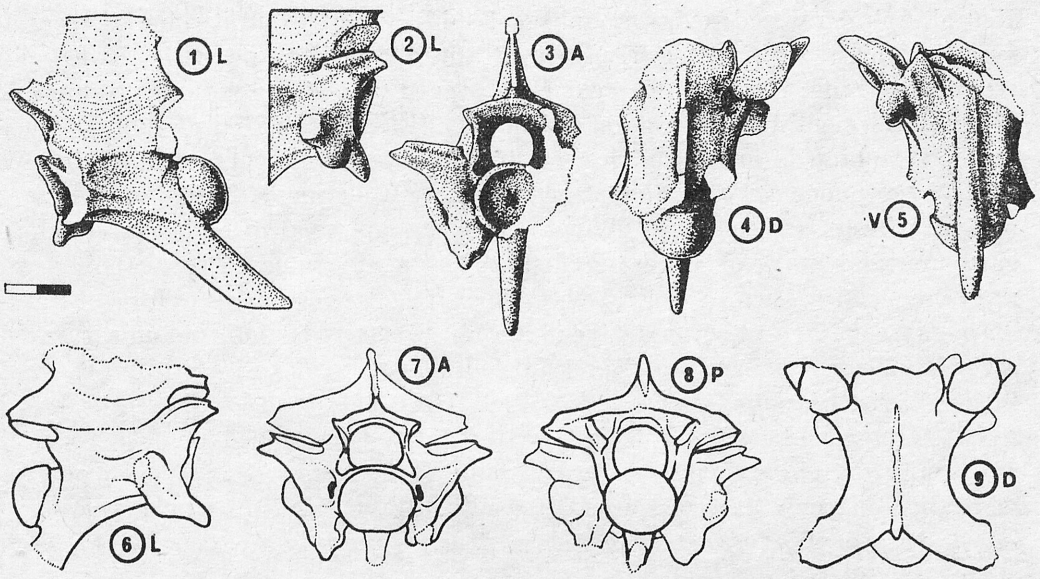


Fig. 31. Vertebrae of *Vipera ammodytes* from W I. 1, 2, 3, 4, 5 — cervical vertebra (ZZSiD, W I—700), 6, 7, 8, 9 — cervical vertebra (ZZSiD, W I—701). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

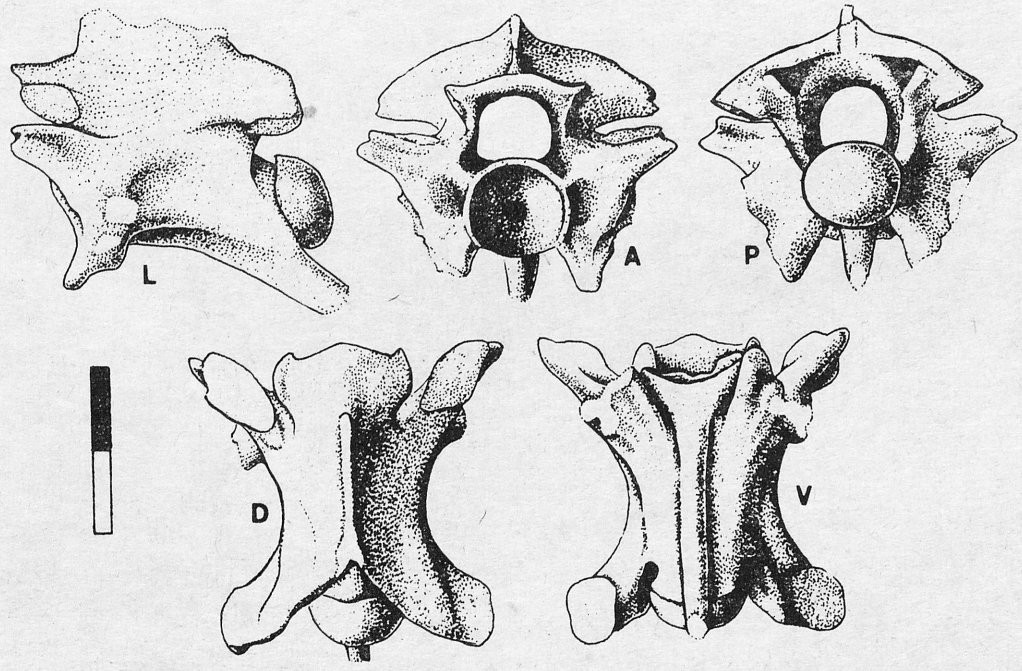


Fig. 32. Trunk vertebra of *Vipera ammodytes* from RK II (ZZSiD, RK II—121). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

Neural arch depressed; epizygapophyseal spine absent. Neural spine of cervical vertebrae high, with posteriorly inclined anterior border and with distinct posterior overhang; these features can be observed on a single vertebra from W I, although its neural spine is damaged in part (Fig. 31: 1). Neural spine of mid-trunk vertebrae is lower and longer, but always prominent. Anterior border of the zygosphene convex and distinctly crenate from above. Postzygapophyseal articular facets are round or obovate. Prezygapophyseal articular facets elongate, prezygapophyseal process very short and acute-shaped. Prezygapophyseal rami are slender, then in ventral view their articular facets are well seen. Paradiapophyses of Recent comparative material have two well defined and separated articular facets, but because of bad erosion this feature can be hardly observed in the fossils. Diapophyses project strongly laterally and are well seen in dorsal view. A dagger-like parapophyseal process is well developed in both cervical and trunk vertebrae; it is slender and long in lateral view and looks anteroventrally. Cotyle is flattened dorso-ventrally. All vertebral foramina well developed, paracotylar foramina located in distinct depressions, usually round in shape.

Mensuration. All vertebrae belonged to rather small specimens. Here follows basic dimensions of mid-trunk vertebrae from all three localities; successively number of vertebrae, range of CL, range of CL/NAW ratio, its mean and standard deviation:

W I: 4 3.64—4.22 1.48—1.66 1.58±0.08
RK I: 2 3.82—3.87 1.61—1.64
RK II: 4 3.07—3.26 1.43—1.66 1.56±0.10

Similar measurements for Recent *Vipera ammodytes* (ZZSiD 292; 60 succeeding vertebrae from 46 to 105) are: 4.54—5.10, 1.42—1.63, 1.53±0.06, similarly for a specimen ZZSiD 319. However, these measurements concern rather larger specimens; for smaller ones (e. g. ZZSiD 318) the CL/NAW ratio is somewhat lower (cf. also Tab. III and Fig. 33).

Additional measurements of hypapophyses of cervical vertebrae are given below. I have measured the length of their posterior border from the tip of hypapophysis to its base just before the condyle rim. Proportion of this value to CL is 0.32 for W I and 0.32 for RK I; for Recent *Vipera ammodytes* it fluctuates from about 0.40 in anterior cervical vertebrae to 0.30 in anterior trunk vertebrae. The value of this ratio for *V. berus*, *V. ursinii* and *V. aspis* probably never exceeds 0.25.

Remarks (Fig. 57). Except for these fossils no viperid remains are known from the Pliocene of Central Europe. As mentioned in the prevailing chapter (cf. Chapter Va, p. 52), a close relative of *Vipera ammodytes*, *V. gedulyi* BOLKAY, was described from the Upper Miocene (MN 13) of Polgárdi, Hungary. SZUNYOGHY (1932) also reported remains of two living species, *V.* cf. ? *ammodytes* and *V.* cf. *aspis* from Polgárdi. Unfortunately, these records, based exclusively on skull bones, are not comparable with the fossils from the Polish Pliocene. Description of a viperid basiparasphenoid from the Middle Pleistocene of KG

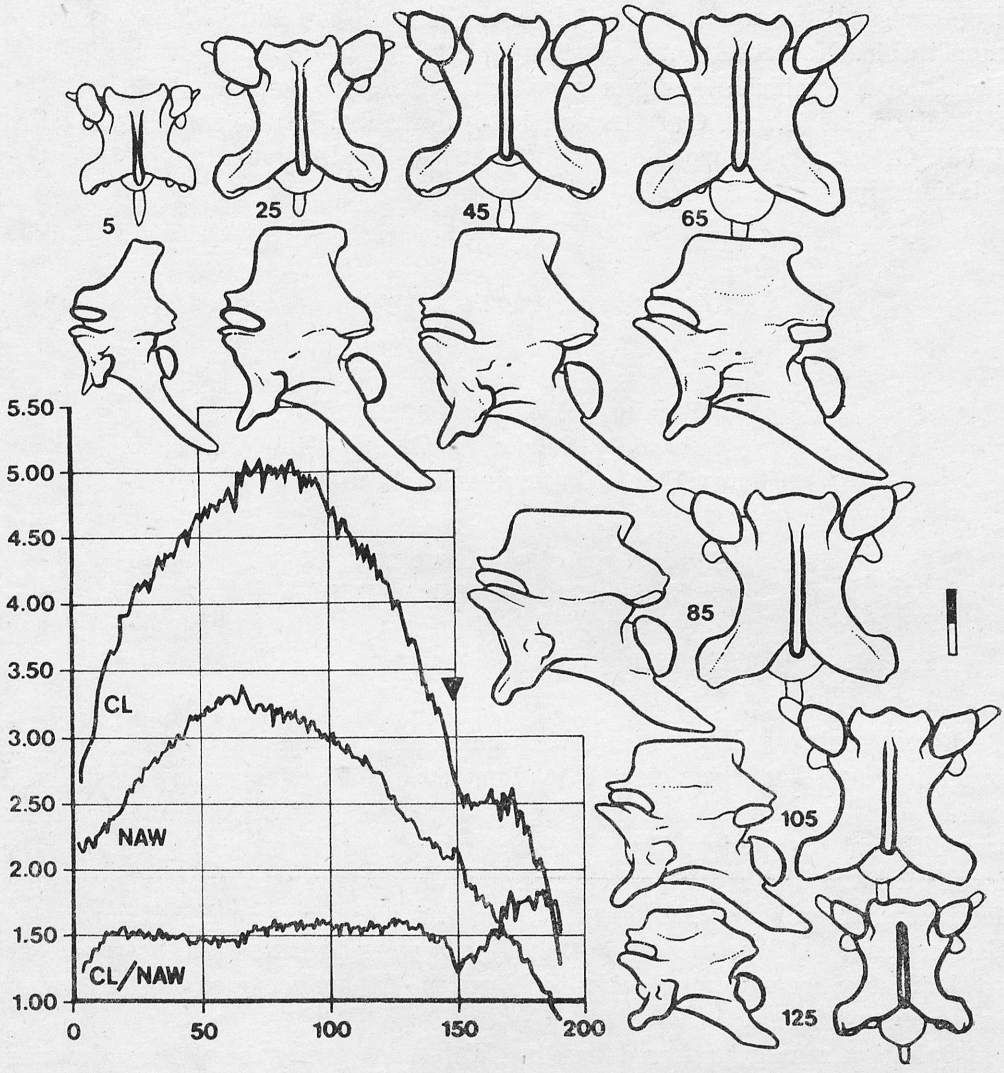


Fig. 33. Intracolumnar variation in CL, NAW and CL/NAW of vertebrae of *Vipera ammodytes* (ZZSiD 292). Vertical axis — dimensions in mm; horizontal axis — no. of succeeding vertebrae; black triangle — position of cloacal vertebrae. Figures show dorsal and lateral views of every 20th precaudal vertebra. Scale equals 2 mm

as belonging to *V.* aff. *ammodytes* (SZYNDLAR, 1981) is incorrect (cf. Chapter Vc, p. 123).

Present European distribution of *Vipera ammodytes* is restricted to the south-eastern part of the continent, northward not exceeding southern Austria and Hungary. However, until very recently this species inhabited Moravia (REMES, 1932, cit. after OLIVA et al., 1968). Fossil records from Poland indicate that in the past the range of *V. ammodytes* reached further northwards.

BOLKAY's (1920) hypothesis that the presumably widespread *Vipera gedulyi*

from Polgárdi was an ancestor of Recent *V. ammodytes* and *V. latasti* is not demonstrable. Nevertheless, *V. ammodytes* and *V. latasti*, the latter inhabiting the Iberian Peninsula and northwestern Africa, are considered to be closely related species (e. g. SAINT GIRONS, 1978) derived from the same stock (GASC, 1968). Osteological morphology of both species is also indicative of their close relationship.

Vc. QUATERNARY

Family *Colubridae* OPPEL, 1811
Subfamily *Colubrinae* OPPEL, 1811
Genus *Elaphe* FITZINGER in WAGLER, 1833

Elaphe longissima (LAURENTI, 1768)
(Figs. 34—37, Table XIV)

Material. — See Table XIII.

Fossil finds of *Elaphe longissima* predominate among ophidian remaint in Poland and have been found in almost all Polish Quaternary localities. Is can be clearly seen in Polish materials that vertebrae of *E. longissima* represent two different morphological patterns, correlated with their geological age. That is why I have divided the whole material into two separate sections: younger fossils are described as *Elaphe longissima* and older ones as *E.* aff. *longissima*. Snakes from localities where both patterns were present have been assigned to the first or second group accordingly which of them occurred most frequently in larger specimens.

Ophidian remains referred here as *Elaphe longissima* have been described previously as follows:

ZA: *Coluber* or *Elaphe* sp. — MŁYNARSKI, 1977, p. 19;
KG: *Elaphe* cf. *longissima* (LAURENTI) — MŁYNARSKI, 1977, p. 21; *Elaphe longissima* (LAURENTI) — SZYNDLAR, 1981, pp. 85—87, Figs. 9—10;
ZS: *Elaphe* sp. — KOWALSKI et al., 1967, p. 23;
JO: *Elaphe longissima* (LAURENTI) — MŁYNARSKI in KOWALSKI et al., 1963, p. 10;
GI: *Elaphe longissima* (LAURENTI) — MŁYNARSKI, 1961b, pp. 4—5, pl. 3.

Moreover, the present description considers records from six other Upper Pleistocene localities.

Cranial bones. Many cranial bones from numerous localities practically does not differ from those of Recent *Elaphe longissima*. Some small differences

List of materials of *Elaphe* aff. *longissima* and *Elaphe longissima*

	Elaphe aff. *longissima*				*Elaphe longissima*										
	ZB	KD	KA	JZ	ZA	KG	RZ	WA	ZD	ND	ZS	RA	CI	JO	GI
frontal (R)							1	1							
——— (L)							1								
parietal						15	1	3						2	
basioccipital						3								1	
basiparasphenoid				5	1	22		2						4	1
maxilla (R)				1		>9	1							2	1
——— (L)				1		>5								1	
pterygoid (R)						>5		2						2	
——— (L)						>3	1							3	1
ectopterygoid (R)						>1								1	1
palatine (R)						>2	1							4	
——— (L)						>2	1							2	1
squamosal (L)															3
quadrate(R)						>3								2	1
——— (L)															4
compound bone (R)				1		>3								5	1
——— (L)						>1								2	2
dentary (R)				1		64		1							
——— (L)		1		2	13	52		1		1				5	
nasal (R)															1
—— (L)															1
premaxilla						1									1
septomaxilla (L)							1								
cervical vertebrae	13	2	±800	>1000	35	>1370	34	11			1		2	152	433
trunk vertebrae	64	257			348		167	128	8	28	21	2	7	736	
caudal vertebrae	8	19			16		27	4	2	2			1		
ribs							±200	88			4				

are probably the result of the scant comparative material at my disposal than from dissimilarity of fossil forms.

Frontal (Fig. 35: 1). Only two bones from RZ and WA. Frontal aperture of round or obovate section. All three processes in prefrontal articular area distinctly developed: septomaxillary process small, rectangular in lateral view; internal prefrontal process has the shape of a thin and broad collar; external prefrontal process thick, triangular in dorsal view, projecting outside internal process. Anterior border of the bone concave in dorsal view.

Parietal (Fig. 34: 3, 35: 1, and 36: 3). A number of parietals preserved in perfect state originate from younger localities; some fragmentary parietals from KG represent posterior portions of the bones. Descending parts of the parietals strongly convex. Dorsal surface flat, without any furrows. Parietal foramina situated near each other in the posterior half of the dorsal surface. Parietal crests converge on each other before reaching posterior border of the bone.

Basioccipital (Fig. 34: 2 and 36: 2). A few well preserved bones from JO and KG. Basioccipital crest moderately developed with the lateral lobes usually better marked than the median one (basioccipital process). Median crest distinct, divergent anterior to occipitocondylar tubercle. The latter structure separated off by a deep furrow.

Basiparasphenoid (Fig. 34: 1, 35: 2, and 36: 1). Several tens of bones, originating from various localities dated from Cromerian (ZA) until Holocene, differ little from one another. Basipterygoid process moderately developed; suborbital flanges distinct. Pterygoid crest strongly inclined anteriorly. Basipterygoid crest absent or underdeveloped with exception of a case (KG). A deep and broad groove extends throughout the ventral side of the parasphenoid process. Posterior orifices of Vidian canal situated near postero-lateral border of the bone; anterior orifices hidden deeply under pterygoid crests. Foramina of dorsal side and notches for sympathetic nerves well marked.

Prootic (Fig. 36: 5). A single left prootic from KG has not been previously described (SZYNDLAR, 1981). Its postero-ventral portion is missing, but otherwise the bone is preserved in a perfect state. Posterior border of prootic is the anterior wall of the fenestra ovalis and forms a sinus deeply penetrating into the bone. Supraoccipital crest underdeveloped. The bar dividing rami of the trigeminal nerve strongly built; below the opening for mandibular branch of the trigeminal nerve it forms a triangular extension directed posteriorly. The internal wall, where the facial nerve foramen should be expected, is broken off. A foramen for maxillary branch of the trigeminal nerve is big and roung; in Recent *Elaphe longissima* (ZZSiD 20, 21, 291) the foramen is strongly flattened antero-posteriorly and provided with a deep groove below, absent in the fossil. A smaller round foramen, probably for a sympathetic nerve, is present below the bar dividing trigeminal nerve orifice; a similar foramen, but much smaller, is present only in one specimen of Recent *Elaphe longissima* (ZZSiD 291).

Maxilla (Fig. 34: 4, 35: 5, and 36: 6). Some complete bones originate from younger localities; from the older ones only small maxillary fragments are avail-

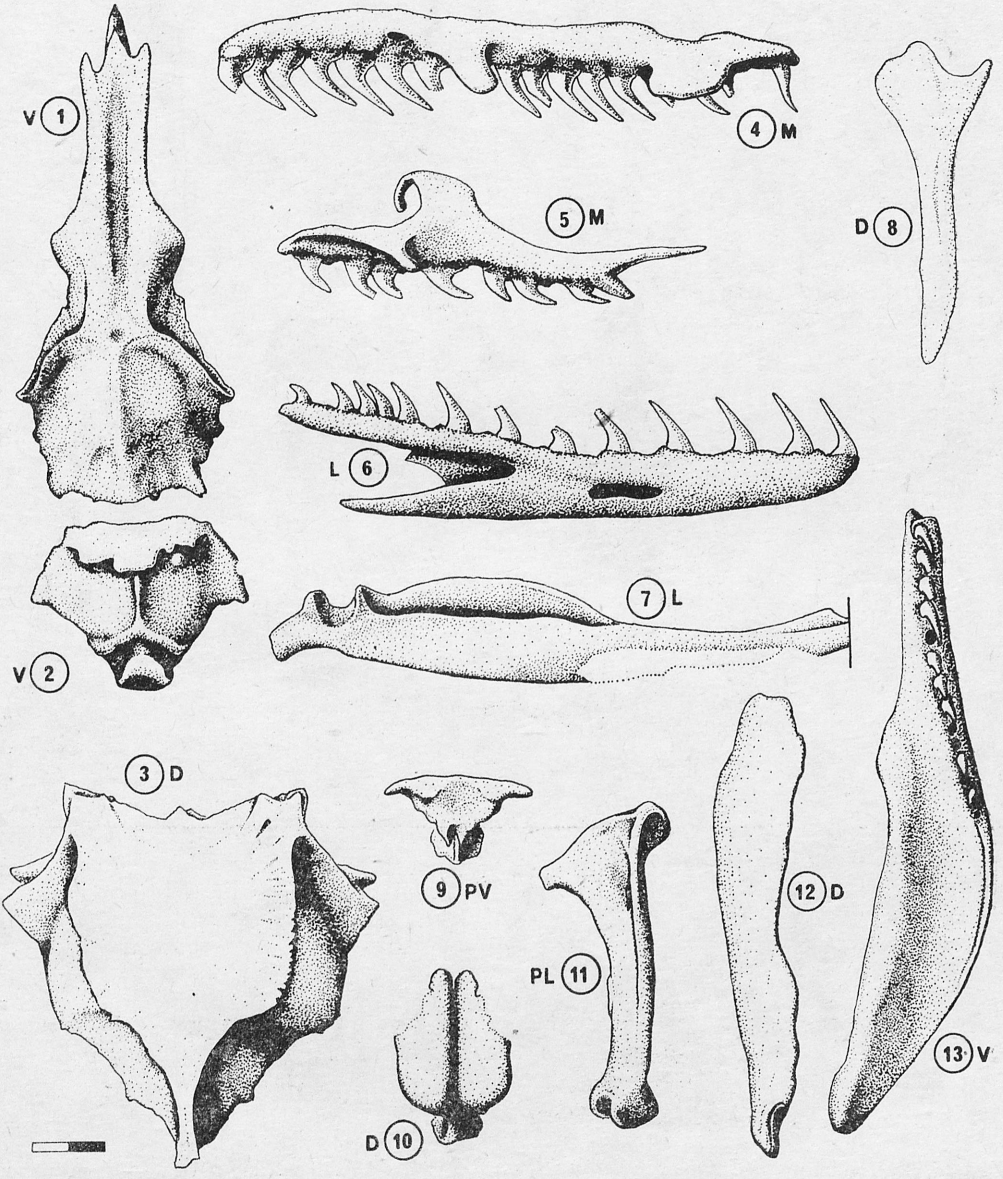


Fig. 34. Cranial bones of *Elaphe longissima* from JO and GI. 1 — basiparasphenoid (ZZSiD, JO-4), 2 — basioccipital (ZZSiD, JO-3), 3 — parietal (ZZSiD, JO-1), 4 — right maxilla (ZZSiD, JO-10), 5 — right palatine (ZZSiD, JO-20), 6 — right dentary (ZZSiD, JO-35), 7 — right compound bone (ZZSiD, JO-30), 8 — left ectopterygoid (ZZSiD, JO-19), 9 — premaxilla (ZZSiD, GI-19), 10 — nasals (ZZSiD, GI-18), 11 — right quadrate (ZZSiD, JO-28), 12 — left squamosal (ZZSiD, GI-6), 13 — right pterygoid (ZZSiD, JO-14). D — dorsal, L — lateral, M — medial, PL — postero-lateral, PV — postero-ventral, V — ventral views. Scale equals 2 mm

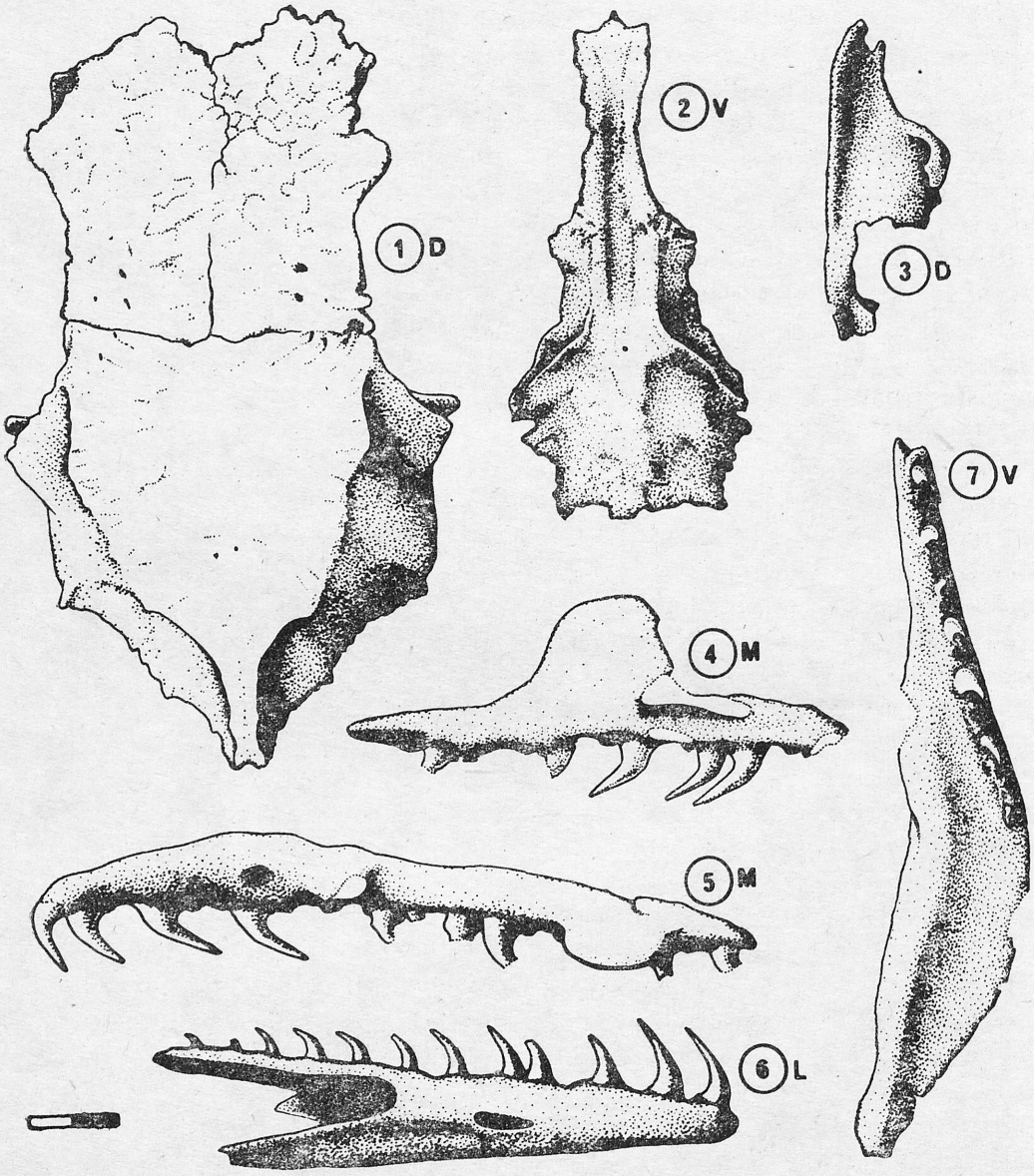


Fig. 35. Cranial bones of *Elaphe longissima* from RZ and WA (not catalogued). 1 — frontals and parietal (RZ), 2 — basiparasphenoid (WA), 3 — right septomaxilla (RZ) 4 — left palatine (RZ), 5 — right maxilla (RZ), 6 — right dentary (WA), 7 — right pterygoid (WA). D — dorsal, L — lateral, M — medial, V — ventral views. Scale equals 2 mm

able. The bone is elongate, slightly bent in dorsal or ventral view. Teeth isodont, large, strongly hooked backward. Complete maxillae (JO, JN, RZ) have 18—19 teeth (or tooth sockets) with no diastema (Recent: 18—21). Prefrontal process, located at the 8th and 9th teeth, slender and tapering, projecting posteroventrally. Ectopterygoid process, situated usually at the level of the 15—17th

teeth, is twice longer than wide (longer side joined with maxillary trunk). Two teeth are present behind ectopterygoid process.

Pterygoid (Fig. 34: 13 and 35: 7). Complete bones preserved in JO and WA localities. In dorsal or ventral view inferior border arched, lateral border slightly concave with weakly developed pterygoid flange. Ectopterygoid process underdeveloped. Pterygoid crest absent, but the anterior half of the bone is convex dorsally. Lateral border of the bone forms a crest inclined upwards. Between the convexity and the lateral crest a deep groove is present extending from the pterygoid flange almost to the posterior end of the bone. Tooth row straight, occupying much less than 1/2 of the bone total length. Teeth small, isodont. Complete specimens have 11—15 teeth (Recent: 12—14). Pterygoid remains from KG are fragmentary and their reference to this species is uncertain.

Ectopterygoid (Fig. 34: 8). External ramus broad, square; internal ramus slender and tapering, at right angle to the former one. Body straight, flattened dorso-ventrally, with tapering posterior tip.

Palatine (Fig. 34: 5, 35: 4, and 36: 7). Teeth isodont, their number in completely preserved specimens (JO, RZ) 10—14 (Recent: 11). Teeth large, strongly hooked backwards. Maxillary process long, slender and tapering, projected posteriorly. Maxillary nerve foramen situated in the middle of the maxillary process base, provided with a deep furrow directed anteriorly. Vomeral process, located between the level of the 5th and 9th teeth, inclined anteriorly. In some specimens it is provided with long and ventrally curved choanal process.

Squamosal (Fig. 34: 12). Shape of three bones from GI resembles those of the living *Elaphe longissima*, but because of lack of any structures on the bone surface its taxonomic value is small and thus correct determination of the species is dubious.

Quadrate (Fig. 34: 11 and 36: 10). Several well preserved quadrates originate from JO, GI and KG. Their trunk is relatively thick and of equal thickness throughout its length. Stapedial process distinct. Quadrate crest present only in proximal part of the trunk. Dorsal edge thickened and overhanging on both sides. In internal view the antero-dorsal overhang forms a spur, distinctly separated off.

Dentary (Fig. 34: 6, 35: 6, and 36: 8). Remarkably proterodontic. Complete dentaries have 22—23 (JO), 23 (ND) or 24 (WA) teeth each (Recent: 24—25). Anterior end of the bone is slightly curved medially. Mental foramen strongly elongate, lying at the level of the 8—10th teeth. Compound notch on the lateral surface usually approaches by the 14th tooth. Meckel's groove closes completely at the level of the 6th tooth.

Compound bone (Fig. 34: 7 and 36: 9). Compounds are preserved in JO, GI, and KG materials. Medial flange is twice as high as lateral flange. Posterior portion of the lateral flange is slightly concave. Supraangular foramen situated just before anterior end of mandibular fossa. Retroarticular process thick, slightly curved postero-ventrally.

Nasal (Fig. 34: 10). Only a poir of joined nasals is preserved in the GI ma-

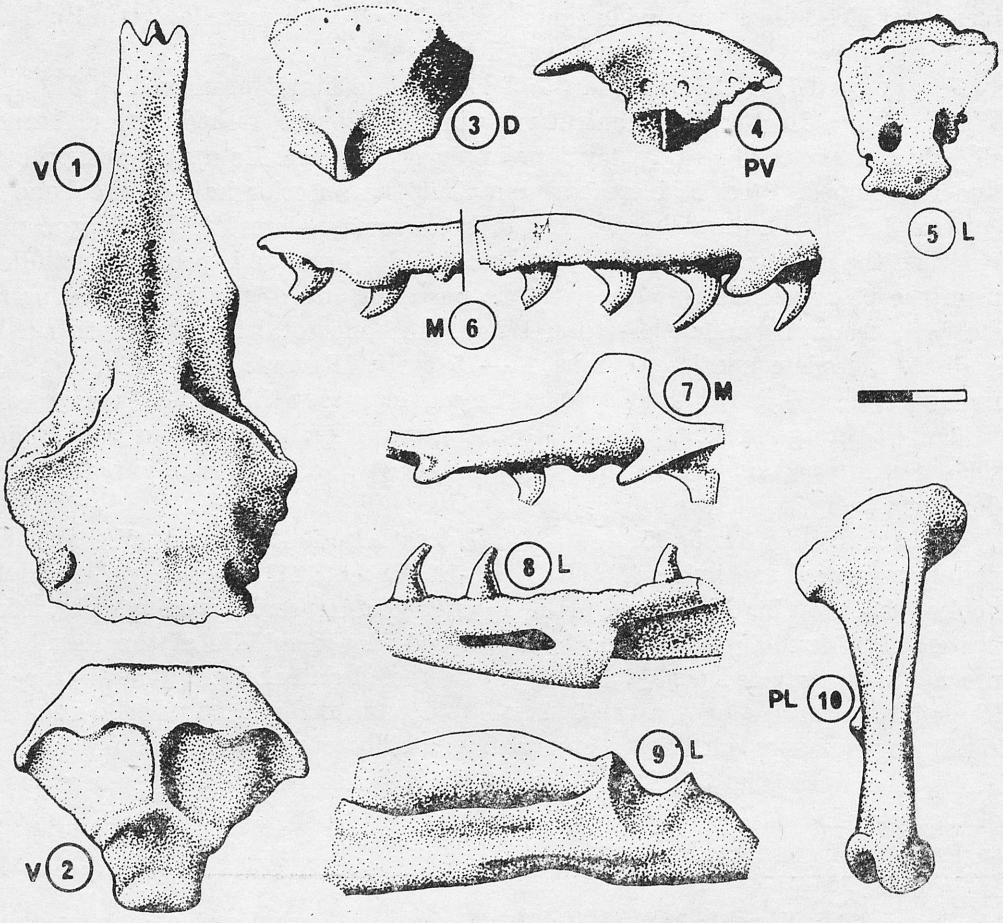


Fig. 36. Cranial bones of *Elaphe longissima* from KG. 1 — basiparasphenoid (ZZSiD, KG-5), 2 — basioccipital (ZZSiD, KG-4), 3 — parietal (ZZSiD, KG-1), 4 — premaxilla (ZZSiD, KG-31), 5 — left prootic (ZZSiD, KG-32), 6 — left maxillae, posterior and anterior fragments (ZZSiD, KG-19 and 20), 7 — left palatine (ZZSiD, KG-23), 8 — left dentary (ZZSiD, KG-29). 9 — left compound bone (ZZSiD, KG-27), 10 — right quadrate (ZZSiD, KG-24). D — dorsal, L — lateral, M — medial, PL — postero-lateral, PV — postero-ventral, V — ventral views, Scale equals 2 mm

terial. Shape of horizontal sheets resembles that of Recent *Elaphe longissima*, but (as in the case of squamosals) correct determination of the species on the basis of nasals is dubious.

Premaxilla (Fig. 34: 9 and 36: 4). Only few bones from GI and KG. Lateral arms long and tapering. Processes on their posterior borders underdeveloped. Vomeral processes short, situated at right angles to nasal process. Nasal process is provided with two broad sheets extending laterally. Ventral openings of premaxillary channels well marked and situated near to each other.

Septomaxilla (Fig. 35: 3). A single well preserved left septomaxilla originates from the RZ material. The sheet-like bone is provided distally with long

and slender ascending nasal process, projected high dorsally. Posterior portion of the sheet is convex. A deep fossa divides anterior portion of the bone and medial lamella, the latter forming a distinct crest. Anterior tip of the bone has a form of bipartite rostrum. Posteriorly, median margin is elongate into a long arm provided with bipartite frontal process.

Mid-trunk vertebrae (Fig. 37: 6—10). In large specimens centrum short, triangular from below. Well developed haemal keel, thick and rounded, rarely thin and sharp (RZ) or flattened (JO), extending from the cotyle posteriorly to the base of the condyle, where it ends in an acute point, which is usually flattened and broadened, forming a spatulate shape of haemal keel when seen from below. Often haemal keel is not well defined anteriorly. Subcentral ridges fairly well developed posterior to parapophyses, but diminishing posteriorly before the base of the condyle. Grooves between the haemal keel and subcentral ridges usually moderate in length. Epizygapophyseal spine usually absent; if present (JO, GI, RZ), it forms a slightly developed callosity rather than a spur-like process. Neural canal usually round in anterior view. Neural spine always strongly overhangs posteriorly and slightly anteriorly. In larger specimens its antero-dorsal margin is almost always thickened (JO, GI, RZ); thickening is usually absent in smaller vertebrae (KG, WA, also Recent: e. g. ZZSiD 20 and 291). Anterior border of zygosphene usually strongly crenate in smaller vertebrae (KG, Recent specimens); in larger vertebrae zygosphene shows various different patterns (crenate, concave with median tubercle, notched crenate), but development of both lateral and median lobes is here indistinct and the zygosphenal border is practically straight in dorsal view (JO, GI, RZ, WA). Postzygapophyseal articular facets are usually of obovate or irregular shape, in large vertebrae often extended laterally. Prezygapophyseal processes relatively long, in large vertebrae obtuse, often with widened ends; in smaller ones slender, acute in shape. Interzygapophyseal ridges moderately developed, parallel to the axis of the centrum. Lateral foramen well marked. Paradiapophyses well developed; division between para- and diapophyseal articular facets usually hardly visible. Parapophysis usually rectangular in lateral view and usually longer than diapophyses, though in some cases inversely (WA). In lateral view parapophyses are shifted anteriorly towards diapophyses. Cotyle rounded or slightly flattened dorso-ventrally. Paracotylar foramina barely seen.

Mensuration. Centrum length (CL) of vertebrae of the fossil *Elaphe longissima* reaches almost eight millimetres in large specimens. I present here measurements of largest vertebrae from some localities. Samples have included 60 vertebrae each; the three ranges successively indicate range of CL, range of CL/NAW ratio, and its mean with standard deviation:

JO: 6.26—7.51 1.06—1.24 1.15±0.04
GI: 4.47—7.46 1.05—1.29 1.14±0.05
WA: 5.09—7.31 1.09—1.23 1.16±0.03
RZ: 7.07—7.97 1.08—1.18 1.14±0.02
KG: 4.95—7.00 1.05—1.30 1.20±0.06

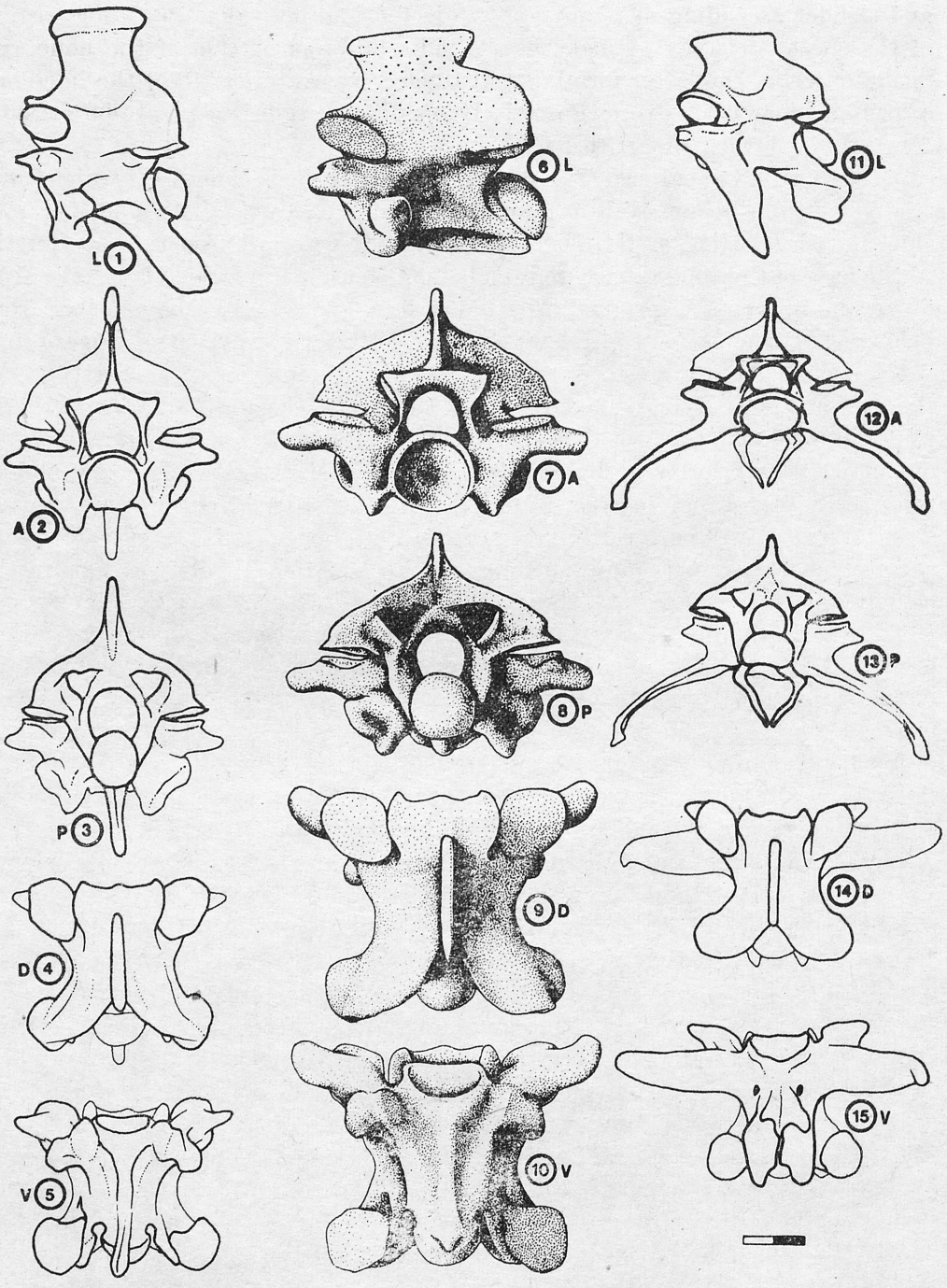


Fig. 37. Vertebrae of *Elaphe longissima* from JO. 1, 2, 3, 4, 5 — cervical vertebra (ZZSiD, JO-55), 6, 7, 8, 9, 10 — trunk vertebra (ZZSiD, JO-201), 11, 12, 13, 14, 15 — caudal vertebra (ZZSiD, JO-938). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

Table XIV

Measurements and ratios of trunk vertebrae of *Elaphe longissima* and *Elaphe* aff. *longissima*

	OR	$\bar{X}\pm SD$	OR	$\bar{X}\pm SD$	OR	$\bar{X}\pm SD$	OR	$\bar{X}\pm SD$
	GI (N = 33)		JO (N = 42)		WA (N = 49)		RZ (N = 33)	
PR-PO	4.74—7.46		6.26—7.51		5.09—7.31		7.11—7.97	
CL	3.81—5.62		4.86—5.80		4.03—5.86		5.75—6.18	
PO-PO	5.50—8.88		7.37—8.72		6.57—8.97		8.73—9.70	
NAW	3.26—5.06		4.18—5.04		3.52—5.14		4.94—5.35	
ZW	2.61—3.85		3.32—4.15		3.16—4.01		3.92—4.33	
CTH	1.73—2.85		2.15—2.90		1.99—2.93		2.64—3.03	
CTW	1.91—2.73		2.29—2.91		2.36—3.05		2.71—3.05	
PR-PR	5.58—9.00		7.50—9.35		6.95—9.29		8.89—9.88	
CL/NAW	1.09—1.20	1.15±0.03	1.11—1.19	1.15±0.03	1.11—1.19	1.15±0.02	1.13—1.17	1.15±0.01
PO-PO/NAW	1.60—1.79	1.68±0.05	1.62—1.92	1.74±0.06	1.56—1.87	1.74±0.06	1.64—1.89	1.77±0.07
CTW/CTH	0.96—1.22	1.12±0.07	0.96—1.13	1.03±0.05	1.01—1.19	1.08±0.04	0.95—1.07	1.02±0.03
ZW/NAW	0.76—0.88	0.83±0.03	0.74—0.96	0.82±0.05	0.75—0.94	0.80±0.04	0.74—0.85	0.88±0.11
PR-PR/PR-PO	1.12—1.33	1.23±0.05	1.13—1.32	1.21±0.05	1.15—1.37	1.27±0.06	1.16—1.36	1.26±0.06
CL/ZW	1.31—1.50	1.40±0.05	1.22—1.56	1.41±0.08	1.22—1.57	1.44±0.08	1.35—1.52	1.44±0.05
PR-PR/NAW	1.69—1.88	1.77±0.05	1.70—1.99	1.80±0.06	1.67—1.97	1.80±0.05	1.75—1.94	1.83±0.06
	KG (N = 24)		JZ (N = 35)		KD (N = 26)			
PR-PO	5.10—7.00		5.52—7.69		5.13—7.68			
CL	4.23—5.33		4.66—7.69		4.24—6.06			
PO-PO	6.28—8.10		6.77—8.98		5.95—8.76			
NAW	3.57—4.78		4.02—5.65		3.49—5.46			
ZW	3.31—4.03		3.18—4.36		2.92—4.51			
CTH	1.81—2.52		1.89—2.65		1.84—3.08			
CTW	2.09—2.74		2.23—2.96		2.15—3.15			
PR-PR	6.20—8.20		7.25—9.32		6.18—9.65			
CL/NAW	1.06—1.20	1.15±0.04	1.05—1.23	1.15±0.06	1.04—1.25	1.15±0.06		
PO-PO/NAW	1.65—1.79	1.70±0.04	1.54—1.86	1.71±0.08	1.55—1.84	1.67±0.07		
CTW/CTH	0.99—1.21	1.12±0.06	0.86—1.34	1.12±0.09	0.92—1.25	1.12±0.08		
ZW/NAW	0.76—0.96	0.87±0.05	0.75—0.92	0.84±0.05	0.73—0.92	0.82±0.04		
PR-PR/PR-PO	1.11—1.37	1.25±0.06	1.06—1.33	1.23±0.06	1.12—1.36	1.25±0.07		
CL/ZW	1.22—1.44	1.33±0.06	1.26—1.56	1.39±0.07	1.25—1.63	1.41±0.08		
PR-PR/NAW	1.67—1.86	1.77±0.06	1.53—1.89	1.77±0.09	1.53—2.02	1.76±0.10		

It can be observed that CL/NAW mean fluctuates about 1.15 value. It is characteristic that mean value CL/NAW for the vertebrae from KG, being smaller on an average than those from the other localities, is higher ($\overline{X} = 1.20$). A full account of numerical data is gathered in the table XIV, which contains measurements of selected vertebrae in order to obtain precisely a mean $\overline{X} = 1.15$. Skeletons of Recent *Elaphe longissima* I have at my disposal have been useless here as CL/NAW ratios of their greatest trunk vertebrae are too high; for instance, mensuration of 60 vertebrae (71—130) from the Polish specimen ZZSiD 291 (ca 130 centimetres long when alive) gives the following: CL range 5.85—6.25, CL/NAW range 1.34—1.47, $\overline{X} = 1.40 \pm 0.03$. It is interesting that the CL/NAW ratio of a much smaller snake from Bulgaria (ZZSiD 20) is distinctly higher: respectively CL range 3.47—3.72, CL/NAW range 1.15—1.22, $\overline{X} = 1.19 \pm 0.03$, $N = 5$; unfortunately, except for these five bones, no other trunk vertebrae are available from this incomplete skeleton (cf. also remarks in Chapter IV, p. 29). For further comments see p. 100.

Intracolumnar variation (Fig. 39). Several axes, preserved in materials from JO and KG, do not differ from those of Recent snakes. Neural spine has a wing-like form, tapering upwards and overhanging posteriorly. A strongly developed spine is present on postzygapophyseal portion of the neural arch. Transverse processes long and slender, projecting posteriorly in lateral view.

Cervical vertebrae (Fig. 37: 1—5) are numerous in majority of the materials. Centrum is shorter and neural arch more vaulted than in trunk vertebrae. Neural spine is much higher than long and overhangs to a similar degree anteriorly and posteriorly. Thickening of the dorsal edge of neural spine occurs sporadically in cervical vertebrae (RZ, here also postero-dorsal portion thickened). Hypapophysis long and slender, usually tapering in lateral view, though occasionally with widened tip (RZ, also a part of Recent snakes). Epizygapophyseal spine occurs rarely as well developed as in trunk vertebrae. Division of paradiapophyses not well marked. Parapophyseal process short, projecting anteriorly; in some exceptional cases a posterior extension of parapophysis is also present (WA).

Posterior trunk vertebrae do not differ much from those of the middle part of the column. Neural spine is somewhat lower, subcentral grooves deeper and haemal keel more expanded dorso-ventrally.

A single cloacal vertebra (JO) has no overhanging neural spine; its anterior and posterior borders are rectangular in lateral view (in living snakes neural spine overhangs). Dorsal branches of lymphapophyses are twice shorter than the ventral ones, these latter being of elongate rhomboid shape in lateral view. Haemapophyses missing.

Caudal vertebrae (Fig. 37: 11—15), numerous in most localities, show intracolumnar variation in their pleurapophyses and neural spines. Pleurapophyses in anterior caudal vertebrae are broad and have obtuse tips, projecting downwards vertically or even slightly posteriorly when seen from the lateral side. In mid-caudal vertebrae slender and acute pleurapophyses project antero-

ventrally; in terminal ones pleurapophyses are more slender and project much more anteriorly than ventrally. Neural spine overhangs posteriorly in anterior vertebrae, in the middle ones its posterior border is usually rectangular in lateral view, and in terminal vertebrae haemapophyses are strongly built and always distinctly widened distally.

Remarks: vide infra (p. 100).

Elaphe aff. *longissima* (LAURENTI, 1768)
(Fig. 38, Table XIV)

Material. — See Table XIII.

The material described below consists of vertebrae from four Early Pleistocene localities: ZB, KD, KA and JZ. Additionally, several cranial bones come from JZ. Material from JZ, recently excavated, has not been earlier worked out. Fossils from the remaining localities have been described previously as follows:

ZB: *Colubridae* indet. — MŁYNARSKI, 1977, p. 18;
(?) *Elaphe* cf. *quatuorlineata* (LACÉPÉDE) — MŁYNARSKI, 1977, p. 18;
Coluber sp. (cf. *robertmertensi* MŁYNARSKI) — MŁYNARSKI, 1977, p. 19;
KD: *Colubridae* indet. — MŁYNARSKI, 1961a, pp. 15—16, pl. VI; 1962, p. 181;
KA: *Colubridae* indet. — MŁYNARSKI, 1961a, p. 16, pl. V; 1962, p. 181;
JZ: cf. *Elaphe* sp. — BOSÁK et al, 1982, Table 1 (p. 221) *.

As for supposed remains of *Elaphe* cf. *quatuorlineata* from ZB, its determination was based on a single palatine bone (MŁYNARSKI, 1977, pp. 18 and 29). This palatine has not been traced in ZZSiD collection, but the presence of *E. quatuorlineata* in ZB, being unconfirmed by vertebrae, is dubious.

These snake remains do not differ drastically from those described above as *Elaphe longissima*. I use here "aff." not because of incertitude of their taxonomic attachment, but in order to stress a certain morphological dissimilarity between the two groups.

Cranial bones. Skull remains from JZ consist of five basiparasphenoids (three of them completely preserved), posterior fragments of two maxillae, two fragmentary dentaries and an almost complete right compound bone. The basiparasphenoids are at first glance identical with those of *Elaphe longissima*, but differ from them in some details. On the ventral side, a furrow extending throughout parasphenoid process is very deep and posteriorly reaches the junction of pterygoid crests. Basisphenoid crest well developed. On the dorsal side, notches for sympathetic nerves are distinct only near lateral borders of the bone, they do not reach sympathetic nerve foramina, the latter situated

* Determination based on a different material than that used in the present study.

forward to anterior foramina of abducens nerves. Maxillary fragments are identical with those of *E. longissima*; they consist of ectopterygoid process, occupying the level of three tooth sockets, and followed posteriorly by two additional sockets. A small compound bone has its medial flange more than twice as high than lateral flange. Antero-dorsal border of the medial flange is steeper and retroarticular process is somewhat more slender than in geologically younger *E. longissima*. The greatest and best preserved dentary fragment has its mental foramen lying at the level of the 10—12th teeth; Meckel's groove closes completely at the level of the 7th tooth.

Vertebrae. The basic difference between vertebrae of *Elaphe longissima* and vertebrae described here is in the shape of postzygapophyseal portions of the neural arch; laminae of the neural arch extend considerably anterior and posterior to postzygapophyses. In consequence, interzygapophyseal ridges are strongly developed, and posterior margins of the neural arch ("aliform processes") project distinctly beyond posterior borders of postzygapophyses. Because of development of the former structures, the narrowing between pre- and postzygapophyses is poorly marked. This pattern is present either in majority of vertebrae (JZ) or at least in large trunk vertebrae (remaining localities). Another characteristic feature of these vertebrae is the shorthness of their prezygapophyseal processes, observed (if preserved) in the majority of the specimens. Haemal keel strongly developed, always rounded and not very broad in dorsal view with exception of several specimens from KA, which have the keels broad and flattened. Epizygapophyseal spine absent or underdeveloped. Anterior border of zygosphene in larger vertebrae usually straight with weakly marked lateral

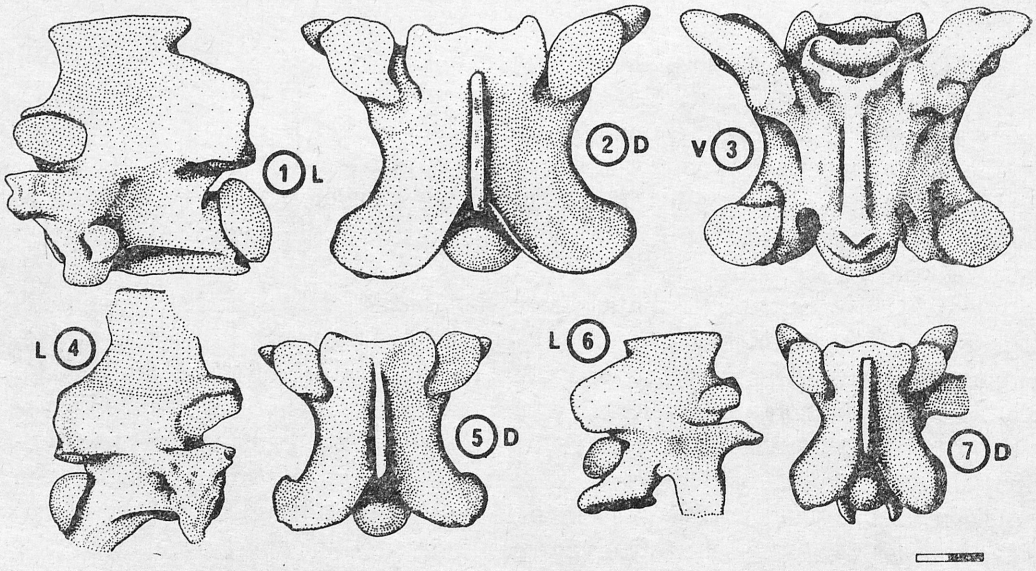


Fig. 38. Vertebrae of *Elaphe* aff. *longissima* from JZ (not catalogued) 1, 2, 3 — trunk vertebra, 4, 5 — cervical vertebra, 6, 7 — caudal vertebra. D — dorsal, L — lateral, V — ventral views. Scale equals 2 mm

Statistical comparison of trunk vertebrae of *Elaphe longissima*, *Elaphe* aff. *longissima*, and *Elaphe paralongissima* sp. n. (data from Tables X and XIV)

	Elaphe longissima GI (N = 33)	*Elaphe longissima* JO (N = 42)	*Elaphe longissima* WA (N = 49)	*Elaphe longissima* RZ (N = 33)	*Elaphe longissima* KG (N = 24)	*Elaphe* aff. *longissima* JZ (N = 35)	*Elaphe* aff. *longissima* KD (N = 26)	*Elaphe paralongissima* W II (N = 27)
Elaphe longissima JO (N = 42)	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p >.05 PR-PR/NAW: p >.05							
Elaphe longissima WA (N = 49)	PO-PO/NAW: p <.01 PR-PR/PR-PO: p <.05 CL/ZW: p <.05 PR-PR/NAW: p >.05	PO-PO/NAW: p >.05 PR-PR/PR-PO: p <.01 CL/ZW: p >.05 PR-PR/NAW: p >.05						
Elaphe longissima RZ (N = 33)	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p <.05 PR-PR/NAW: p <.01	PO-PO/NAW: p >.05 PR-PR/PR-PO: p <.01 CL/ZW: p >.05 PR-PR/NAW: p <.05	PO-PO/NAW: p <.05 PR-PR/PR-PO: p >.05 CL/ZW: p >.05 PR-PR/NAW: p >.05					
Elaphe longissima KG (N = 24)	PO-PO/NAW: p >.05 PR-PR/PR-PO: p >.05 CL/ZW: p <.01 PR-PR/NAW: p >.05	PO-PO/NAW: p <.05 PR-PR/PR-PO: p <.05 CL/ZW: p <.01 PR-PR/NAW: p >.05	PO-PO/NAW: p <.05 PR-PR/PR-PO: p >.05 CL/ZW: p <.01 PR-PR/NAW: p >.05	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p <.01 PR-PR/NAW: p <.01				
Elaphe aff. *longissima* JZ (N = 35)	PO-PO/NAW: p <.05 PR-PR/PR-PO: p >.05 CL/ZW: p >.05 PR-PR/NAW: p >.05	PO-PO/NAW: p >.05 PR-PR/PR-PO: p >.05 CL/ZW: p >.05 PR-PR/NAW: p >.05	PO-PO/NAW: p >.05 PR-PR/PR-PO: p <.05 CL/ZW: p <.01 PR-PR/NAW: p <.05	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p <.01 PR-PR/NAW: p <.01	PO-PO/NAW: p >.05 PR-PR/PR-PO: p <.05 CL/ZW: p <.01 PR-PR/NAW: p >.05			
Elaphe aff. *longissima* KD (N = 26)	PO-PO/NAW: p >.05 PR-PR/PR-PO: p >.05 CL/ZW: p >.05 PR-PR/NAW: p >.05	PO-PO/NAW: p <.01 PR-PR/PR-PO: p <.05 CL/ZW: p >.05 PR-PR/NAW: p <.05	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p >.05 PR-PR/NAW: p <.05	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p =.05 PR-PR/NAW: p <.01	PO-PO/NAW: p >.05 PR-PR/PR-PO: p >.05 CL/ZW: p <.01 PR-PR/NAW: p >.05	PO-PO/NAW: p <.05 PR-PR/PR-PO: p >.05 CL/ZW: p <.01 PR-PR/NAW: p >.05		
Elaphe paralongissima W II (N = 27)	PO-PO/NAW: p <.05 PR-PR/PR-PO: p >.05 CL/ZW: p =.05 PR-PR/NAW: p <.01	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p >.05 PR-PR/NAW: p <.01	PO-PO/NAW: p <.01 PR-PR/PR-PO: p <.01 CL/ZW: p >.05 PR-PR/NAW: p <.01	PO-PO/NAW: p <.01 PR-PR/PR-PO: p <.01 CL/ZW: p >.05 PR-PR/NAW: p <.01	PO-PO/NAW: p <.01 PR-PR/PR-PO: p <.05 CL/ZW: p <.01 PR-PR/NAW: p <.01	PO-PO/NAW: p <.01 PR-PR/PR-PO: p >.05 CL/ZW: p <.05 PR-PR/NAW: p <.01	PO-PO/NAW: p <.05 PR-PR/PR-PO: p <.05 CL/ZW: p >.05 PR-PR/NAW: p <.01	

and median lobes (KA, KD, ZB); in specimens from JZ always distinctly crenate with well defined three lobes. Neural spines are damaged in vertebrae from KA, KD and ZB, in these from JZ neural spine is as high as long, slightly overhanging anteriorly and strongly posteriorly. Zygapophyseal articular facets relatively large, these of prezygapophyses usually round or oval-shaped. Parapophyses longer than diapophyses and shifted anteriorly in lateral view. Lateral foramina situated within deep depressions, dorsally covered by strongly developed interzygapophyseal ridges. Paracotylar and subcentral foramina weakly marked. Cotyle large and round.

Vertebrae from remaining columnar parts resemble these of *Elaphe longissima*, but some of them have posteriorly strongly expanded "aliform process", even to a higher degree than in trunk vertebrae. Considerable development of postzygapophyseal area of neural arch can be observed in a cervical vertebra from KD and caudal vertebrae from JZ.

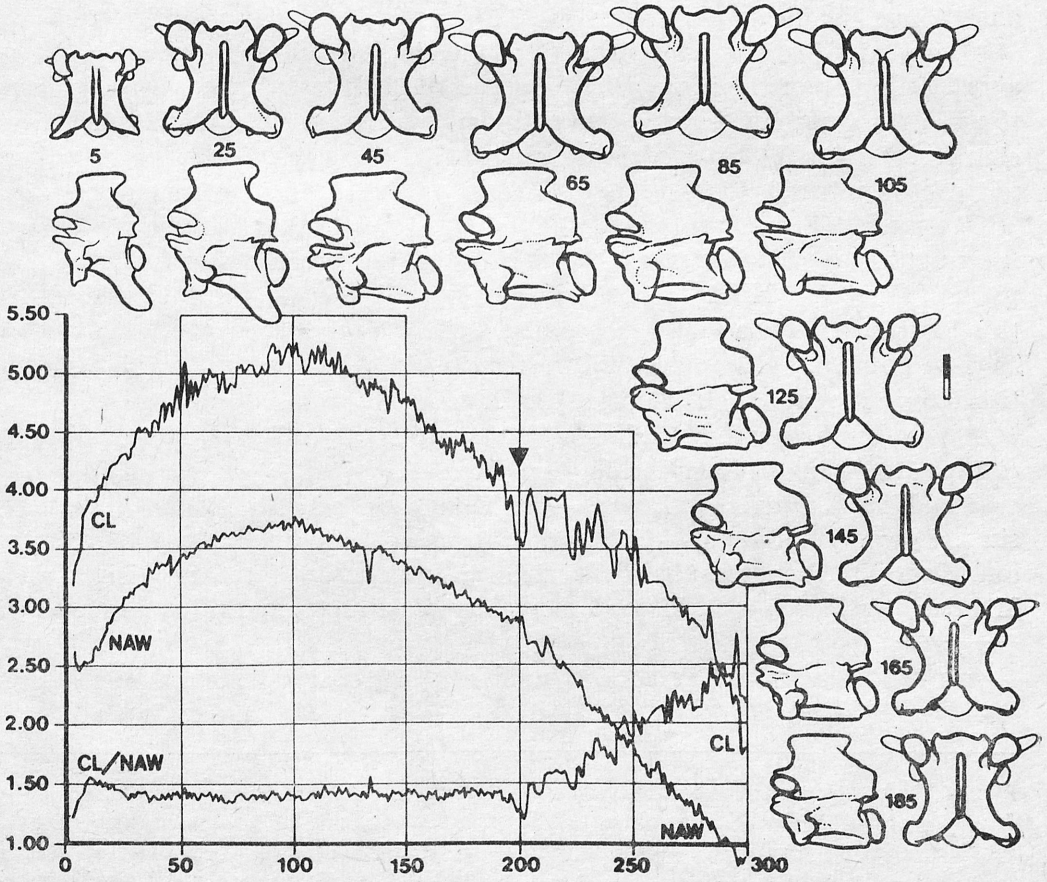


Fig. 39. Intracolumnar variation in CL, NAW and CL/NAW of vertebrae of *Elaphe longissima* (ZZSiD 291). Vertical axis — dimensions in mm; horizontal axis — no. of succeeding vertebrae; black triangle — position of cloacal vertebrae. Figures show dorsal and lateral views of every 20th precaudal vertebra. Scale equals 2 mm

Mensuration. Measurements and ratios of vertebrae from JZ and KD are contained in Table XIV. Sampling of vertebrae from KD has been very difficult because of destruction of the material; in this connection measurement taken from the fossils cannot be accurate.

Table XV shows results of statistical comparison among samples from 7 localities dated from the Early Pleistocene until Holocene, thus including both *Elaphe longissima* and *E.* aff. *longissima*. It can be seen from the table that differences between the youngest and oldest forms, representing different morphological patterns, are not higher (even lower) than differences between forms originating from localities of closer age. For instance, there are no significant differences between Early Pleistocene and Holocene snakes — JZ vs. JO: $p>.05$ for all four ratios, similarly for KD vs. GI. On the other hand, high differences can be observed among vertebrae from localities of much closer age than the above pairs — for GI vs. RZ we have highly significant differences ($p<.01$) for two ratios, significant difference ($p<.05$) for one ratio, and only once a non-significant difference ($p>.05$); similarly for GI vs. WA etc.

The above analysis demonstrates that in the long history of *Elaphe longissima*, lasting from the Early Pleistocene until the present time, basic proportions of its vertebrae have not varied significantly in spite of morphological changes. I suppose that variability observed between particular samples does not exceed intraspecific variability among snakes living contemporaneously.

Remarks (Fig. 40). Fossil remains of *Elaphe longissima* have been reported from numerous sites in Central Europe. The oldest record comes from the Uppermost Miocene (MN 13) of Polgárdi, Hungary. Several cranial bones from this locality have been described as belonging to an extinct species, *Zamenis kormosi* Bolkay (1913, p. 224, pl. 12: Figs. 4—8); these remains were later identified by Szunyoghy (1932, p. 10) as *Elaphe longissima*.

The only Pliocene find of *E. longissima* was reported by Szunyoghy (supra cit., p. 10) from Beremend, Hungary (MN 16).

In addition, remains of *E. longissima* have been found in several Quaternary sites: Lower Pleistocene — Betfia * in Rumania (Szunyoghy, 1932, p. 10) and Deutsch Altenburg-2, 4 in Austria (Rabeder, 1974, p. 148, Fig. 1: 1), Middle Pleistocene — St. Margarethen, Austria (Rabeder, 1977a, p. 92, pl. 1:

* Betfia = Püspökfürdö of Bolkay (1913) and Szunyoghy (1932). In older literature Betfia is also known by names Episcopia or Somlyó-hegy.

Fig. 40. Past and present Central European distribution of *Elaphe longissima*. Abbreviations of names of Polish localities: see Fig. 1. Abbreviations of names of foreign localities: BD — Beremend, BO — Brassó, BT — Betfia, DA — Deutsch Altenburg-2, 4, EB — Euerwanger Bühl, LO — Lobsing, PI — Pisede, PL — Polgárdi, SM — St. Margarethen, WE — Weimar-Ehringsdorf, TA — Taubach. The area of present distribution of *Elaphe longissima* is dotted (after Arnold and Burton, 1978, and other sources); 19th century localities of the occurrence of *Elaphe longissima* in Poland and southern Zealand are indicated by asterisks. For further

comments see p. 100

RZ
WA
ZB, ZA
KA, KI
KG
KD
RA
JZ
ZD
JO
ND, ZS, CI, GI
PI
TA
WE
EB
LO
DA
SM
PL
BT
BO
BD

Fig. 11; 1977b, p. 117) and Brassó, Rumania (SZUNYOGHY, 1932, p. 10); Upper Quaternary (all localities in Germany) — Weimer-Ehringsdorf and Taubach (MŁYNARSKI and ULLRICH, 1975, p. 139; 1977, p. 168), Euerwanger Bühl (MARKERT, 1975, pp. 220—223; 1976, p. 76) and Pisede (PETERS, 1977, pl. 2: Figs. 17 and 24, pl. 3: Fig. 1). With exception of Upper Quaternary records, all descriptions have been based exclusively on skull bones.

Cranial bones described as belonging to an extinct snake, *Coluber lobsingensis* HELLER (1960, pp. 27—28, pl. 3: Figs. 14 and 15), from the Upper Pleistocene of Lobsing, Germany, seem to represent — judging on the basis of HELLER's (supra cit.) illustrations — simply *Elaphe longissima*.

Present range of *E. longissima* is restricted to the southern part of Europe, excluding the Iberian Peninsula; the south-eastern part of Poland (49°—50°N) is presumably the northernmost area inhabited by this thermophilous reptile. Fossil records indicate that during warmer periods of the Quaternary *E. longissima* invaded areas lying far northwards from its present range. Northernmost fossil localities of *E. longissima* in Poland, WA and RZ, lie at the latitude ca. 52.5°N; in Germany, its northernmost fossil locality, Pisede (PETERS, 1977), is situated at about 54°N.

History of dispersal of this snake in Central Europe during Atlantic Stade of the Holocene, though indirectly, is especially well documented. Older herpetological literature provides interesting data on occurrence of isolated insular colonies of *Elaphe longissima* lying northward from bounds of its present continuous range. These colonies, restricted to small areas of warm microclimate, surely were not invaders from the South, but — on the contrary — remnants (so called xerothermic relicts) of wider Holocene population of *E. longissima*. In Poland, even in latter part of the 19th century, *E. longissima* inhabited several localities in the Kraków—Wieluń Upland (ca. 51°N) (e. g. WAŁECKI, 1883; cf. also BOCHEŃSKI et al., 1968). Occurrence of *E. longissima* in Danish Zealand (ca. 56°N) until 1863 (PFAFF, 1945, cit. after DEGERBØL and KROG, 1951) indicates that during the Holocene the continuous range of this reptile must have reached at least the southern shore of the Baltic Sea.

Genus *Coronella* LAURENTI, 1768

Coronella austriaca LAURENTI, 1768
(Figs. 41 and 42, Table XVI)

Material. — Fossil remains of *Coronella austriaca*, consisting almost exclusively of trunk vertebrae, originate from the following localities: ZB — 3 vertebrae, KI — 26, ZA — 2, KD — 17, KA — 6, KG — at least 30, ND — 3. Moreover, material from KG contains 6 basioccipitals, one left frontal and one right quadrate.

So far, fossil remains of this snake have been mentioned from only one locality in Poland, i. e. KG:

Coronella cf. *austriaca* (LAURENTI) — MŁYNARSKI, 1977, p. 21;

Coronella austriaca (LAURENTI) — SZYNDLAR, 1981, pp. 87—89, Fig. 11.

In fact, *C. austriaca* occurred in six other sites; presumably because of small size of its bones presence of this snake has not been noticed earlier.

Basioccipital (Fig. 41: 2) Six completely preserved bones, described earlier by SZYNDLAR (1981, p. 87, Fig. 11: 1). The bone is rounded in ventral view, approximately as long as wide. Basioccipital and median crests present, but weakly developed. Basioccipital process absent. Occipitocondylar tubercle moderately separated. Basioccipital tubercle underdeveloped.

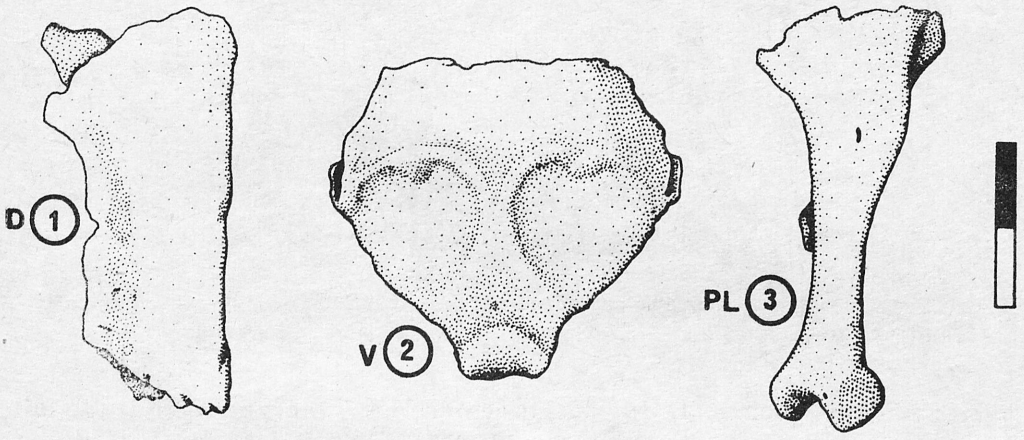
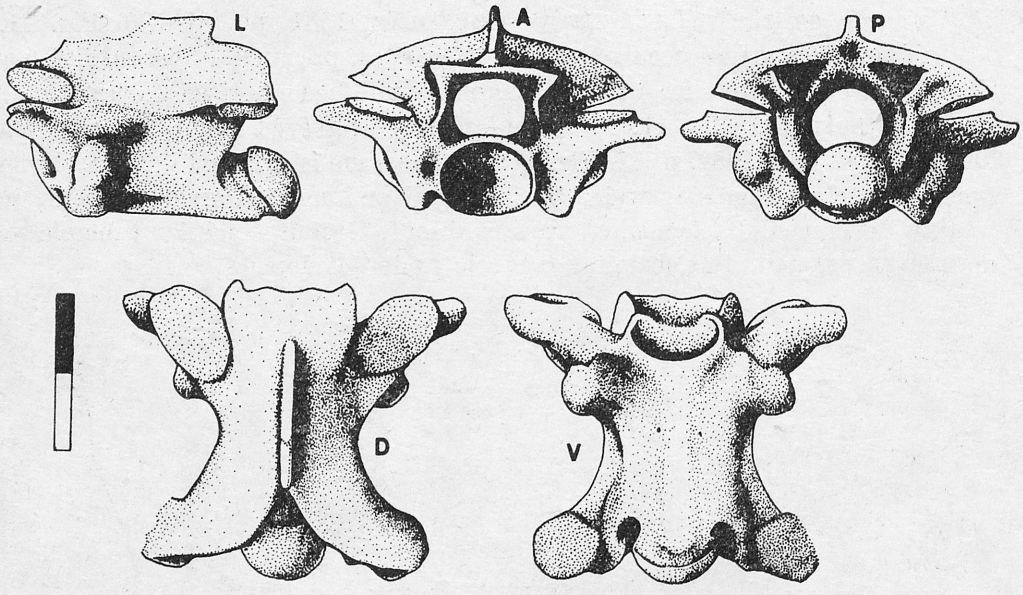


Fig. 41. Cranial bones of *Coronella austriaca* from KG. 1 — left frontal (ZZSiD, KG-8007) 2 — basioccipital (ZZSiD, KG-8001), 3 — right quadrate (ZZSiD, KG-8008). D — dorsal, PL — postero-lateral, V — ventral views. Scale equals 2 mm

Frontal (Fig. 41: 1). A single left bone, completely preserved, not described previously. Frontal aperture round in cross section. Septomaxillary process small, tapering in anterior view, and rounded in median view. Premaxillary processes moderately developed: external process tapering, internal process somewhat wider in anterior view.

Quadrate (Fig. 41: 3). A single right bone, completely preserved, not described previously. The bone is relatively short and broad. Stapedial process prominent and elongate. Antero-dorsal corner of the bone produces large robust spur, projecting inside. Trochlea quadrati strongly built, very wide in posterior view.

Vertebrae (Fig. 42). Vertebrae of *Coronella austriaca* are of small size, with CL rarely exceeding value 3.00 mm in adult specimens. In dorsal view, because of strong narrowing in the middle of the vertebral centrum together with broad extension of postzygapophyses, vertebrae have peculiar X-like shape. Centrum is moderately long, cylindrical, almost completely devoid of haemal keel, subcentral grooves and subcentral ridges alike; only anteriormost and posteriormost trunk vertebrae are provided with weakly defined, wide and rounded keel. Neural arch extremely strongly flattened, without epizygapophyseal



Figl 42. Trunk vertebra of *Coronella austriaca* from KG (ZZSiD, KG-8050). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

spines; postzygapophyseal area of the neural arch is downswept. Neural canal somewhat square in outline from the front, usually narrower than strongly depressed condyle. Neural spine extremely low, in some cases almost underdeveloped, usually without anterior and posterior overhangs; slight posterior overhangs can be observed in some vertebrae of Recent examples (ZZSiD 293) and those from KG, KA and ZB. Zygosphene flat, a little wider than the cotyle. In dorsal view, zygosphene usually crenate, with lateral lobes always projected forwards anterior to the median lobe; sometimes the median lobe is notched crenate (some vertebrae from KG and KD) or practically absent (KA). Zygapophyseal articular facets always relatively large. Postzygapophyseal facets usually round; prezygapophyseal facets round or oval. Prezygapophyseal processes short, for the most part obovate (Recent: ZZSiD 18, 293, 348; KG, KA), rarely acute (KD, KI). Interzygapophyseal ridges prominent in postzygapophyseal region, but not overly developed. All foramina (subcentral, lateral and paracotylar) always well marked; paracotylar foramina usually of large size. Paradiapophyses weakly divided into parapophyseal and diapophyseal portions; in anterior view, paradiapophyses usually strongly expanded laterally. Cotyle oblique, distinctly separated from the centrum by a long neck.

Remarks. From outside Poland fossil records of *Coronella austriaca* are restricted to younger Quaternary: Brassó in Rumania (Bolkay, 1913, p. 225), Breitenberghöhle, Germany (Brunner, 1957, p. 377, Fig. 16: 1), Bacho Kiro, Bulgaria (Młynarski, 1982, p. 30), Dietfurt, Spitzbubenhöhle and Euerwanger

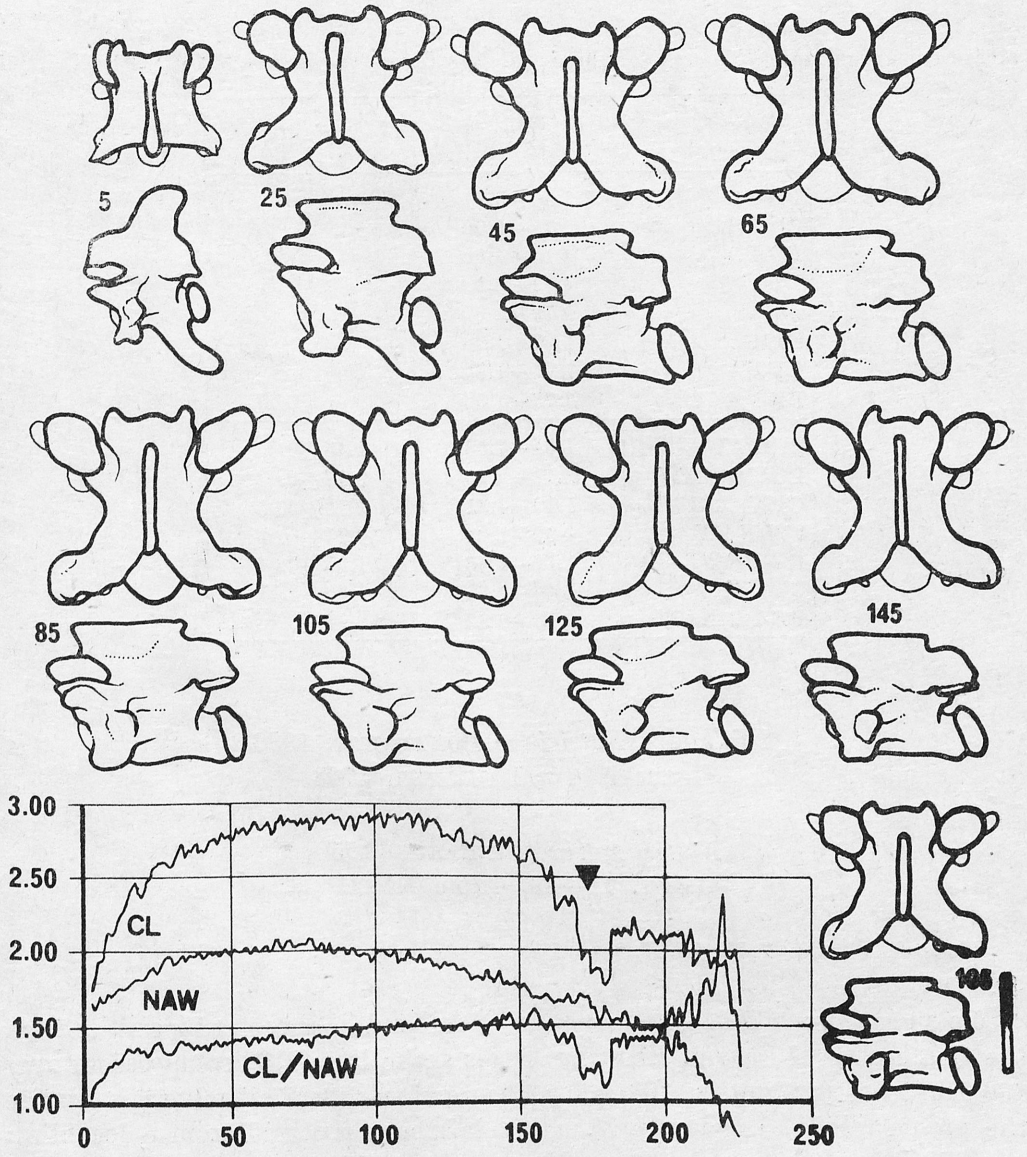


Fig. 43. Intracolumnar variation in CL, NAW and CL/NAW of vertebrae of *Coronella austriaca* (ZZSiD 293). Vertical axis — dimensions in mm; horizontal axis — no. of succeeding vertebrae; black triangle — position of cloacal vertebrae. Figures show dorsal and lateral views of every 20th precaudal vertebra. Scale equals 2 mm

Bühl in Germany (MARKERT, 1975, pp. 220—224; 1976, pp. 73—76) as well as Pisede, Germany (PETERS, 1977).

Presently, *C. austriaca* is widespread in Europe, northwards reaching areas of Southern Scandinavia. All known fossil localities of this snake are included in its present range.

Table XVI

Measurements and ratios of trunk vertebrae of Recent *Coronella austriaca* (ZZSiD 293) (N = 60)

	OR	$\overline{X} \pm SD$
PR-PO	3.50—3.77	
CL	2.78—2.96	
PO-PO	4.13—4.50	
NAW	1.89—2.10	
ZW	1.72—2.00	
CTH	1.06—1.28	
CTW	1.34—1.52	
PR-PR	4.23—4.58	
CL/NAW	1.34—1.53	1.45±0.05
PO-PO/NAW	2.11—2.25	2.17±0.03
CTW/CTH	1.10—1.31	1.18±0.05
ZW/NAW	0.90—1.04	0.96±0.03
PR-PR/PR-PO	1.12—1.28	1.21±0.04
CL/ZW	1.40—1.69	1.50±0.07
PR-PR/NAW	2.15—2.32	2.24±0.04

Subfamily *Natricinae* Bonaparte, 1838
Genus *Natrix* Laurenti, 1768

Natrix natrix (Linnaeus, 1758)
(Figs. 44—49, Table XVIII)

Material. — See Table XVII.

Fossil remains of *Natrix natrix* have been found in almost all localities from the Quaternary of Poland. Remains of this snake from KG, composed of over 100 000 bones (Szyndlar, 1981), form more than 2/3 of all materials used in the present study. Previously *N. natrix* has been reported from 8 localities:

ZB: *Natrix* cf. *natrix* (L.) — Młynarski, 1977, p. 18;
KI: *Natrix* cf. *natrix* (L.) — Młynarski, 1977, p. 19;
ZA: *Natrix* cf. *natrix* (L.) — Młynarski, 1977, p. 20;
KG: *Natrix* cf. *natrix* (L.) — Młynarski, 1977, p. 20;
Natrix natrix (L.) — Szyndlar, 1981, pp. 91—93, Figs. 13, 14;
Palaeomalpolon borealis gen. sp. n. — Szyndlar, 1981, pp. 89—90, Fig. 12;
ZY: *Natrix natrix* (L.) — Młynarski in Bałuk et al., 1979, p. 122;
NI: *Natrix natrix* (L.) — Kowalski, 1961;
GI: *Natrix natrix* (L.) — Młynarski, 1961b, pp. 2—4, pl. 1, 2;
JO: *Natrix natrix* (L.) — Młynarski in Kowalski et al., 1963, pp. 10—11.

Table XVII

List of materials of *Natrix natrix*

	ZB	KD	KA	KI	ZA	KG	ZY	RZ	NI	RA	JO	GI	DS
frontal (R)												2	
——— (L)												3	
parietal						37					1	3	
supraoccipital												1	
exoccipital (R)												1	
basioccipital						22					1	7	
prootic (R)						1						1	
——— (L)												1	
basiparasphenoid					1	145					3	4	
maxilla (R)					1	>17						4	
——— (L)					2	>17							
pterygoid (R)						>2							
——— (L)						>4							
ectopterygoid (R)						>1						1	
——— (L)						>2						3	
palatine (R)					1	>2						1	
——— (L)					1	>2						1	
squamosal												3	
quadrate (R)						>3					1	1	
——— (L)						>2						2	
compound bone (R)						25						1	
——— (L)						28						2	
dentary (R)					2	±240						1	
——— (L)					2						1		
vomer (L)												1	
premaxilla						5						2	
precaudal vertebrae	79	94	64	203	>2000	±106500	7	2	1	10	105	1357	>48
caudal vertebrae	8		1	3	>46								
ribs											>10	>100	

Frontal (Fig. 44: 1). Five bones from GI. Frontal aperture round in cross section. Septomaxillary process distinct, with widening distal portions. Prefrontal process broad and thin, weakly developed. Anterior border of the bone convex in dorsal view.

Parietal (Fig. 44: 2 and 45: 1). Several complete bones from GI and JO, and about 40 fragments from KG. Postorbitals (fused anteriorly with parietal) form distinct crests extending throughout descending parts of the parietal. On dorsal side of the parietal a median furrow is present, especially deep near its posterior border. Parietal crests do not converge on each other before reaching posterior border of the bone. Anterior border V-shaped in dorsal view.

Supraoccipital (Fig. 44: 10). A single supraoccipital from GI is fused with a parietal and prootics. Sagittal crest and occipital crests well developed; the latter distinctly dominate the former in posterior view. Supraoccipital foramina not seen.

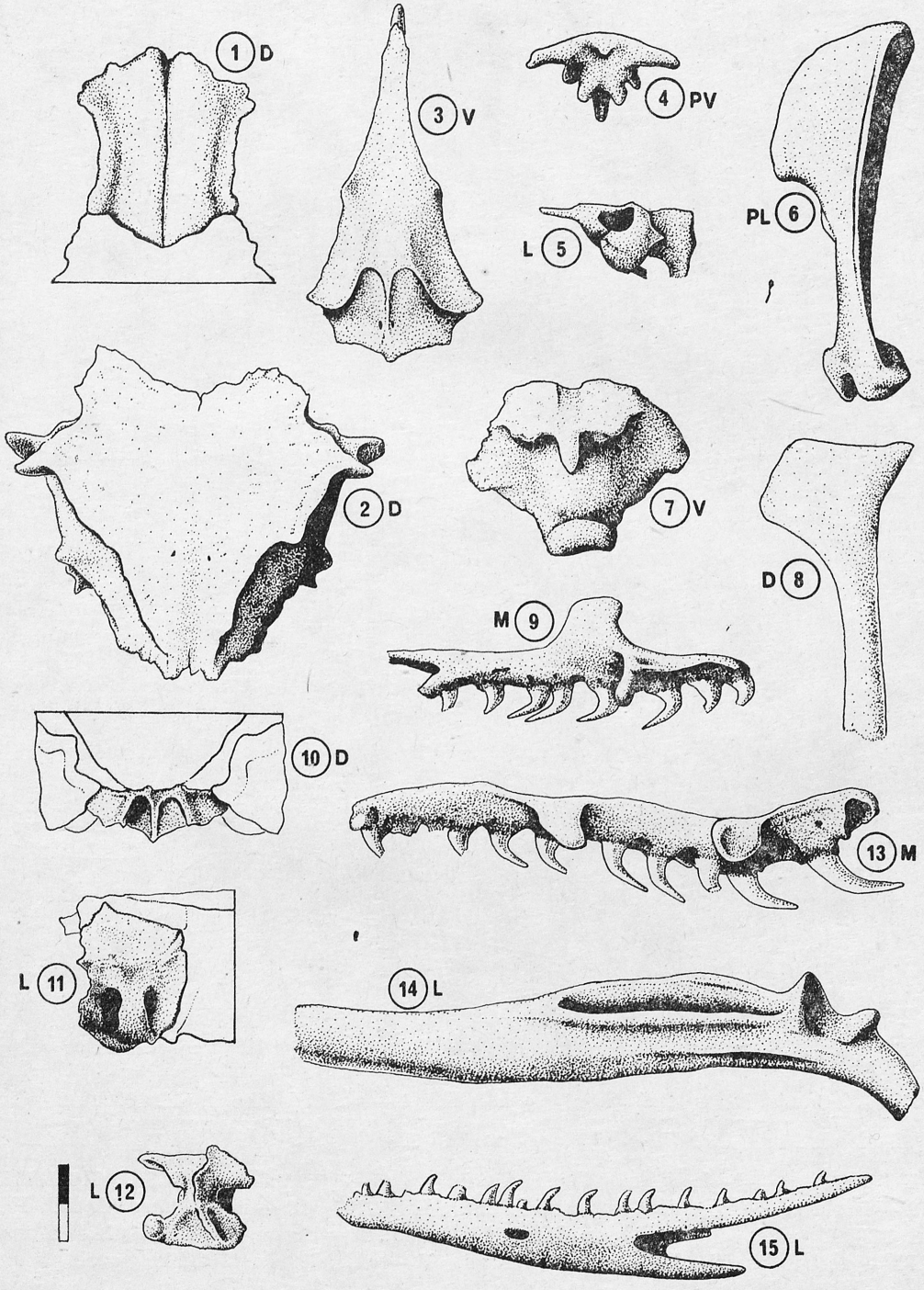
Exoccipital (Fig. 44: 12). A single right bone from GI, before preparation fused with a supraoccipital and a prootic. Occipital crest strongly developed. Anterior border of the exoccipital, being the posterior wall of fenestra ovalis, forms a sinus deeply penetrated into the bone. Between the dorsal end of the occipital crest and postero-dorsal portion of circumfenestral crest a solid bony bar is present, covering posteriorly recessus scalae tympani. Vagus-hypoglossal nerve foramen, accompanied by at least one additional foramen, is located in a furrow before the dorsal end of the occipital crest. Several small foramina can be observed in recessus scalae tympani, one of them probably being the glossopharyngeal nerve foramen. Another small foramen is present before the exoccipital condyle. Parotic process strongly developed, extending backward in lateral view.

Basioccipital (Fig. 44: 7 and 45: 7). Numerous bones from KG, GI and JO. The bones are usually wider than long. Basioccipital crest distinct; basioccipital process strongly developed, extending far backward in dorsal view. Median crest absent. Basioccipital tubercles well developed, but indistinctly separated. Occipitocondylar tubercle strongly built, distinctly separated from the bone.

Prootic (Fig. 44: 11 and 45: 4). Two well preserved right bones from KG and GI. Posterior border of the bone, forming anterior wall of fenestra ovalis, does not possess a distinct recess. Supraoccipital crest prominent. A bar dividing orifices for rami of trigeminal nerves well developed, rectangular. Orifice of mandibular branch of the trigeminal nerve forms a broad concavity after

Fig. 44. Cranial bones of *Natrix natrix* from JO and GI. 1 — frontals (ZZSiD, GI-500 and 501), 2 — parietal (ZZSiD, GI-506), 3 — basiparasphenoid (ZZSiD, GI-520), 4 — premaxilla (ZZSiD, GI-545), 5 — left vomer (ZZSiD, GI-544), 6 — right quadrate (ZZSiD, GI-537), 7 — basioccipital (ZZSiD, GI-511), 8 — left ectopterygoid (ZZSiD, GI-528), 9 — left palatine (ZZSiD, GI-532), 10 — supraoccipital (ZZSiD, GI-509), 11 — right prootic (ZZSiD, GI-518), 12 — right exoccipital (ZZSiD, GI-510), 13 — right maxilla (ZZSiD, GI-524), 14 — left compound bone (ZZSiD, GI-540), 15 — left dentary (ZZSiD, JO-1009). D — dorsal, L — lateral, M — medial, PL — nostero-lateral, PV — postero-ventral, V — ventral views. Scale equals 2 mm

the dividing bar. In the bone from GI there is a vertical groove below the concavity; the groove is absent in the prootic from KG. Orifice for maxillary branch of the trigeminal nerve forms a large and round foramen; somewhat smaller



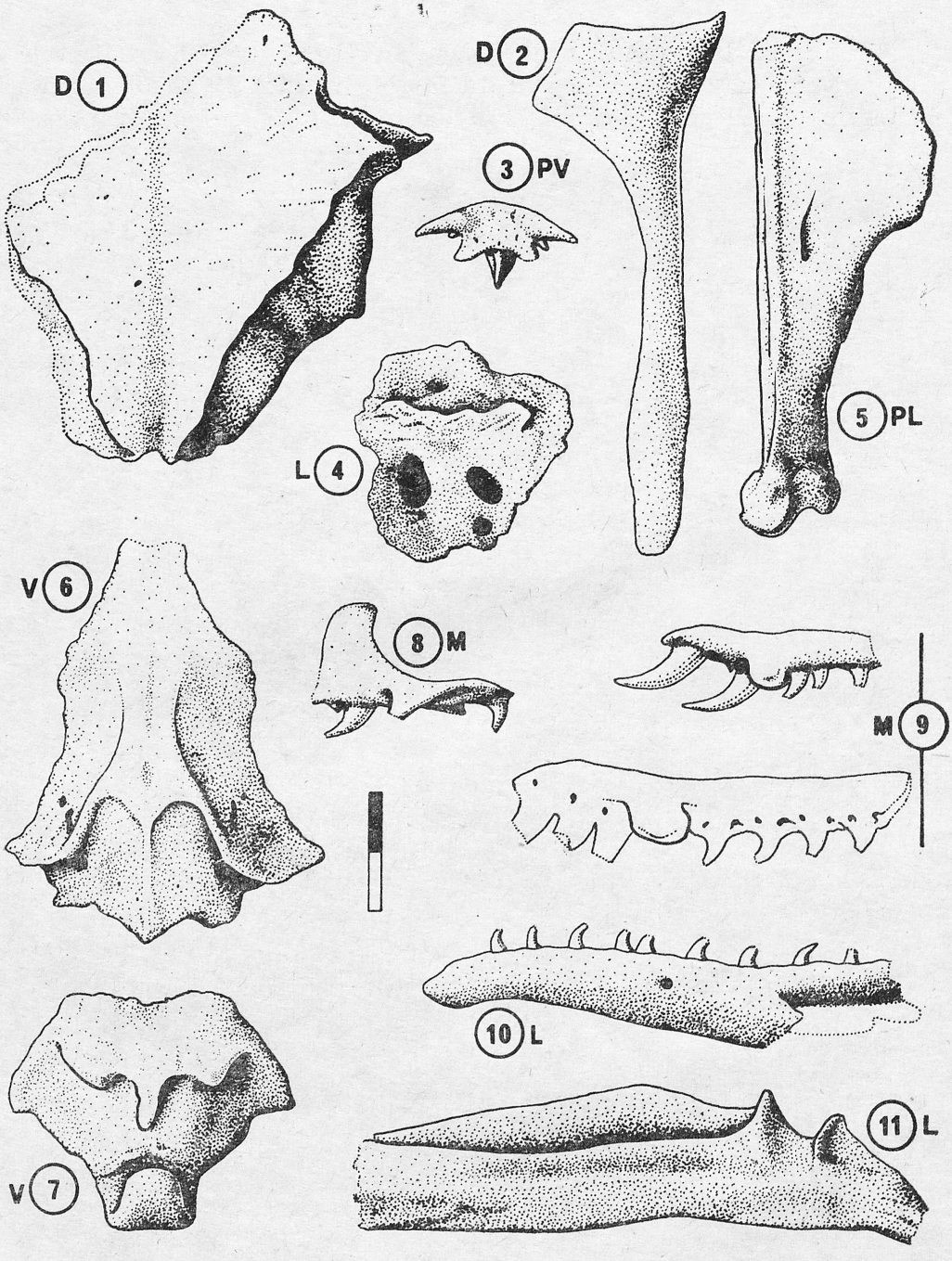


Fig. 45. Cranial bones of *Natrix natrix* from KG. 1 — parietal (ZZSiD, KG-10000), 2 — left ectopterygoid (ZZSiD, KG-10171), 3 — premaxilla (ZZSiD, KG-10176), 4 — right prootic (ZZSiD, KG-10165), 5 — left quadrate (ZZSiD, KG-10174), 6 — basiparasphenoid (ZZSiD, KG-10055), 7 — basioccipital (ZZSiD, KG-10032), 8 — left palatine (ZZSiD, KG-10173), 9 — left maxillae, posterior fragments (ZZSiD, KG-10167), 10 — left dentary (ZZSiD, KG-10178), 11 — left compound bone (ZZSiD, KG-10175). D — dorsal, L — lateral, M — medial, PL — postero-lateral, PV — postero-ventral, V — ventral views. Scale equals 2 mm

foramen for sympathetic nerve is located below (KG; Recent snakes). In the bone from GI both foramina are covered by the anterior margin of the central bar and not seen in lateral view. Very small facial nerve foramen is situated centrally in the concavity after the central bar.

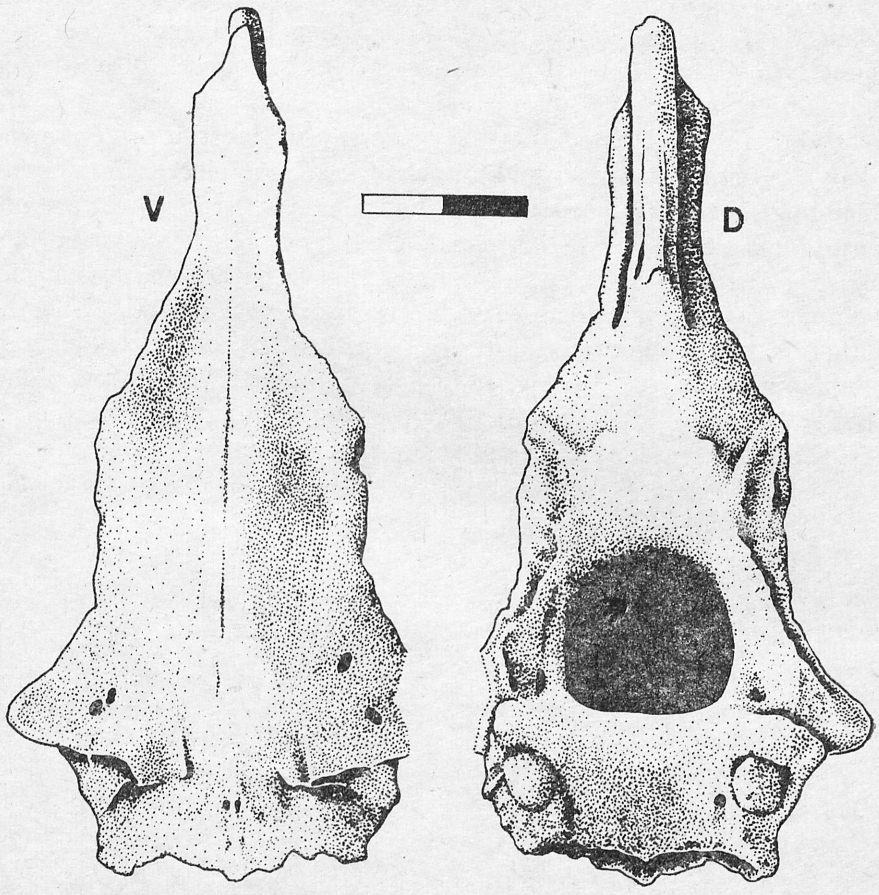


Fig. 46. Basiparasphenoid of *Natrix natrix* from KG (ZZSiD, KG-110000) (previously described as *Palaeomalpolon borealis* by SZYNDLAR, 1981; ex no. RF/290/80). D — dorsal, V — ventral views. Scale equals 2 mm

Basiparasphenoid (Fig. 44: 3, 45: 6, 46, 47: 1, and 48). Basiparasphenoids of *Natrix natrix* come from ZA, KG, JO and GI. The bones are characterized by considerable morphological variability, especially well seen in very abundant material — above 140 bones — from KG. One basiparasphenoid from KG has been described earlier as belonging to a new genus and species, *Palaeomalopolon borealis* SZYNDLAR (1981, p. 89). This allocation, based only on general shape of the bone, was erroneous (for further comments vide infra). Basiparasphenoid of *Natrix natrix* has usually the shape of an elongated triangle. Distinct pterygoid processes are displaced up to the posterior margin of the bone. Suborbital flanges moderately developed with exception of a single bone from

ZA where the flanges project far aside. Pterygoid crests strongly inclined posteriorly; in one case (the bone from ZA) the crests are provided with tubercular processes. Basipterygoid crest distinct, very rarely absent (ZA; several bones from KG including "*Palaeomalpolon*"; Recent ZZSiD 323). Vidian canal always very short. Posterior orifice of Vidian canal situated near the posterior border of the bone; sometimes cerebral foramen is distinctly separated off (one bone from GI and several bones from KG). A groove is often present between posterior orifice of Vidian canal and the margin of the bone. Anterior orifice of Vidian canal, located anteriorly to pterygoid crest, is sometimes accompanied by a foramen for pterygoid branch of trigeminal nerve. Few bones from KG including that of "*Palaeomalpolon*" have shallow furrows between anterior and posterior foramina of Vidian canal. On dorsal side of the bone, anterior foramina for abducens nerves and foramina for sympathetic nerves are located in a common depression closely to each other; external orifices of notches for sympathetic nerves are covered dorsally by prominent, but rarely entirely closed, bony appendices (see also Fig. 48 for location of artery and nerve foramina).

Maxilla (Fig. 44: 13, 45: 9, and 47: 3). Several complete bones have been ound in the Holocene localities; numerous bones from older localities, chiefly

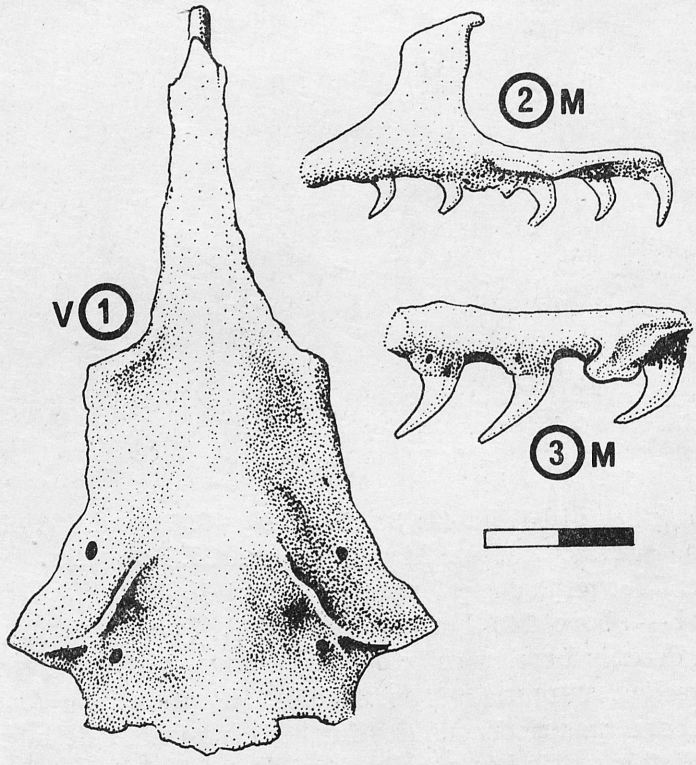


Fig. 47. Cranial bones of *Natrix natrix* from ZA. 1 — basiparasphenoid (ZZSiD, ZA-311), 2 — left palatine (ZZSiD, ZA-312), 3 — left maxilla, anterior fragment (ZZSiD, ZA-313). M — medial, V — ventral views. Scale equals 2 mm

from KG, are preserved only in fragmentary state. The bone is elongate, distinctly curved in dorsal or ventral view. The bone is opisthomegadontic, the 2—4 (usually three) last teeth always considerably greater than the previous ones. Complete maxillae from GI have 21 teeth each (Recent: 20—23). Prefrontal process, located at the level of the 10th and 11th teeth, projects laterally; a tip on its intero-posterior end protrudes backward. Ectopterygoid process, situated at about the 20th tooth, is tapering and projecting intero-anteriorly.

Pterygoid. The fossil materials do not contain any complete bones; only a few small fragments, for the most part representing anterior portions of the bones, originate from KG. Straight tooth-ramus occupies 2/3 of the bone length; toothless posterior portion of the bone curved aside after the last tooth (observation on Recent materials). Pterygoid crest well developed, distinctly inclined laterally. Teeth, rather big and all of equal size, are curved medially and thus well seen from above. Ectopterygoid process prominent.

Ectopterygoid (Fig. 44: 8 and 45: 2). Several bones from GI and KG. External and internal rami of maxillary articulation are weakly separated from each other, forming together a sheet of irregular tetragon shape. In dorsal view, stem of the bone is slightly curved laterally; its posterior portion widened. In lateral view, the bone is distinctly curved upward.

Palatine (Fig. 44: 9, 45: 8, and 47: 2). Complete palatines are known from GI, moreover fragmentary bones (posterior portions missing) have been found in KG and ZA localities. The bone is isodontic; number of teeth in completely preserved specimens (GI) 16 (Recent: 15—16). Posterior edge of maxillary process and anterior edge of vomerine process are opposite. Maxillary process relatively short and widening at the tip; maxillary nerve foramen situated on the anterior edge of its elongate (antero-posteriorly) base. Vomerine process, located between the level of the 7th and 9th teeth, inclined anteriorly; the area before the process is distinctly concave in dorsal view.

Squamosal. 3 bones from GI probably belonged to *Natrix natrix*, though reference to the species based on squamosal cannot be certain.

Quadrate (Fig. 44: 6 and 45: 5). Several bones from the Holocene localities and KG. Distal portion of the bone slender, its proximal (dorsal) portion elongate ventro-posteriorly. Antero-lateral border of the quadrate slightly concave (GI, JO, Recent materials) or straight (KG); quadrate crest rather weakly developed and restricted only to the median area of the bone. Stapedial process small.

Compound bone (Fig. 44: 14 and 45: 11). Numerous examples, for the most part preserved in good condition (without anterior portions), come from KG and GI. Medial flange insensibly higher (by 1/3) than lateral flange. There is a distinct furrow throughout the length of the medial flange, situated near its dorsal border. Supraangular foramen located far from the anterior end of mandibular fossa. Retroarticular process very long, strongly curved downward (lacking in most fossils).

Dentary (Fig. 44: 15 and 45: 10). Dentaries are straight and slender; in

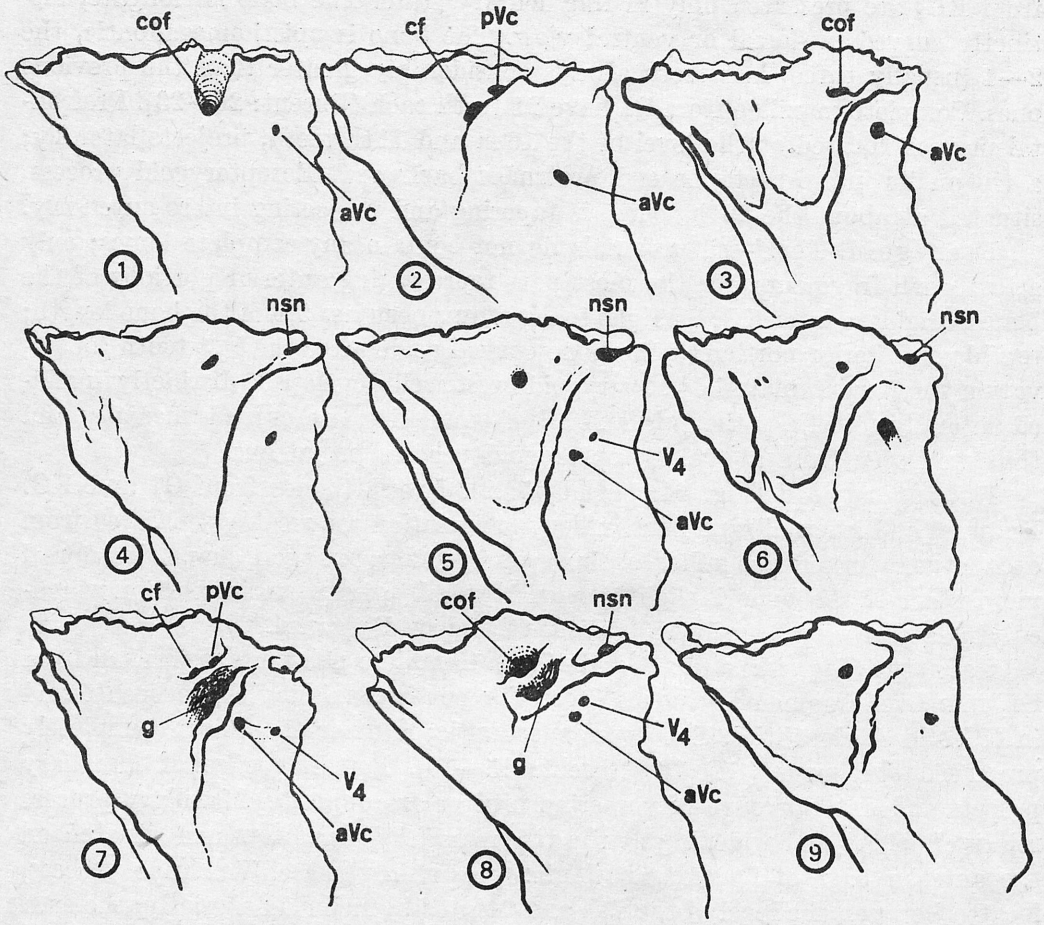


Fig. 48. Some patterns of disposition of foramina in postero-ventral basisphenoid area of *Natrix natrix*: 1 — Recent (ZZSiD 323), 2 — from GI, 3, 4, 5, 6, 7 — from KG, 8 — from KG (previously *Palaeomalpolon*), 9 — from ZA. Abbreviations: aVc — anterior orifice of Vidian canal (for palatine branch of facial nerve (VII)), cf — cerebral foramen (for palatine branch of facial nerve (VII)), cof — common foramen (for cerebral artery and facial nerve: cf + pVc), g — groove, nsn — notch for sympathetic nerve, pVc — posterior orifice of Vidian canal (for cerebral branch of internal carotid artery), V_4 —foramen for pterygoid branch of trigeminal nerve. Not to scale

dorsal view anterior end of the bone strongly curved inside. The bone is generally isodontic except 2—3 minute anteriormost teeth. A complete dentary from JO has 31 small teeth (Recent: 29). Very small mental foramen lies at the level of the 12th tooth. Compound notch on the lateral surface approaches by the 18th or 19th tooth. Meckel's groove closes completely by the 8th or 9th tooth.

Vomer (Fig. 44: 5). A single bone from GI, preserved in good state. Postero-inferior process usually forms a bony ring, but in this example its ventral portion is missing. Posterior margin of the ring has the form of a broad lamina in lateral view; postero-superior process is not distinctly separated off. Lamina

spheroidea palatina shifted posteriorly, and so cavum vomeris is well seen in lateral view. Premaxillary process long and thin, well separated at the base.

Premaxilla (Fig. 44: 4 and 45: 3). 2 bones from GI and 5 from KG. Lateral arms long and tapering, provided with well developed processes on their posterior borders. Palatine process short, situated at acute angle to the nasal process. Ventral openings of premaxillary channels situated far from each other. Premaxillary channels pierce the anterior wall of the bone and are directed laterally in form of deep grooves; on lateral borders of the nasal process, where the grooves leave the bone, deep notches are produced.

Mid-trunk vertebrae (Fig. 49: 6—10). Centrum long and narrow, with flat ventral surface. Hypapophysis strongly developed, usually sigmoid in lateral view; distal tip blunt, extending posteriorly to near the level of the condyle tip. Anterior keel flattened. Subcentral ridges sharp, but diminishing posteriorly, extending from diapophyses to the base of the condyle. Grooves between subcentral ridges and anterior keel have the form of shallow depressions located around subcentral foramina. There is often a deep groove between the parapophyseal process and cotyle; the groove may penetrate as far as the paracotylar foramen. Similarly, a narrow sinus produced from the neural canal reaches the paracotylar foramen from the opposite (upper) direction. Neural arch moderately vaulted, without epizygapophyseal spines. Posterior border of the neural arch deeply V-shaped. Postzygapophyseal area of the neural arch upswept. Neural spine longer than high, usually thickened on its upper edge, at least anteriorly; in some vertebrae, however, especially these belonging to smaller snakes (e. g. from KG) thickening is absent. Neural spine of trunk vertebrae strongly overhangs both anteriorly and posteriorly; posterior overhang almost always stronger defined, forming often long tapering projection. Practically all vertebrae from older localities (ZB, KI) lack their neural spines; neural spine of vertebrae from KD, KA and ZA is relatively lower than that of vertebrae originating from younger localities. Zygosphene flat, always distinctly crenate from above, with the upper edge of articular surfaces projected above the level of the zygosphenal lip. Within zygantrum two big foramina are seen; moreover, less but well defined foramina are present on posterior walls of postzygapophyseal rami. Postzygapophyseal articular facets reniform or oval in shape. Prezygapophyseal articular facets oval. Prezygapophyseal processes long, strongly flattened dorso-ventrally, usually with distinctly widening tip in dorsal view; in smaller specimens prezygapophyseal processes are more slender. Interzygapophyseal ridges sharp and well developed, usually parallel to the axis of the centrum. Lateral foramina well marked, in large specimens located in deep depressions and bordered ventrally by a short strong ridge. Paradiapophyses with two well defined articular facets; diapophyses projecting strongly aside. Parapophyseal processes strongly built and often flattened dorso-ventrally, projecting anteriorly; they are usually obtuse in ventral view, more rarely acute. Cotyle flattened; ventral edge of the cotyle rim provided with two small tubercles.

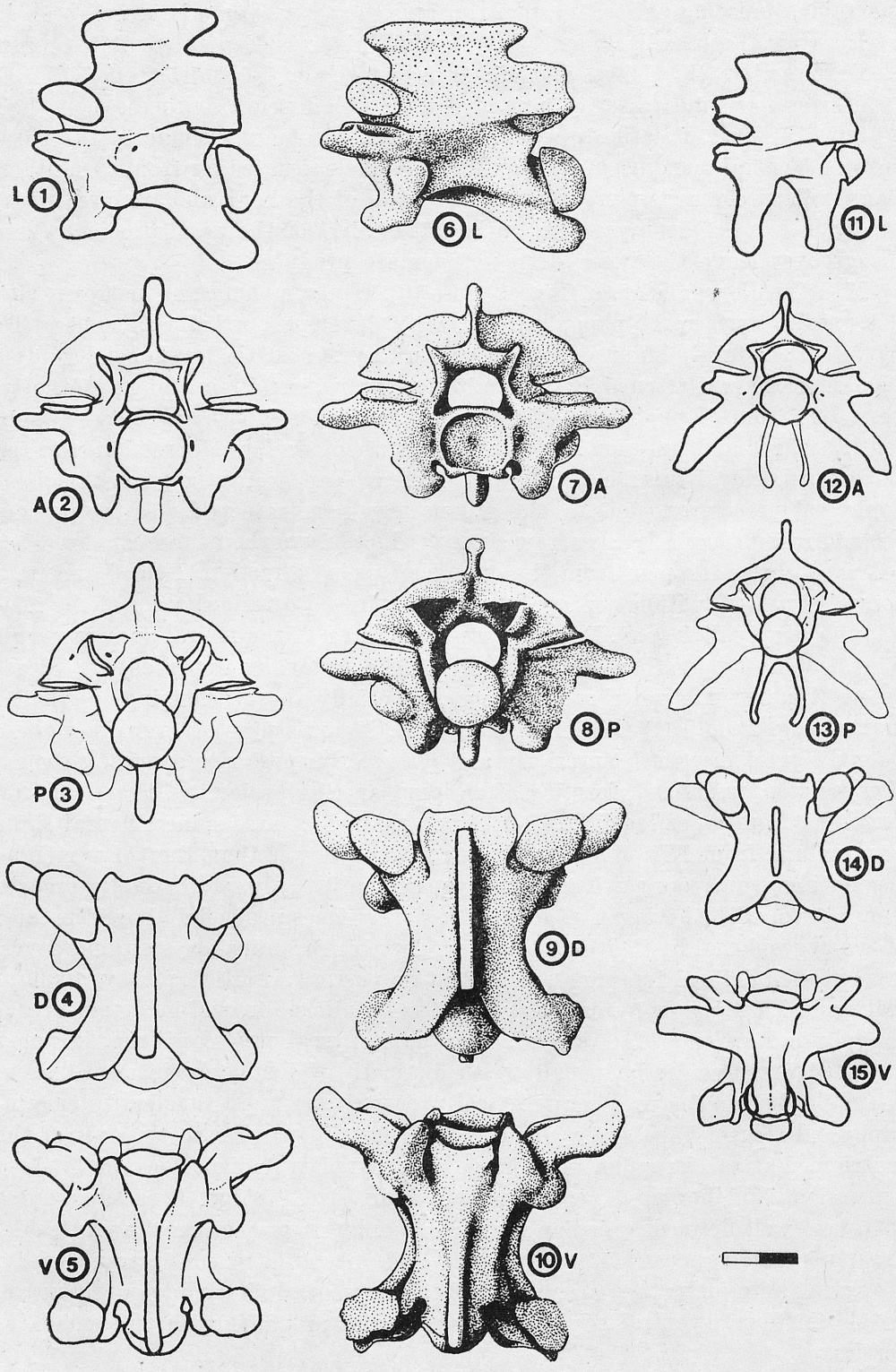

L 1
6 L
11 L
A 2
7 A
12 A
P 3
8 P
13 P
D 4
9 D
14 D
V 5
10 V
15 V

Table XVIII

Measurements and ratios of trunk vertebrae of *Natrix natrix*

	Recent ZZSiD 289 (N = 21)		JO (N = 16)		KG (N = 40)	
	OR	$\bar{X}\pm SD$	OR	$\bar{X}\pm SD$	OR	$\bar{X}\pm SD$
PR-PO	4.78—5.01		4.39—6.18		4.21—6.09	
CL	4.03—4.31		3.81—5.36		3.51—4.97	
PO-PO	4.80—5.18		4.35—6.56		4.11—5.94	
NAW	2.50—2.67		2.36—3.31		2.23—3.09	
ZW	2.52—2.71		2.00—2.76		2.03—2.85	
CTH	1.42—1.62		1.36—1.86		1.18—1.71	
CTW	1.61—1.76		1.48—2.05		1.25—2.06	
PR-PR	4.88—5.27		4.36—6.28		4.17—6.08	
CL/NAW	1.61—1.64	1.62±0.001	1.55—1.70	1.62±0.05	1.56—1.69	1.62±0.04
PO-PO/NAW	1.82—2.00	1.94±0.04	1.80—2.03	1.92±0.08	1.76—2.12	1.95±0.08
CTW/CTH	1.02—1.19	1.11±0.05	0.97—1.16	1.09±0.05	0.94—1.33	1.13±0.07
ZW/NAW	0.96—1.04	1.01±0.02	0.81—0.96	0.89±0.05	0.74—1.05	0.94±0.06
PR-PR/PR-PO	1.00—1.07	1.04±0.02	0.99—1.06	1.02±0.02	0.94—1.16	1.03±0.05
CL/ZW	1.55—1.69	1.61±0.03	1.64—2.00	1.83±0.10	1.57—2.10	1.74±0.11
PR-PR/NAW	1.87—2.01	1.96±0.04	1.81—2.05	1.93±0.07	1.84—2.16	2.00±0.08

Mensuration. I present below some results of mensuration of greatest trunk vertebrae belonging to *Natrix natrix* from the Holocene and Pleistocene localities. Successively follows: number of vertebrae, range of CL, range of CL/NAW ratio, and its mean with standard deviation:

JO: 30 3.81—5.99 1.45—1.90 1.63±0.11
GI: 60 4.17—5.60 1.57—2.07 1.74±0.10
KG: 60 3.35—4.98 1.48—1.84 1.64±0.08
ZA: 31 3.77—5.04 1.50—1.93 1.71±0.11

It is somewhat surprising that, as opposed to *Elaphe longissima*, vertebrae of *Natrix natrix* from all Pleistocene sites (including localities not taken into account in the above specification) have considerably smaller size than those from the Holocene (JO and GI). In this connection, in order to compare statistically vertebrae from some localities (here KG vs. Recent; Table XIX) I had to avoid use of most the largest vertebrae from JO and the whole GI sample. Because of these reasons comparison between the JO sample and the remaining ones can be inadequate. Comparison between Recent (ZZSiD 289) and KG *Natrix natrix* shows highly significant difference ($p<.01$) only for one ratio; for three remaining ratios the differences are not significant ($p>.05$).

Fig. 49. Vertebrae of *Natrix natrix* from GI. 1, 2, 3, 4, 5 — cervical vertebra (ZZSiD, GI-607), 6, 7, 8, 9, 10 — trunk vertebra (ZZSiD, GI-547), 11, 12, 13, 14, 15 — caudal vertebra (ZZSiD, GI-608). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

Table XIX

Statistical comparison of trunk vertebrae or Recent and fossil *Natrix natrix* (data from Table XVIII)

	Recent (N = 21)		
JO (N = 16)	PO-PO/NAW: p > .05 PR-PR/PR-PO: p > .05 CL/ZW: p < .01 PR-PR/NAW: p > .05	JO (N = 16)	
KG (N = 40)	PO-PO/NAW: p > .05 PR-PR/PR-PO: p > .05 CL/ZW: p < .01 PR-PR/NAW: p > .05	PO-PO/NAW: p > .05 PR-PR/PR-PO: p > .05 CL/ZW: p < .01 PR-PR/NAW: p < .01	KG (N = 40)

The CL/NAW ratio of *N. natrix* vertebrae very rarely reaches 1.90; there are only few vertebrae exceeding this value. It seems that occurrence of vertebrae with very elongate centra is more frequent in materials from older localities; this observation is of a special importance because of resemblance between these vertebrae and vertebrae of *N. longivertebrata*.

Intracolumnar variation (Fig. 50). With exception of the first several bones all vertebrae of the precaudal region of the column of *Natrix natrix* show little morphological differences among one another.

Several dozens of axes originate from KG * and GI. Neural spine much higher than long, provided with anterior and posterior overhangs and has slightly inclined antero-ventrally dorsal edge. Neural arch provided with epizygapophyseal spines. Transverse processes slender and rather short, directed posteriorly in lateral view. Odontoid process heavy built, obtuse. Intercentra robust with strongly widened tips.

Cervical vertebrae (Fig. 49: 1—5), as is typical for most snakes, are relatively shorter, have much more vaulted neural arch and longer hypapophysis than trunk vertebrae. Neural spine of cervical vertebrae is relatively higher; posterior overhang of the neural spine is well defined, but anterior overhang is slight. Parapophyseal process directed antero-ventrally. The lip of the zygosphene usually higher than the upper edge of the articular facets. Besides, other vertebral structures resemble those of trunk vertebrae.

Posterior trunk vertebrae have lowered neural spines with slight overhangs; hypapophysis stronger built, but shorter than in mid-trunk vertebrae.

Cloacal vertebrae (KG; Recent ZZSiD 289, 323) have extremely low neural spine. Dorsal ramus of the lymphapophysis is much shorter than ventral ramus. Haemapophyses are missing in both fossil and comparative materials, but presumably they were relatively long.

* Previously described erroneously as atlases belonging to *Colubridae* indet. (Szyndlar, 1981, p. 93).

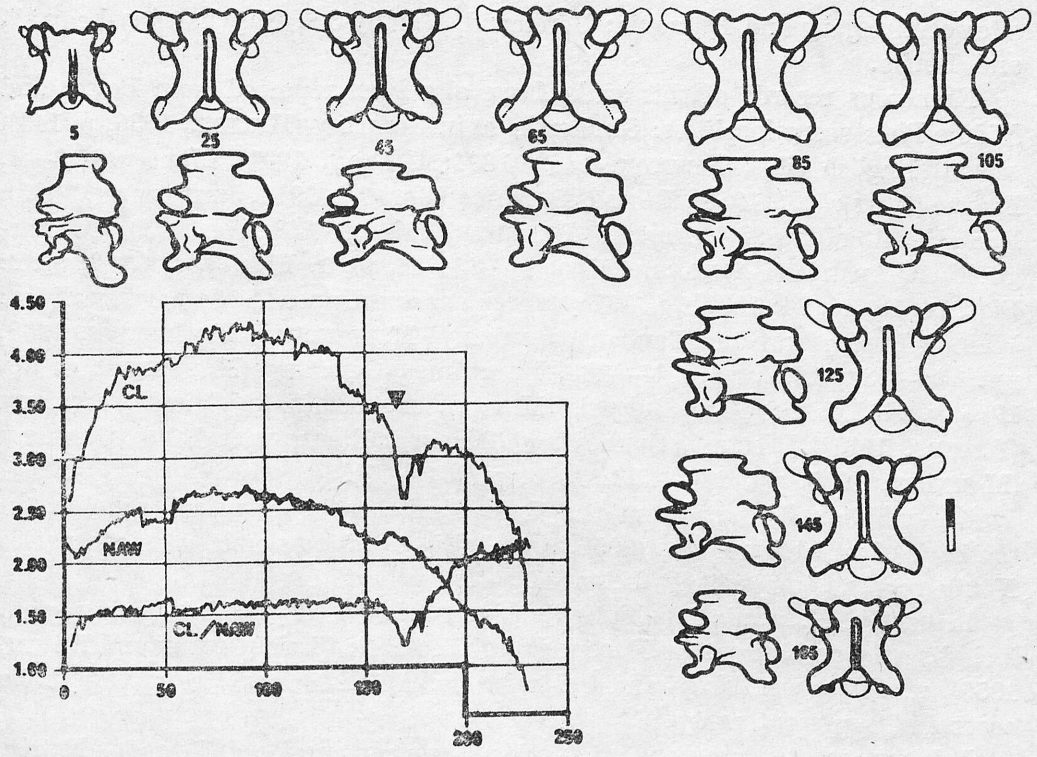


Fig. 50. Intracolumnar variation in CL, NAW and CL/NAW of vertebrae of *Natrix natrix* (ZZSiD 289). Vertical axis — dimensions in mm; horizontal axis — no. of succeeding vertebrae; black triangle — position of cloacal vertebrae. Figures show dorsal and lateral views of every 20th precaudal vertebra. Scale equals 2 mm

Caudal vertebrae (Fig. 49: 11—15) always have long and slender pleurapophyses and haemapophyses. Pleurapophyses project antero-ventrally with exception of anterior caudal vertebrae where pleurapophyses usually are directed ventrally. The neural spine distinctly overhangs anteriorly, but there is no posterior overhang and the posterior border of the spine is even inclined anteriorly, especially in posterior caudal vertebrae.

Remarks (Fig. 51). Fossil remains of *Natrix natrix* have been reported from various European localities more often than those of any other snake.

The oldest record of the snake, originating from the Uppermost Miocene (MN 13) of Polgárdi and described by Bolkay (1913) and Szunyoghy (1932), has been discussed earlier (cf. Chapter V a, p. 50).

Mais and Rabeder (1977, p. 85) mentioned the occurrence of *N. natrix* in the Upper Pliocene (MN 16) of Deutsch Altenburg-20, Austria, however, these authors neither described nor figured the remains.

Bolkay (1913, p. 223), Szunyoghy (1932, p. 8) and Kretzoi (1956, p. 259) reported remains of *N. natrix* from several Upper Pliocene and Early Pleistocene

sites of Hungary and Rumania: Beremend, Villány-3 *, Nagyharsány-hegy **, and Betfia.

Numerous records of this snake have also been reported from Lower and Middle Pleistocene localities: Gundersheim in Germany (HELLER, 1936, p. 143), several English sites (NEWTON, 1882, 1894; HINTON, 1901), Montoussé 3—4, France (CLOT et al., 1976), Brassó, Rumania (BOLKAY, 1913, SZUNYOGHY, 1932), Deutsch Altenburg-2, 4, Austria (RABEDER, 1974, p. 148, Fig. 2: 1), St. Margarethen, Austria (RABEDER, 1977a, pp. 83—86, pl. 1: Figs. 3, 4, 6, 13, pl. 2: Figs. 14, 18, 19, 24; 1977b, p. 117), as well as from Upper Quaternary localities: Weimar-Ehringsdorf and Taubach, Germany (MŁYNARSKI and ULLRICH, 1968, pp. 138—139; 1977, pp. 167—168, Burgtonna, Germany (MŁYNARSKI et al., 1978, p. 225), Bacho Kiro, Bulgaria (MŁYNARSKI, 1982, p. 30), Pisede, Germany (PETERS, 1977), Dietfurt, Spitzbubenhöhle and Euerwanger Bühl, Germany (MARKERT, 1975, pp. 220—223; 1976, pp. 70—76).

An ophidian dentary from the Late Pleistocene of Breitenberghöhle, on the basis of which BRUNNER (1957, p. 377, Fig. 16: 5) has erected a new species *Natrix rusticus*, most likely belonged to *N. natrix*.

Presently, *N. natrix* inhabits extensive territories of the Palearctic region, including the greater part of Europe up to the Arctic Circle (GISLÉN and KAURI, 1959), northwestern Africa and Central Asia. All fossil localities of this snake occur in its present range.

It is somewhat surprising that another European species of the genus *Natrix*, i. e. *N. tesselata*, is absent in Polish fossil materials. Present range of this East European snake reaches the southern frontier of Poland. Fossil remains of this snake have been reported from several Hungarian and Rumanian sites, dated from the Uppermost Miocene until Middle Pleistocene: Polgárdi, Beremend, Villány-3, Nagyharsány-hegy, Betfia, Villány-6, and Brassó (BOLKAY, 1913, p. 223; SZUNYOGHY, 1932, p. 9; KRETZOI, 1956, p. 259). These records, based exclusively on skull bones, have been neither figured nor described in detail.

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* Villány-3 = Villány of BOLKAY (1913) and = Kalkberg near Villány of SZUNYOGHY (1932).

** The age of the older collections from Nagyharsány-hegy described by BOLKAY (1913) and SZUNYOGHY (1932) (= Nagyharsány-hegy near Villány) agrees with the age of the fauna from Villány-3 (Prof. D. JÁNOSSY, pers. comm., 1982).

Fig. 51. Past and present Central European distribution of the genus *Natrix*. Abbreviations of names of Polish localities: see Fig. 1. Abbreviations of names of foreign localities: BD — Beremend, BO — Brassó, BR — Breitenberghöhle, BT — Betfia, BU — Burgtonna, DA — Deutsch Altenburg-2, 4 and 20, EB — Euerwanger Bühl, Dietfurt and Spitzbubenhöhle, GU — Gundersheim, NH — Nagyharsány-hegy, PI — Pisede, PL — Polgárdi, SM — St. Margarethen, TA — Taubach, VY — Villány-3, WE — Weimar-Ehringsdorf. The area of present distribution of *Natrix tesselata* is lined; *Natrix natrix* inhabits the whole area covered by the map (after ARNOLD and BURTON, 1978, and other sources). For further comments see

p. 119

ZY
RZ
MA
ZA, ZB
W I, W II
RK I, RK II
KA
KI
KG
KD
RA
JO
NI, GI, DS
BT
BO
PL
VY, NH
BD
DA
SM
PI
BU
TA
WE
BR
EB
GU

Recently, *N. tesselata* has also been reported from the Upper Quaternary of Euerwanger Bühl and Spitzbubenhöhle (MARKERT, 1975, pp. 220—223; 1976, pp. 74—76).

Family *Viperidae* LAURENTI, 1768
Subfamily *Viperinae* LAURENTI, 1768
Genus *Vipera* LAURENTI, 1768

Vipera berus (LINNAEUS, 1758)
(Figs. 52—55, Table XXI)

Material. — See Table XX.

Ophidian remains, referred here to *Vipera berus*, originate from ten localities. Previous descriptions concern vipers from two sites:

KA: *Viperidae* indet. — MŁYNARSKI, 1961a, pp. 16—17; 1962, p. 182;
KG: *Vipera* cf. *berus* (LINNAEUS, 1758) — MŁYNARSKI, 1977, p. 21;
Vipera berus (LINNAEUS, 1758) — SZYNDLAR, 1981, pp. 93—94. Figs. 15 and 16;
Vipera aff. *ammodytes* (LINNAEUS, 1758) — ibidem, p. 94, Fig. 17.

With exception of materials from ZA and KG that contain abundant viper remains including skull bones, in most localities the presence of *Viperinae* is recorded on the basis of only a few vertebrae. Perhaps that is why vipers have been omitted in previous descriptions.

Basiparasphenoid (Fig. 52: 1—3 and 53: 1). 5 bones altogether, one from ZA and four from KG, one among the latter complete (remaining bones have parasphenoid processes missing). Two bones from KG were earlier described as belonging to *Vipera* aff. *ammodytes* (SZYNDLAR, 1981, p. 94, Fig. 17: 1).

Basipterygoid processes underdeveloped. Suborbital flanges developed to varying degree. Pterygoid crest absent. As is typical for vipers, the basisphenoid crest is distinct, extending from the posterior border of the bone to the central area where it forks into two separate crests reaching the suborbital flanges. Posterior border of the bone has medially bifurcated process. Pterygoid process very short. Cerebral foramen distinctly separated from the posterior

Table XX

List of materials of *Vipera berus*

	KD	KA	ZA	KG	CI	RA	ND	NI
Basiparasphenoid			1	4				
Maxilla (R)			1	1				
Vertebrae	79	4	±5600	>30	1	9	4	12

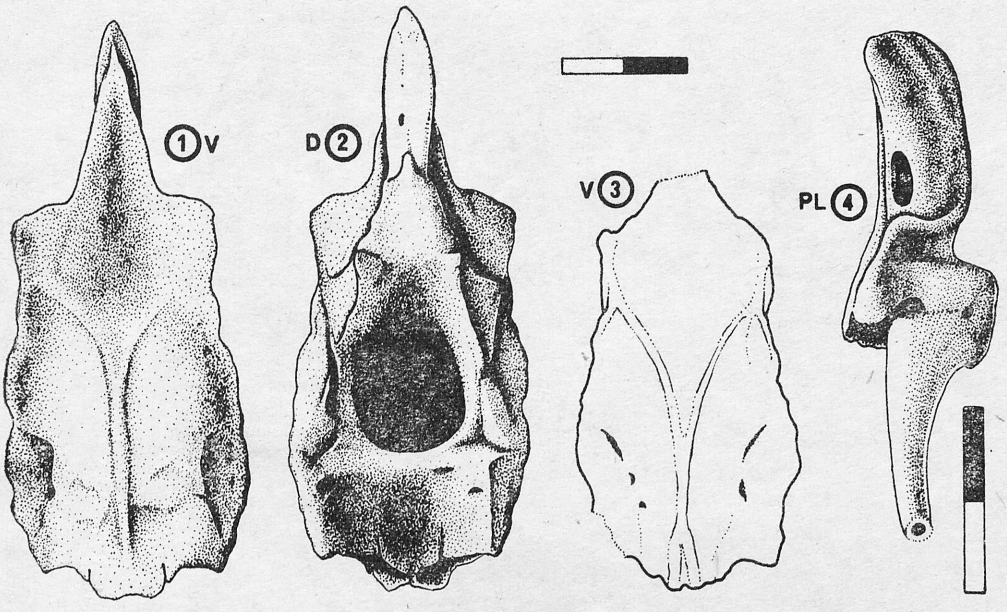


Fig. 52. Cranial bones of *Vipera berus* from KG. 1, 2, 3 — basiparasphenoids (ZZSiD, KG-8500 and 8501), 4 — left maxilla (ZZSiD, KG-8504). D — dorsal, PL — postero-lateral, V — ventral views. Each scale equals 2 mm

orifice of Vidian canal; these foramina are covered ventrally by longitudinal crests. On dorsal side, frontal crest is short and wide, strongly flattened dorso-ventrally, provided with well developed frontal step and trabecular processes. Trabecular grooves very deep, enclosed laterally with prominent crests of suborbital flanges. Anterior and posterior foramina for abducens nerves well marked. Anterior orifices of Vidian canals are situated also on the dorsal side of the bone, immediately before sympathetic nerve foramina. Orifices of Vidian canals are enclosed in both sides by bony crests.

My previous opinion (SZYNDLAR, 1981) that two basiparasphenoids from KG belonged to *Vipera* aff. *ammodytes* was based on the general shape of the bones and considerable development of their suborbital flanges. However, strongly developed suborbital flanges can be found in some specimens of *V. berus* (e. g. ZZSiD 238), moreover, disposition of foramina in the discussed bones is typical for *V. berus* while in *V. ammodytes* it is clearly different. In *V. ammodytes* the posterior orifice of Vidian canal is large and provided with a distinct groove directed laterally; this foramen and cerebral foramen (lying behind) are never covered with a bony crest. Anteriorly, Vidian canal leaves the bone through its lateral border, not dorsal side. Furthermore, frontal crest, trabecular grooves and other details of the basiparasphenoid of *V. ammodytes* are built unlike those of *V. berus*.

Maxilla (Fig. 52: 4 and 53: 2). Two bones from ZA and KG, In anterior view, dorsally to the base of venom fangs, the trunk of the bone is very thin and

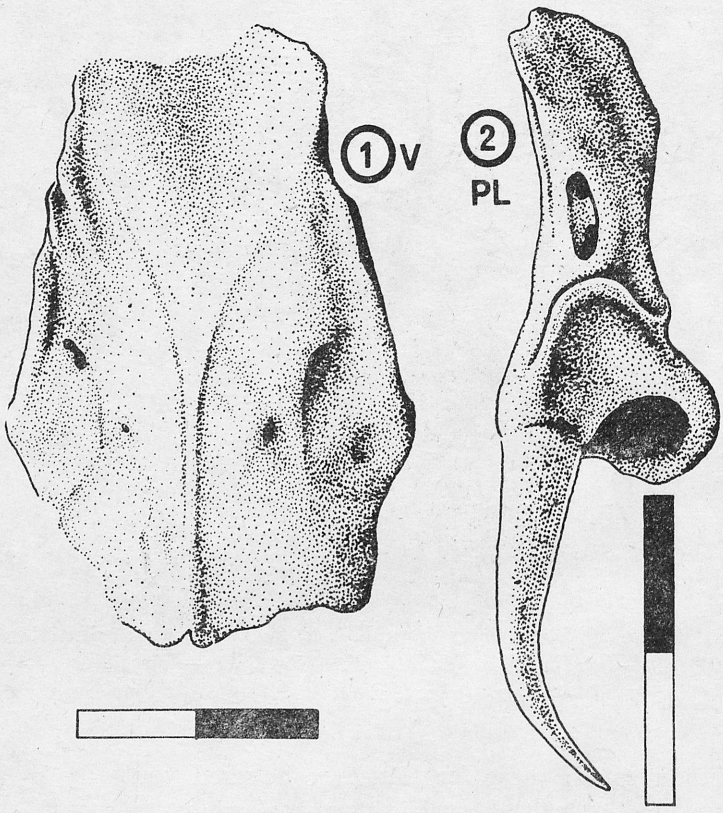


Fig. 53. Cranial bones of *Vipera berus* from ZA. 1 — basiparasphenoid (ZZSiD, ZA-2000), 2 — left maxilla (ZZSiD, ZA-2001), PL — postero-lateral, V — ventral views. Each scale equals 2 mm

sharp-edged. Its uppermost portion is elongated medially into a prominent process of the maxillary-prefrontal articulation; on the opposite side a small round-shaped foramen is present. Orifice of the dental canal, situated on the lateral side of the bone, is elongated dorso-ventrally and encloses two separate foramina. In posterior view, dorsally to the base of the fangs, a very deep fossa is present, limited from above by a distinct crest. Both maxillae have preserved one fang each — this from KG in the lateral socket and that from ZA in medial socket. Proximal lumen of the fangs is lanceolate in shape.

Precaudal vertebrae (Fig. 54 and 55). *Vipera berus*, like other viperid species, has relatively few vertebrae in the column (here about 140 in the precaudal region), but intracolumnar variation is strongly expressed both in morphology and measurements (Fig. 56; cf. also graphs in Brattstrom, 1964, and Thireau, 1967). At the same time it is difficult to distinguish precisely divisions of the precaudal vertebral column. Because of these reasons it will be necessary to describe cervical and trunk vertebrae together.

Centra of trunk vertebrae are cylindrical and elongate, especially in the posterior precaudal region. Hypapophyses of cervical vertebrae long and straight,

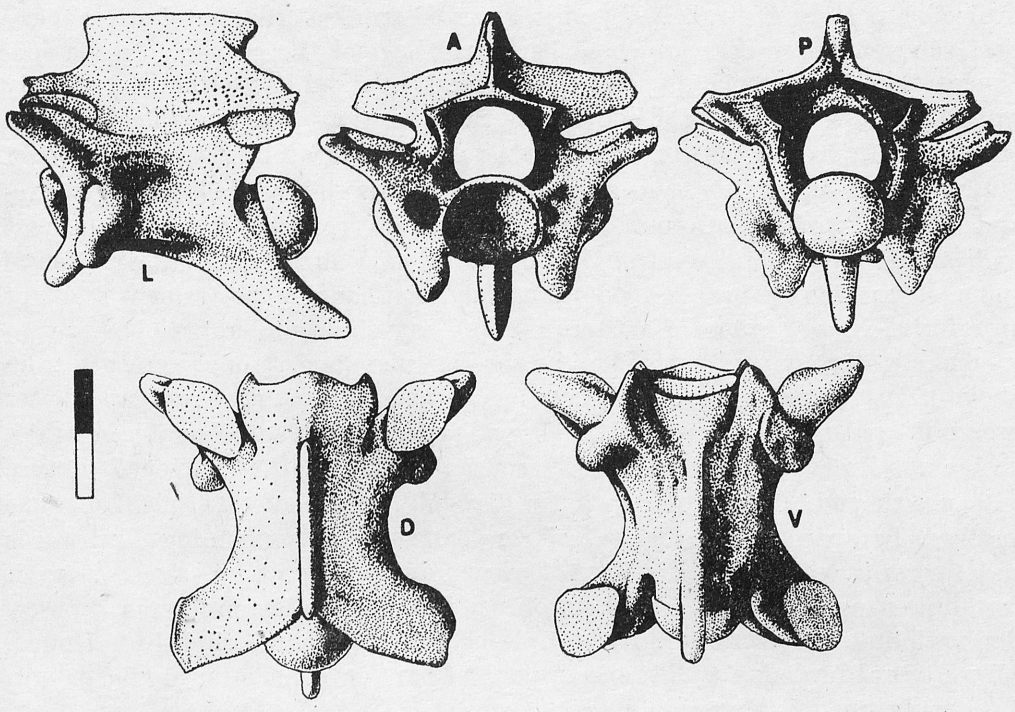


Fig. 54. Cervical vertebra of *Vipera berus* from ZA (ZZSiD, ZA-2003). A — anterior, D— dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

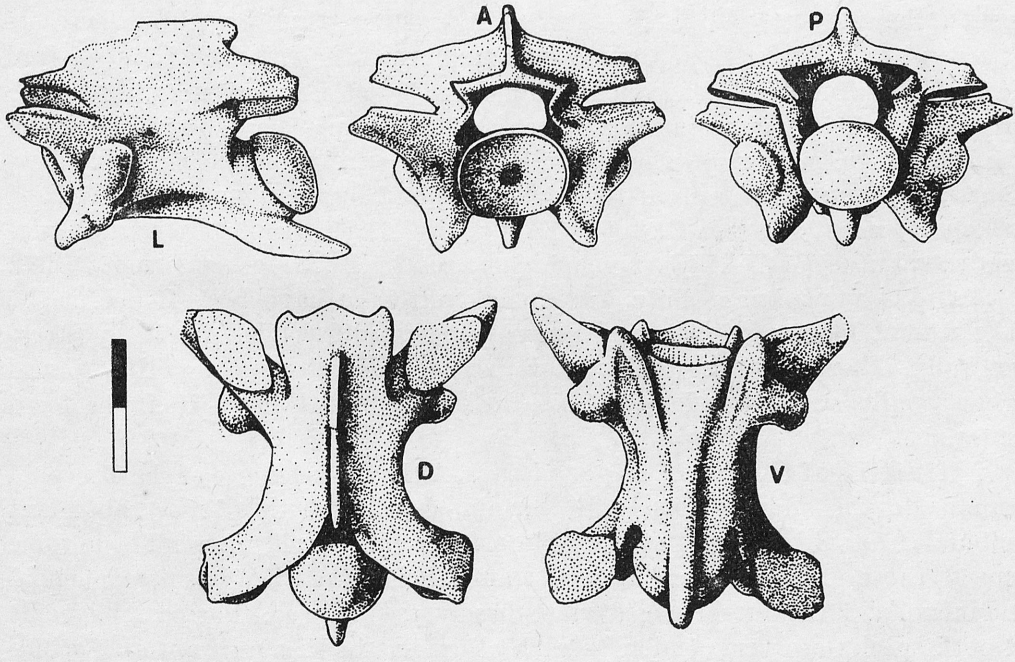


Fig. 55. Trunk vertebra of *Vipera berus* from RA (ZZSiD, RA-13). A — anterior, D — dorsal, L — lateral, P — posterior, V — ventral views. Scale equals 2 mm

projected postero-ventrally. Hypapophyses of trunk vertebrae short, hooked posteriorly, more or less projected backward beyond the cotyle; in some specimens the tip of the hypapophysis is slightly forked. Anterior keel usually widening before reaching the cotyle rim. Subcentral grooves and ridges present only in the anterior portion of the centrum. Neural arch, with exception of anterior vertebrae, flattened and distinctly emarginated between the pre- and postzygapophyses. Neural spine of cervical vertebrae well developed, as high as long, overhanging strongly posteriorly and slightly anteriorly. Neural spine of trunk vertebrae very low, usually overhanging posteriorly and not anteriorly. Neural spine of posterior trunk vertebrae underdeveloped. Zygosphene slightly convex or straight in anterior view and strongly crenate from above. Postzygapophyseal articular facets usually round. Prezygapophyses broad in ventral view; prezygapophyseal articular facets obovate in trunk vertebrae. Prezygapophyseal processes usually short, often flattened, obtuse or acute-shaped. In lateral view, paradiapophyses are not distinct from one another. Parapophyseal processes of cervical vertebrae extending downwards and forwards, often acute in lateral view. Parapophyseal processes of trunk vertebrae usually strongly built and obtuse from below; the processes of posterior vertebrae project anteriorly. Cotyle of trunk vertebrae slightly flattened. All vertebral foramina well marked, paracotylar foramina often doubled, but, if so, only on one side of the cotyle.

Mensuration. As I have mentioned earlier, the degree of intracolumnar variability among vipers is large and it can also be demonstrated by measurements. For instance, CL/NAW ratio of succeeding trunk vertebrae increases at a great rate. Under these terms good sampling of the vertebrae for statistical analysis is difficult; in consequence, homogeneity of samples is doubtful (high value of coefficient of variation for each ratios). Samples have been taken from the ZA and KG materials, where viperid remains were numerous enough. These bones are presumed to represent the trunk region between about 40th and 70th vertebrae; mean value of their CL/NAW ratio is 1.80. In posterior trunk vertebrae value of CL/NAW is much higher, reaching 2.30 or even more (ZA).

Caudal vertebrae. Only few caudal vertebrae have been found in the ZA material. Pleurapophyses, if preserved, are long and slender, directed postero-ventrally. Haemapophyses very short, expanded antero-posteriorly. Neural spine usually strongly reduced. No cloacal vertebra is known from the fossil materials.

Affinities of the fossil *Vipera berus*. Although reference of the discussed remains to the adder seems to be certain, detailed study of most abundant material from ZA shows that vertebrae from this locality resemble in some aspects those of *Vipera ursinii*. Two cranial bones from ZA, basiparasphenoid and maxilla, however, belonged undoubtedly to *V. berus*. Basiparasphenoids of both species are very similar to each other, but in *V. ursinii* anterior orifice of Vidian canal is located on the lateral margin of the bone, unlike in *V. berus* which has the foramen on the dorsal side of the bone. Maxilla of *V. ursinii*

Table XXI

Measurements and ratios of trunk vertebrae of *Vipera berus* and *Vipera ursinii*

	OR	$\bar{X}\pm SD$	OR	$\bar{X}\pm SD$
	Vipera berus Recent ZZSiD 22 (N = 25)		*Vipera berus* KG (N = 21)	
PR-PO	4.07—4.75		4.59—5.72	
CL	3.40—3.95		3.83—5.51	
PO-PO	4.04—4.46		4.38—5.81	
NAW	1.99—2.13		2.15—2.70	
ZW	1.92—2.13		1.94—2.61	
CTH	1.31—1.55		1.38—1.77	
CTW	1.52—1.79		1.80—2.09	
PR-PR	4.10—4.52		4.69—6.35	
CL/NAW	1.70—1.88	1.80±0.05	1.72—1.90	1.80±0.06
PO-PO/NAW	2.03—2.18	2.11±0.04	1.95—2.28	2.08±0.09
CTW/CTH	1.05—1.24	1.15±0.04	1.08—1.32	1.21±0.07
ZW/NAW	0.92—1.03	0.98±0.03	0.86—1.07	0.97±0.06
PR-PR/PR-PO	0.94—1.03	0.98±0.03	0.92—1.10	1.01±0.04
CL/ZW	1.74—1.96	1.84±0.06	1.66—2.06	1.86±0.12
PR-PR/NAW	2.05—2.22	2.14±0.05	2.04—2.37	2.16±0.09
	Vipera berus ZA (N = 33)		*Vipera ursinii* Recent ZZSiD 294 (N = 23)	
PR-PO	4.23—6.36		4.30—4.64	
CL	3.62—5.29		3.59—3.92	
PO-PO	4.20—5.93		4.18—4.37	
NAW	2.04—2.89		2.03—2.13	
ZW	1.92—2.56		1.90—2.03	
CTH	1.27—1.82		1.28—1.43	
CTW	1.58—2.09		1.38—1.58	
PR-PR	4.25—6.04		4.78—4.95	
CL/NAW	1.68—2.16	1.80±0.11	1.70—1.90	1.80±0.06
PO-PO/NAW	1.82—2.24	2.04±0.10	1.97—2.09	2.04±0.03
CTW/CTH	1.11—1.36	1.21±0.06	1.03—1.16	1.11±0.04
ZW/NAW	0.86—1.01	0.94±0.05	0.92—0.98	0.94±0.01
PR-PR/PR-PO	0.87—1.06	0.98±0.04	0.91—1.00	0.95±0.03
CL/ZW	1.71—2.29	1.91±0.13	1.81—2.00	1.91±0.06
PR-PR/NAW	1.92—2.25	2.09±0.10	2.01—2.12	2.06±0.03

is relatively much shorter than that of *V. berus* and has the orifice of dental canal lying on the posterior wall of the bone. Also caudal vertebrae of both species differ distinctly from each other. *V. berus*, with exception of some posteriormost caudal vertebrae, has pleurapophyses considerably longer than haemapophyses, therefore unlike *V. ursinii*, which has pleurapophyses and haemapophyses of similar length. Unfortunately, except ZA, caudal vertebrae of

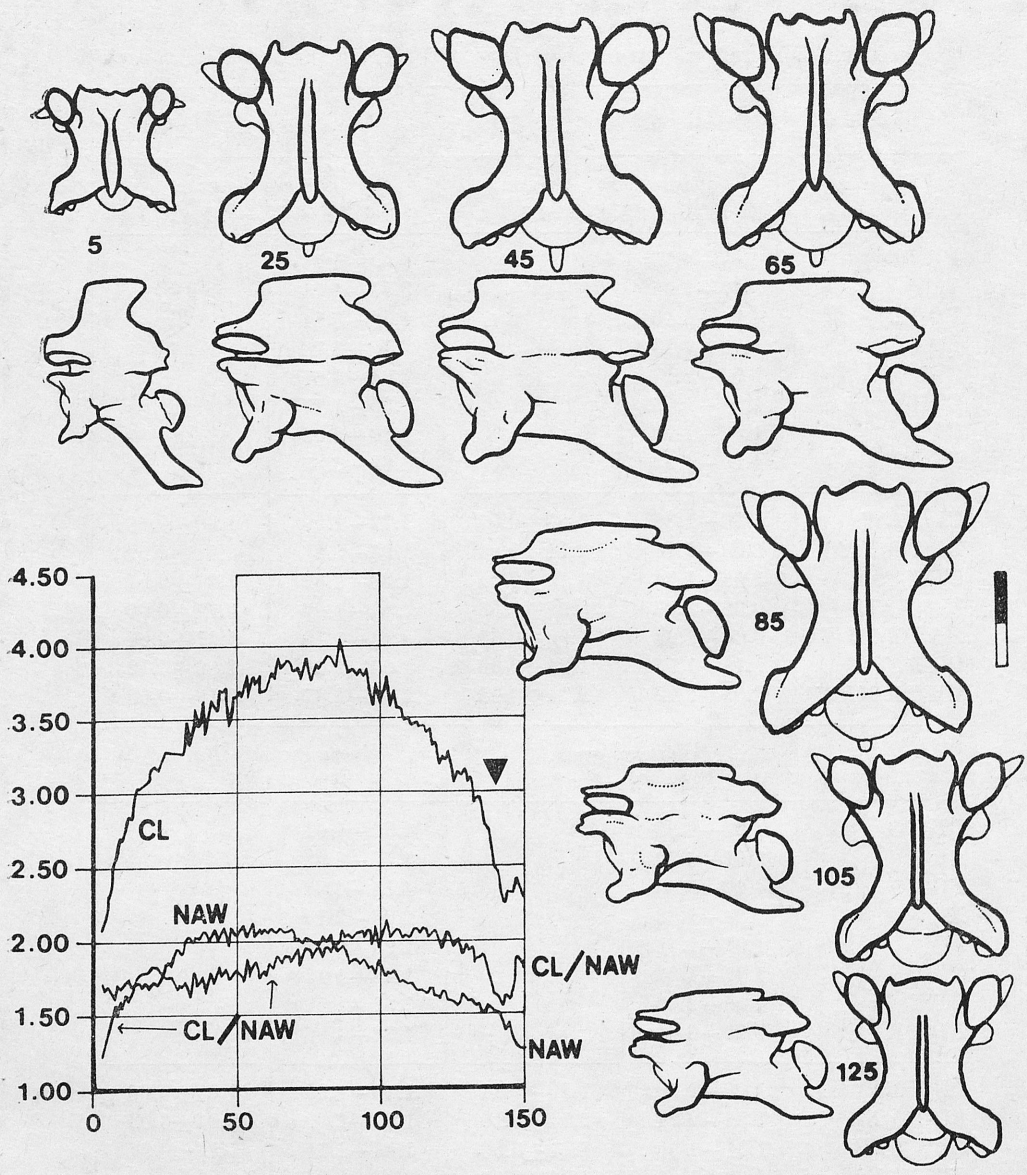


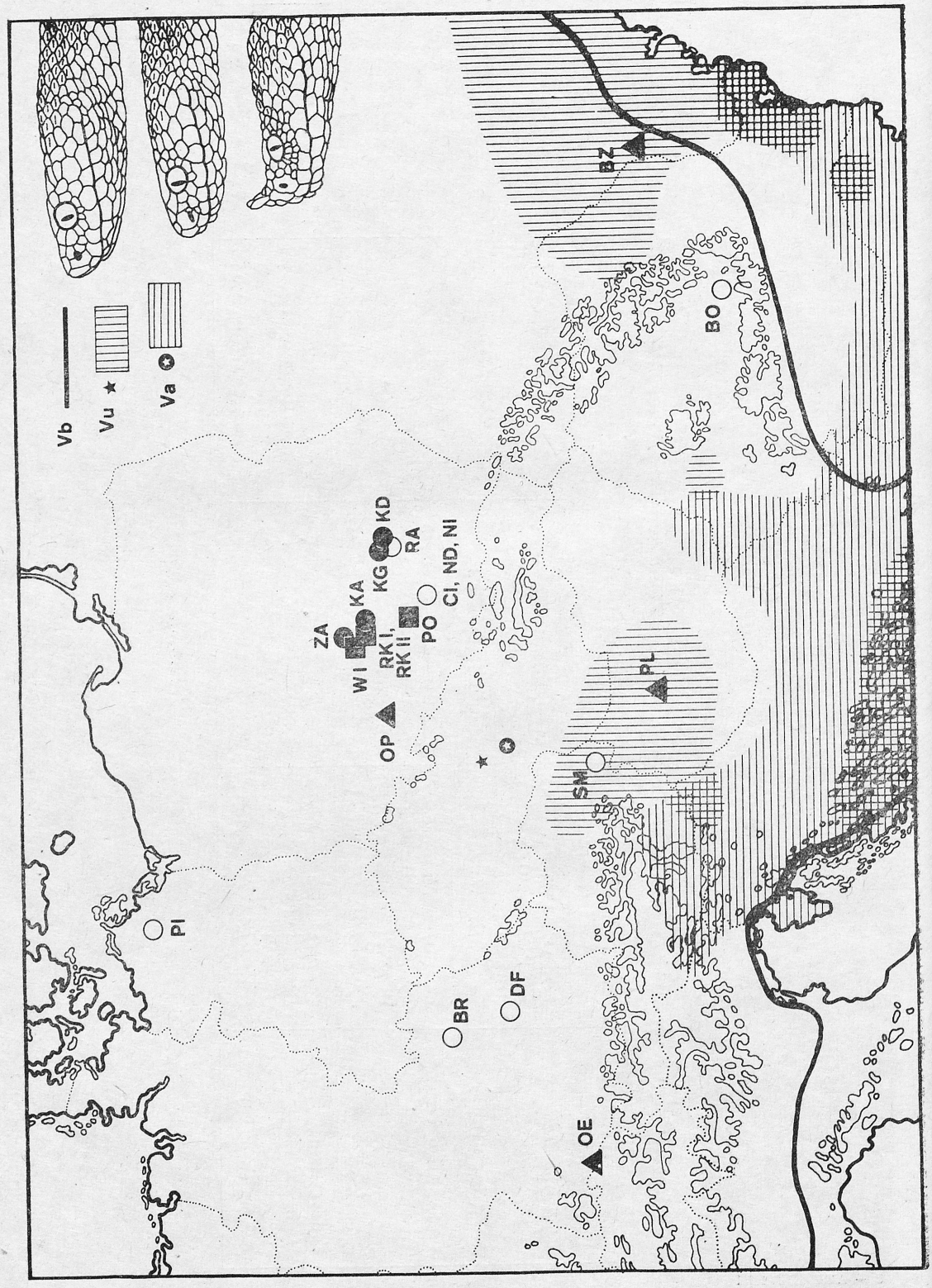
Fig. 56. Intracolumnar variation in CL, NAW and CL/NAW of vertebrae of *Vipera berus* (ZZSiD 22). Vertical axis — dimensions in mm; horizontal axis — no. of succeeding vertebrae: black triangle — position of cloacal vertebrae. Figures show dorsal and lateral views of every 20th precaudal vertebra. Scale equals 2 mm

V. berus have not been found in another locality. Morphological differences between trunk vertebrae of two species are rather indistinct: *V. ursinii* has relatively longer hypapophysis, slender prezygapophyseal processes, non overhanging anteriorly neural spine and narrow anterior keel in ventral view. These features, though present in many vertebrae from ZA, rarely occur altogether;

Table XXII

Statistical comparison of trunk vertebrae of Recent and fossil *Vipera berus*, and Recent *Vipera ursinii* (data from Table XXI)

	Vipera berus Recent (N = 25)			
Vipera berus KG (N = 21)	PO-PO/NAW: p > .05 PR-PR/PR-PO: p < .01 CL/ZW: p > .05 PR-PR/NAW: p > .05	*Vipera berus* KG (N = 21)		
Vipera berus ZA (N = 33)	PO-PO/NAW: p < .01 PR-PR/PR-PO: p > .05 CL/ZW: p < .05 PR-PR/NAW: p < .05	PO-PO/NAW: p = .05 PR-PR/PR-PO: p < .01 CL/ZW: p > .05 PR-PR/NAW: p < .01	*Vipera berus* ZA (N = 33)	
Vipera ursinii Recent (N = 23)	PO-PO/NAW: p < .01 PR-PR/PR-PO: p = .01 CL/ZW: p = .01 PR-PR/NAW: p < .01	PO-PO/NAW: p < .05 PR-PR/PR-PO: p < .01 CL/ZW: p = .05 PR-PR/NAW: p < .01	PO-PO/NAW: p > .05 PR-PR/PR-PO: p < .01 CL/ZW: p > .05 PR-PR/NAW: p > .05	*Vipera ursinii* Recent (N = 23)


Vb
Vu
Va
BZ
BO
KD
RA
KA
KG
ZA
WI
RK I,
RK II
PO
CI, ND, NI
OP
PL
SM
PI
BR
DF
OE

the predominating morphological pattern is typical for Recent *V. berus*. The main similarity of the ZA viperid vertebrae to *V. ursinii* is inherent in their measurements. Indeed, statistical comparison (see Table XXII) of ZA vs. Recent *V. ursinii* shows no significant differences ($p>.05$) for three ratios, while ZA vs. Recent *V. berus* inversely shows significant and highly significant differences ($p<.05$ and $p<.01$) for three ratios. Similar differences can be observed between ZA and KG, conversely; vertebrae from the latter locality, except in one case, shows no significant differences ($p>.05$) with Recent *V. berus*.

Another similarity between *V. ursinii* and the ZA remains concerns posterior trunk vertebrae. In *V. ursinii* CL/NAW ratio for this vertebral region reaches 2.30 (ZZSiD 294, 346) and similar situation can be observed in the vertebrae from ZA. In adult specimens of *V. berus* (ZZSiD 22, 328) CL/NAW ratio of posterior trunk vertebrae does not exceed 2.10, like that of the vertebrae from the remaining fossil localities.

However, because of difficulties discussed above, numerical data taken from viperid skeletons are less credible than in the case of other snakes and therefore have less taxonomic importance than the morphological features. On the other hand, *V. berus* and *V. ursinii* are closely related species, thus presence of common features in specimens from the Lower Pleistocene can be the evidence of a common ancestor. Unfortunately, viperid remains from the oldest Pleistocene localities, consisting of infrequent fragmentary vertebrae, cannot be used to confirmation of this view.

Remarks (Fig. 57). Beyond of Poland, fossil records of *Vipera berus* have been reported from few localities of younger Quaternary: Middle Pleistocene of East England (NEWTON, 1882; 1894, p. 190, pl. 10: 8, 9), Middle Pleistocene of St. Margarethen, Austria (RABEDER, 1977a, pp. 92—93, pl. 1: Fig. 3, pl. 2: Fig. 21), Middle Pleistocene of Brassó, Rumania (BOLKAY, 1913, p. 226, Fig. 5; SZUNYOGHY, 1932, p. 10), Late Pleistocene of Breitenberghöhle, Germany (BRUNNER, 1957), and Upper Quaternary of Dietfurt and Spitzbudenhöhle, Germany (MARKERT, 1976, pp. 70—75).

V. berus, being a boreal species, presently inhabiting extensive areas of north-central Eurasia, eastwards reaching the coasts of the Pacific Ocean. In Europe, its range covers the greater part of the continent, excluding areas of the mediterranean peninsulas; northwards, the adder is recorded up to about 68°30'N (TERHIVUO, 1981).

Fig. 57. Past and present Central European distribution of *Viperidae*. Vb — southern limit of present range of *Vipera berus*, Vu — present range of *Vipera ursinii* (vertical lines), Va — present range of *Vipera ammodytes* (horizontal lines); asterisks indicate sites of the occurrence of *Vipera ursinii* and *Vipera ammodytes* in Moravia in the turn of 19th century (PRAŽÁK, 1898, REMES, 1923; cit. after OLIVA et al., 1968). Abbreviations of names of Polish localities: see Fig. 1. Abbreviations of names of foreign localities: BO — Brassó, BR — Breitenberghöhle, BZ — Buzhora, DF — Dietfurt and Spitzbubenhöhle, OE — Oehningen, PL — Polgárdi, SM — St. Margarethen. Present range after ARNOLD and BURTON, 1978, and other sources.

For further comments see pp. 52, 84 and 131

VI. DISCUSSION

History of the ophiofauna in the territory of Poland is especially well documented for the period from the Middle Pliocene until Recent. Ophidian remains coming from older epochs are not numerous and therefore provide only fragmentary data on the composition of snake faunas. Nevertheless, based on the available materials, one can clearly distinguish several different stages in the history of snakes from Poland:

1. Middle Miocene: exclusively extinct genera; Recent genera, if present, remain undeterminable.

2. Upper Miocene/Early Pliocene: both extinct and Recent genera; lack of Recent species.

3. Middle/Upper Pliocene: exclusively Recent genera; both extinct and Recent species, the former species close to the living ones.

4. Early Pleistocene: exclusively Recent species, however, at least in part morphologically somewhat different from snakes living to-day.

5. Younger Quaternary: exclusively modern species, osteologically identical with to-day living snakes. The Quaternary snake fauna does not differ qualitatively from Recent Polish fauna, however, quantitative relations among particular species are different, with increased representation of thermophilous forms.

Constitution of Polish ophiofaunas confirms generally accepted views on the Neogenous and Quaternary snake history in the Holarctic region. As pointed out by Tihen (1964), Auffenberg and Milstead (1965), Gelbach (1965), Hoffstetter (1968), Holman (1977), Rage (1982), and other authors, a great modernization of Holarctic snake faunas, leading to the formation of modern ophidian taxa, took place in the Miocene epoch. In the late Paleogene of this region the ophidian fauna was comprised almost exclusively of primitive groups of snakes, for the most part belonging to the family *Boidae*. Suddenly in the Miocene the archaic snakes were dominated and then replaced by modern colubroids. The presence of both archaic and advanced snakes was typical of Upper Miocene/Early Pliocene times; such a situation can be also observed in the materials from Poland.

The Pliocene is generally considered as a transition period in which many extinct snake species were replaced largely by living forms. This standpoint is also fully valid with reference to Polish records, although there is a confusion because of dissimilarity of Pliocene snake faunas from Poland and adjacent (southern) territories. The question concerns living colubrid species, namely *Elaphe longissima* and *Natrix natrix*, unknown from before the Early Pleistocene from the Polish region, but reported from Hungarian and Austrian Upper Miocene and Pliocene localities (Bolkay, 1913; Szunyoghy, 1932; Mais and Rabeder, 1977). These records, if indeed valid, would suggest that both species appeared during the Neogene in southern Europe and invaded territory of Poland (and afterwards western Europe) prior to the extinction or withdrawal

westwards of the Polish Pliocene snake fauna, thus as early as the beginning of the Quaternary. However, it is improbable that snakes now occupying northern Europe (especially *Natrix natrix*) were restricted during the Pliocene to the areas situated south from Poland. On the other hand, during the Pliocene Polish territory was invaded, beyond a doubt from the South, by a mediterranean species, *Vipera ammodytes*, absent in the Polish Pleistocene. The records from Hungary and Austria, for the most part either undescribed and not figured, or based on solitary cranial bones, need re-examination and might be ignored here with the exception, however, of *Elaphe longissima* from the Upper Miocene of Polgárdi, described on the basis of several bones, thoroughly figured and thus acceptable with confidence (*Zamenis Kormosi* of BOLKAY, 1913, pl. 12: Figs. 4—8). Nevertheless, Polgárdi is the only Miocene site from which Recent ophidian species have been described. No living snake species has been reported from the Neogene of Western Europe; from North America living snake species are not known until the Upper Pliocene (cf. HOLMAN, 1979).

After the beginning of the Pleistocene Holarctic species of snakes were already well established. Most of these species survived up to the present; speciation, if took place, existed rather at the subspecific level. All Quaternary snake remains found in Poland, as well as most of the fossils from other European countries, belonged to Recent species. A few extinct species from the younger Pleistocene of Central Europe, as mentioned in the foregoing chapter (Vc), most likely were indeed living forms. Recent papers concerning West European Pleistocene ophiofaunas describe the fossils, unless restricted only to generic level, as belonging to living species. Some extinct species of snakes from the Pleistocene of France have been described as far back as the middle of the 19th century by POMEL, 1853 (cf. also redescriptions of de ROCHEBRUNE, 1880) and their taxonomic status should be urgently revised *. According to HOLMAN (1981) only two of the 61 identified species of Nearctic Pleistocene snakes are presently considered to be extinct; recently, several extinct ophidian species have been described from the Early Pleistocene of Florida by MEYLAN (1982).

Considering the generally accepted view that European herpetofaunas for the most part were being formed by newcomers from the East (for details see Chapter VII), the territory of Poland must have played in the past an important part as a transit corridor for succeeding waves of invaders from Central Asia or even North America. Unfortunately, because of the scantiness of ophidian remains from the Polish Miocene and Early Pliocene, these hypothetical migrations are poorly documented. There are at least two indirect records supporting this standpoint. The first evidence is presence of the North American genus *Ogmophis* in the Middle Miocene of OP which, considering that its Nearctic origin is certain, could reach Europe only via an Asiatic route. The second evidence is presence of the West European form, *Coluber viridiflavus-C. robertmer-*

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* In opinion of Dr. J.—C. RAGE (pers. comm., 1983) Pleistocene snake species described by POMEL (1853), *Coluber fossilis* and *C. gervaisii*, are both nomina dubia.

tensi, in the younger half of the Polish Pliocene, the range of which must have withdrawn westwards at the end of the Neogene.

Since the Upper Pliocene these parallel movements across Polish territory were replaced by exclusively meridional migrations and retreats of snake fauna resulting from fluctuating ecological conditions during the Pleistocene. It is easy to demonstrate that composition of snake faunas reflects these changes well.

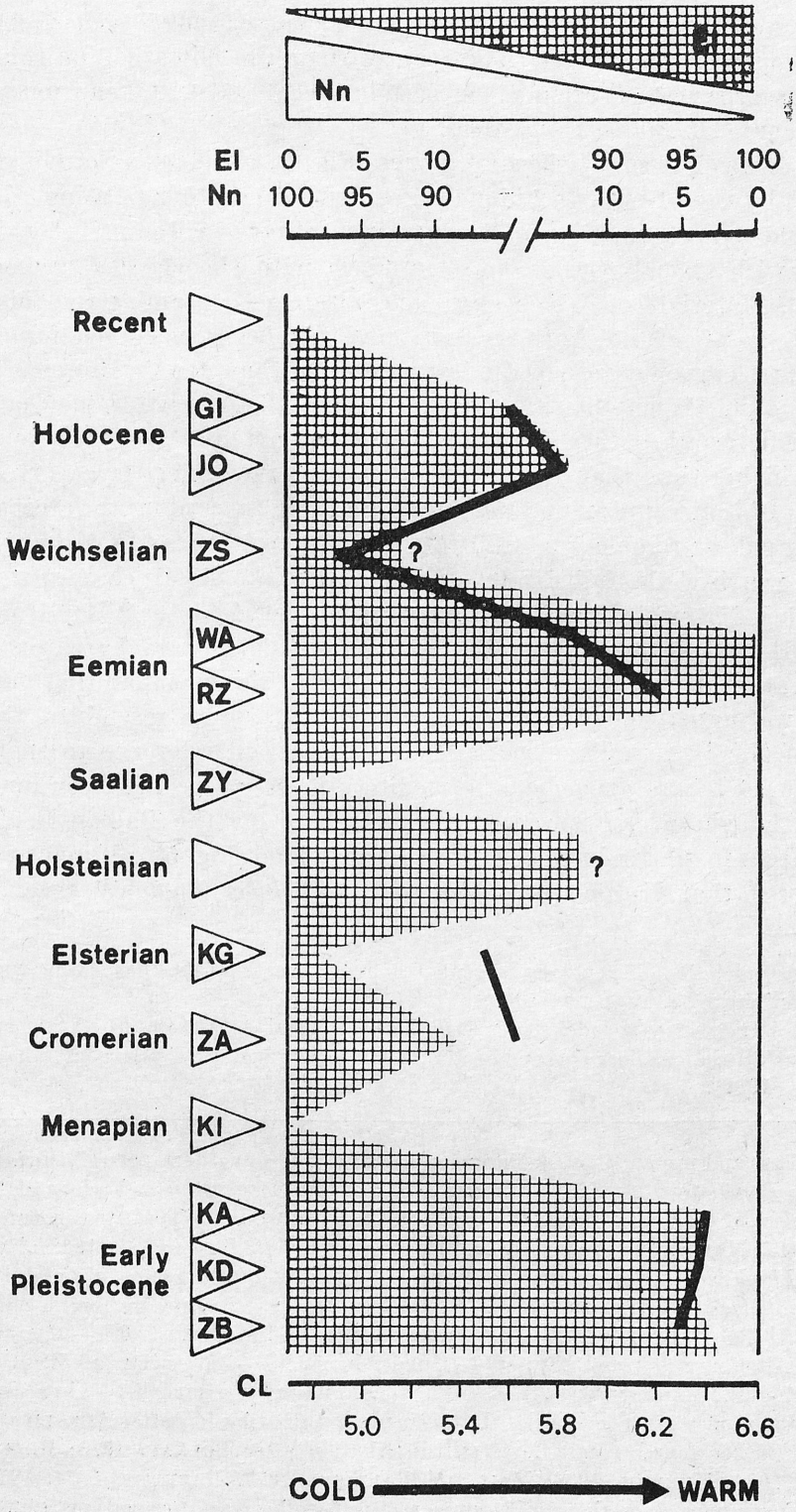
As mentioned above, the ophiofauna of the Polish Pleistocene consisted exclusively of species presently living in our country. Three of them, *Natrix natrix*, *Coronella austriaca* and *Vipera berus*, are eurythermic forms with present range reaching North Europe. As pointed out earlier by MŁYNARSKI (1961b and other papers), the fourth species, *Elaphe longissima*, owing to the fact that the southern frontier of Poland is the northernmost border of its European range, is a good indicator of fluctuations of Quaternary climate. Since *E. longissima*, like other reptiles, is a typical ectotherm depended on external sources of heat, then its presence in a fossil locality simply indicates that the climate of this site was warmer than at the present time; its absence suggest similar or even worse climatic conditions.

However, the above method of determination of paleoclimates provides only an alternative datum: warmer or cooler in comparison with a certain temperature, but does not enable us to compare to one another climatic conditions of various localities. The latter problem can be solved by comparison of the total number of specimens belonging to two species of different thermic requirements; here thermophilous *Elaphe longissima* and eurythermic *Natrix natrix*, as remains of both snakes usually occur together in majority of Polish Quaternary localities. Inference from these comparisons is obvious: the more specimens of *Elaphe longissima* the warmer climate and vice versa. Proportional ratios of both forms in materials from particular localities have been estimated exclusively on the basis of vertebrae (cranial bones are absent in many materials); as the column of *E. longissima* contains more vertebrae than that of *Natrix natrix*, an appropriate correction have been introduced into calculations.

Since use of this method can raise various doubts, e. g. that composition of fossil deposits does not reflect the real relationship between both species, I have confronted the results using another technique, introduced by BRATTSTROM (1967). The latter method is based on the fact that reptiles, as ectothermic animals deriving their heat from the environment, are subject to BERGMANN's rule inversely than endotherms. Consequently, specimens living

Fig. 58. Share of *Elaphe longissima* (squared field) and *Natrix natrix* (white field) in materials from succeeding fossil localities of the Polish Quaternary (proportional composition of both species is indicated in the upper scale). Black line indicates maximum size of vertebrae (CL) of *Elaphe longissima* from succeeding sites (CL value is shown in the lower scale). For further

comments see p. 136


Nn
El 0 5 10 90 95 100
Nn 100 95 90 10 5 0
Recent
Holocene
GI
JO
Weichselian
ZS
?
Eemian
WA
RZ
Saalian
ZY
Holsteinian
?
Elsterian
KG
Cromerian
ZA
Menapian
KI
Early Pleistocene
KA
KD
ZB
CL
5.0 5.4 5.8 6.2 6.6
COLD
WARM

in warmer conditions grow to a larger size than these living in cooler conditions *; on the contrary, the larger snake the warmer the climate. For this purpose I have used basic measurements of vertebral centra (CL) taken from the greatest vertebrae of *Elaphe longissima*.

As it is easily seen at the first glance (Fig. 58), the curves of climatic changes built by use of both techniques agree with each other to a high degree. As one would expect, maxima of temperature coincide with interglacial periods, minima with glacial periods, in accordance with the classical geological evidence **. Materials of Weichselian age, although containing remains of both *Elaphe longissima* and *Natrix natrix*, have not been considered for constructing the first curve because of the low number of these fossils. Presence of *Elaphe longissima* in Weichselian time (ZD, ND, ZS, CI), though somewhat surprising, can be ascribed to the Upton Warren interstadial (average temperature of June higher than that at present by 1° or 2°) and Older Dryas (average temperature of June approximating the present one) according to latest data provided by paleoentomologists (cf. BIRKS and BIRKS, 1980, and references therein).

It is worth while to dedicate some final remarks in this chapter to problems concerning dispersal of mediterranean snakes (cf. Chapter VII) into the territory of Poland. MŁYNARSKI's (1962, 1977) opinion (in part based on erroneous identification of ophidian taxa) that the herpetofauna inhabiting our country during warm periods of the Pliocene and Pleistocene resembled the Recent fauna of the Balkan Peninsula is false, at least in reference to snakes. With exception of *Vipera ammodytes* no mediterranean species has been found in Poland, although several species presently inhabiting the Balkan Peninsula are known from fossil sites situated south from Poland (Fig. 59). Moreover, it should be stressed that *V. ammodytes* (as well as *Coluber jugularis*) reaches further

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* This rule, though generally accepted among herpetologists, has been questioned by several authors (e. g. LINDSEY, 1966).

** It is necessary to add that recent herpetological data from North America do not support at all the classical concept of alternating cool-glacial and warm-interglacial climates (HOLMAN, 1980).

Fig. 59. Past and present Central European distribution of mediterranean *Colubrinae* unknown from the Polish territory. Cj — present range of *Coluber jugularis* (horizontal lines); 19th century sites of the occurrence of this snake in Czechoslovakia are indicated by asterisks (JEITTELES, 1862; MALESEVICS, 1888; KAMMERER, 1901; cit. after OLIVA et al., 1968); Eq — present range of *Elaphe quatuorlineata* (vertical lines); Cg, Cn, Es — present range of *Coluber gemonensis*, *Coluber najadum* and *Elaphe situla* (dotted). Abbreviations of names of fossil localities: BD — Beremend, BO — Brassó, BR — Breitenberghöhle, BT — Betfia, CS — Csarnóta, DA — Deutsch Altenburg-2, 4 and 20, GU — Gundersheim, NH — Nagyharsány-hegy, PL — Polgárdi, SM — St. Margarethen, VY — Villány-3. Names of fossil localities are accompanied by abbreviated names of snake species. Data for present distribution after ARNOLD and BURTON, 1978, and other sources; data for fossil distribution after BOLKAY, 1913; BRUNNER, 1957; HELLER, 1936; KRETZOI, 1956; MAIS and RABEDER, 1977, RABEDER, 1974, 1977a, 1977b. Continuous lines show mid-summer (July) isotherms (after various sources)

Cj
Eq
Cg
Cn
Es
16
18
20
22
GU (Cj)
BR (Es)
DA (Cg—Cj Eq)
SM (Cg)
PL (Cj, Cn)
VY, NH (Cj)
BD, CS (Cj)
BT (Cj)
BO (Cj)

northwards than other mediterranean snakes; at the beginning of the 20th century isolated colonies of both species, no doubt Holocene relicts, still inhabited Moravia, close to the southern frontier of Poland. In this connection, presence of *Vipera ammodytes* in the Polish Pliocene is obvious; northernmost ranges of other mediterranean species probably never reached even the southern part of Poland.

Various reasons might have contributed to the absence of mediterranean snakes in the territory of Poland in the past, e. g. presence of physical barriers (mountains) at southern frontier of Poland. However, an inadequate climatic regime presumably was of the greatest importance. Because of the ectothermic nature of reptile physiology their distribution to the North is determined largely by available heat energy. The most important factor is temperature of summer-time; significance of several other factors such as surface net radiation and number of mid-summer sunshine hours, although obvious, are poorly ununderstood because of the absence of suitable information (SPELLERBERG, 1976). Assuming that mean temperatures of interglaciations were 2° or 3° higher than those of today and displacing mid-summer isotherms for Central Europe accordingly we will find that even in favourable terms ranges of mediterranean snakes could not have reach southern Poland (Fig. 59).

VII. ORIGIN OF MODERN SNAKE FAUNA OF EUROPE

As discussed in the previous chapter, routes of Asiatic migrants that formed Recent European snake fauna must have crossed in the past the territory of Poland. In this connection, paleo-ophiological data from Poland, supplemented by evidence from other countries of Central Europe, can be useful for reconstruction of distributional history of European snakes.

The modern snake fauna of Europe for the most part was being formed by immigrants from the East that invaded the continent during the Pliocene. As pointed out by DARLINGTON (1957), extensive speciation of reptiles is restricted to tropical rather than temperate zones. Indeed, fossil snakes known since the Middle Pliocene of Europe were either Recent species or forms very close to them; evolutionary events occurring in European territory after the Miocene must have been on a limited scale. Some speciation leading to origin of new snake species, however, must have taken place also in Europe. Considering their taxonomic relationship and present distribution, origin of at least the following specific pairs — *Coronella austriaca-C. girondica*, *Natrix tesselata-N. maura* or *Vipera berus-V. seoanei* — resulted from local speciation, the latter phenomenon possible owing to rapid isolations, usual in fluctuating ecological conditions at the end of the Pliocene and during the Pleistocene.

If the previous remarks are valid for advanced snakes *(Colubroidea)*, few members of older families, namely *Boidae* and *Typhlopidae*, are thought to be

survivors of animals widespread in Europe in the past rather than modern immigrants from the East.

The ophidian fauna from the Eocene of Europe is comprised almost exclusively of *Boidae*, *Aniliidae* and *Scolecophidia* (HOFFSTETTER, 1968). *Aniliidae* are unknown from Europe since the beginning of the Neogene; ophidian remains, reported as *Aniliidae* by PAPP et al. (1954) from the Upper Miocene of Viennese Basin, were referred by RAGE (1974) to the subfamily *Boinae*. Large boas of the subfamily *Boinae* were represented in the Miocene of Europe by only few forms (cf. ROEMER, 1870; de ROCHEBRUNE, 1880; PORTIS, 1901; ANTUNES and RAGE, 1974), all these animals disappeared up to the end of the Miocene. Small boids of the subfamily *Erycinae* were widespread in the European Paleogene and Neogene (HOFFSTETTER and RAGE, 1972; see also chapter Va, p. 33); only a single species, *Eryx jaculus*, survided up to the present. *Scolecophidia*, found as fossils in the French and Spanish Miocene (HOFFSTETTER, 1946; ALFÉREZ and BREA, 1981), are not known from subsequent epochs from the European mainland; to-day, the group is represented in Europe by a single species, *Typhlops vermicularis*.

Except these two species, restricted presently to the Balkans, presumably all remaining European snakes are direct descendants of post-Miocene invaders. Miocene immigrants, although even representing modern taxa of colubroid snakes, must have been tropical or subtropical forms, therefore their extinction in the Neogene must have happened in consequence of deterioration of the European climate during the Pliocene. European *Elapidae* belonging to the extinct genus *Palaeonaja*, known from Western Europe from the Lower Miocene (MN 4) until the Middle Pliocene (MN 15; HOFFSTETTER, 1938, 1939; RAGE and ŞEN, 1976; ALBERDI et al., 1981; ALFÉREZ and BREA, 1981), may have represented just Miocene immigrants *.

As known from paleontological evidence, connection between reptile faunas of Europe and Western Asia have existed for a long time. During the Neogene there was a striking similarity, at least at the familial level, between West Asiatic and West European herpetofaunas (RAGE, 1981b); at the same time, herpetofaunas of southwestern Europe and northwestern Africa differed significantly from each other (ANTUNES and RAGE, 1974) and their composition indicates that the Miocene herpetofauna of northwestern Africa was formed in the result of invasions from Asia, not from Europe (RAGE, 1976).

Problems concerning migrations of modern snake faunas from Asia and their inplantation in Europe have been discussed by several authors: with reference to *Elapidae* by HOFFSTETTER (1938, 1939), *Natricinae* by MALNATE (1960), *Viperidae* by KRAMER (1961), SAINT GIRONS (1980) and others, snakes in general by RABB and MARX (1973) and recently by RAGE (1982). The most complete source of information on the latest history of the European snake fauna

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* Recently also found in the Late Miocene (MN 11) of Kohfidisch, Austria (BACHMAYER and SZYNDLAR, in prep.).

is their present distribution, so it is necessary to introduce here some essential data.

The Recent European ophidian fauna shows an interesting division into two distinct groups: eastern * and western species. Except 5 species, known from both eastern and western parts of the European mainland, the remaining 20 species are known exclusively from either East or West. The border line where the ranges of most species from the latter group overlap is situated in the area of the Julian Alps; ranges of particular eastern and western forms overlap to a minimal degree only at the territory of Slovenia. Ranges of 3 eastern snakes, however, cover Italy; nevertheless, distribution of 2 of these species is restricted to the southern part of the Appenine Peninsula. The same distributional pattern is also found among European lizards.

According to the latitudinal distribution of snakes (thus also acordingly to their thermal requirements) one can divide European species into three groups:

1. Mediterranean species — restricted to a narrow strip of land along the Mediterranean Sea including (or not) territories of mediterranean peninsulas; 16 species altogether.

Table XXIII

Distributional division of European snakes

	West European species	East European species
Boreal species	*Vipera berus*	
	Natrix natrix	
	Coronella austriaca	
	Elaphe longissima	
Paramediterranean species	*Vipera aspis*	*Natrix tesselata*
	Natrix maura	*Vipera ursinii*
	Coluber viridiflavus	*Coluber jugularis*
Mediterranean species	*Coronella girondica*	*Vipera ammodytes*
	Vipera seoanei	*Elaphe quatuorlineata*
	Elaphe scalaris	*Elaphe situla*
	Vipera latasti	*Coluber najadum*
	Coluber hippocrepis	*Coluber gemonensis*
	Macroprotodon cucullatus	*Telescopus fallax*
		Typhlops vermicularis
		Eryx jaculus
	Malpolon monspessulanus	

* The term „Eastern Europe", as used in this chapter, is restricted to the area between the Adriatic and Black Seas.

2. Parameditterranean species — distributed further north than the previous group, up to about 49°—50° N; 6 species altogether.

3. Boreal species — distributed much further north, at least up to 60° N; 3 species altogether.

Division of European snakes according to their eastern-western and latitudinal distribution is shown in Table XXIII. The list includes neither species inhabiting European borderlands *(Eryx miliaris, Eirenis collaris, E. modestus, Elaphe dione, E. hohenackeri, Vipera kaznakovi, V. xanthina, Agkistrodon halys)* nor insular species *(Coluber algirus, Vipera lebetina)*.

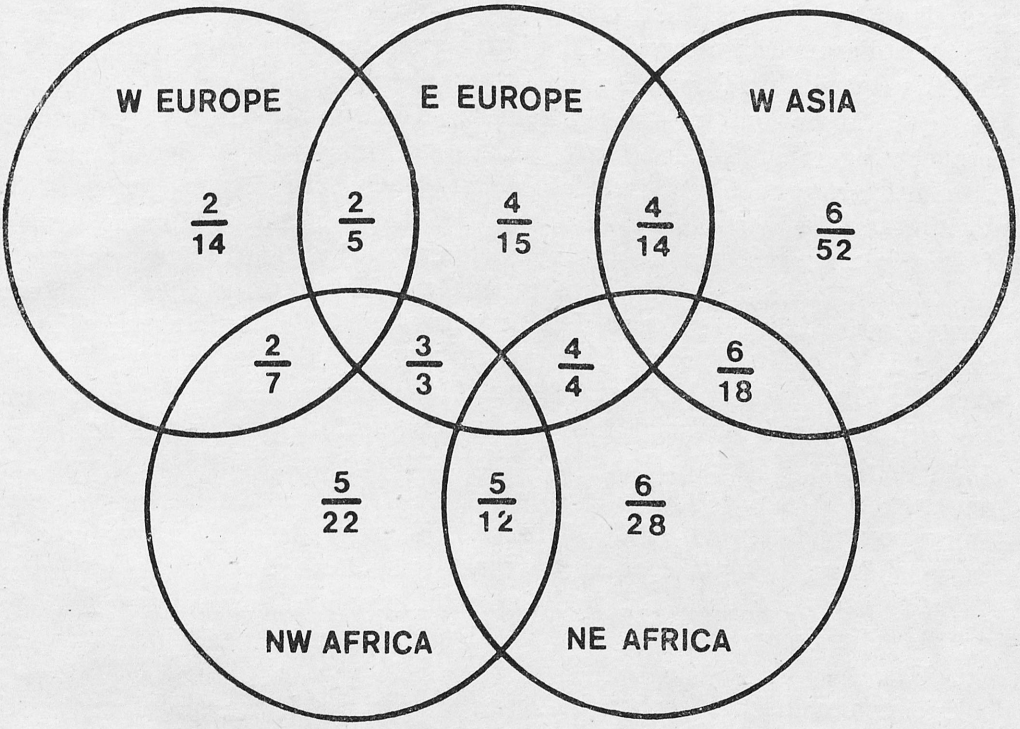


Fig. 60. Frequency distribution of Recent snakes of Europe, Western Asia and Northern Africa. Numerator — number of families; denominator — number of species. Data from Başoglu and Baran 1980; Hoofien, 1972; Marx, 1968; Mertens and Wermuth, 1960; and Pasteur and Bons, 1960

Separation of European snake fauna into eastern and western species, surely not accidental, presumably was caused by effective physiographic barriers, occurring in the past about the area of the present location of the border line between both groups. Indeed, as widely known, the Tethys Sea was connected with the Pannonian Basin of the Paratethys by an inlet located at the territory of Croatia and Slovenia since the Oligocene epoch. Although this inlet disappeared in the Upper Miocene, however, presence of the Alps in the north together with transgression of the Tethys into Lombardia and

Piemonte since the Early Miocene until the beginning of the Quaternary caused the effective physical barrier to persist in the area.

Pliocene migrants from Asia must have invaded Europe with the use of two routes (Fig. 61), separate and remote from each other: northern, at least in part presumably via the territory of Poland, and southern, via Asia Minor—in order to pass round the Paratethys. Snake faunas advancing by the southern way, naturally must have been composed of more thermophilous animals than faunas using the northern way. The former group, after reaching the Balkan Peninsula, migrated northwards along the Adriatic coasts; because of higher thermic requirements, however, their further advance was at last stopped east from the Alps; physical barriers at the base of the Appenine Peninsula prevented their dispersion westwards. The latter group, rounding the Alps from the North, reached French and Italian territory, but did not invade the Iberian Peninsula. Migrations into Iberia from the North were probably hindered by both physiographic barriers (the Pyrenees) and competition of local fauna, for the most part probably of indirect African origin. After disappearance of the maritime barrier between West Asia and Africa at the end of Miocene, a wave of Asiatic migrants, similar to those advancing by South European route, also entered Africa, and therefore around the Mediterranean Basin a homogeneous snake fauna developed. The first invasion of the modern snake faunas from Africa to Iberia could have taken place at the end of the Miocene when the broad inlet between linking of the Tethys Sea and the Atlantic Ocean disappeared. Although the isthmus was of short duration and the ocean appeared again, it seems that the newly formed Strait of Gibraltar was narrow enough to enable some migrations of snakes. As in the case of mammals (Crusafont and Savage, 1973), transtethyian migrations of snakes by other routes, if they took place at all, occurred sporadically.

Analysis of distribution of the Recent European snake fauna provided some important evidence in support of the hypothesis presented above (see also Fig. 60).

Occurrence in both eastern and western parts of Europe is characteristic for northern snakes that have an extensive south-northern and east-western range. All three boreal species inhabit both East and West of Europe.

Except *Natrix maura* the remaining 3 paramediterranean species known from Western Europe are practically absent in the territory of the Iberian Peninsula (occurrence restricted to the northeasternmost part of Spain). Both their northern occurrence and absence in Iberian territory confirm the hypothesis that these species could reach their present range by a North African route.

Among mediterranean snakes only one of 16 species *(Malpolon monspessulanus)* is distributed also in the East and the West. Except the European endemic *Coluber gemonensis*, all mediterranean snakes from Eastern Europe are also known from West Asia.

Except *Coronella girondica*, the remaining 6 western mediterranean species

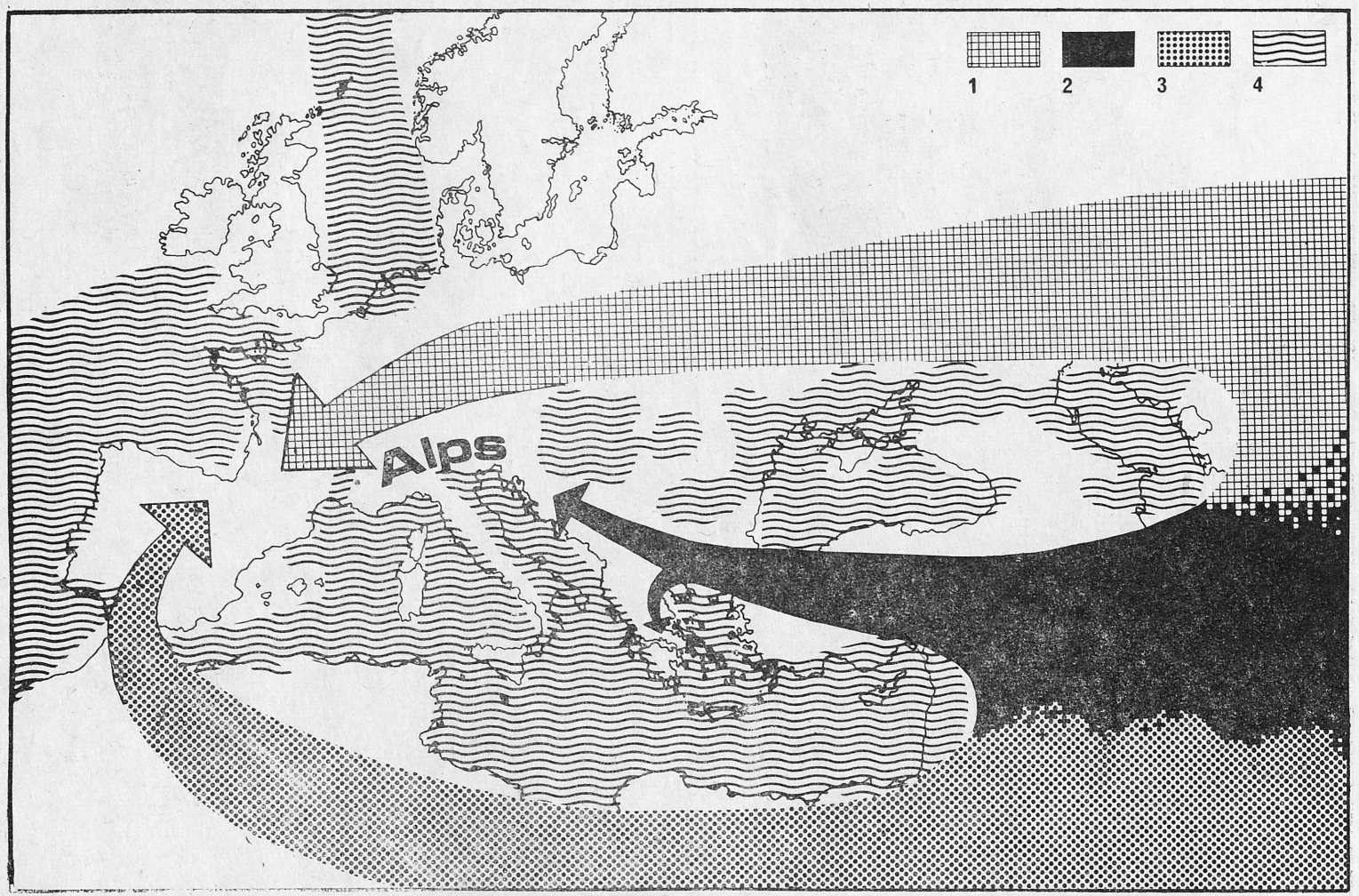
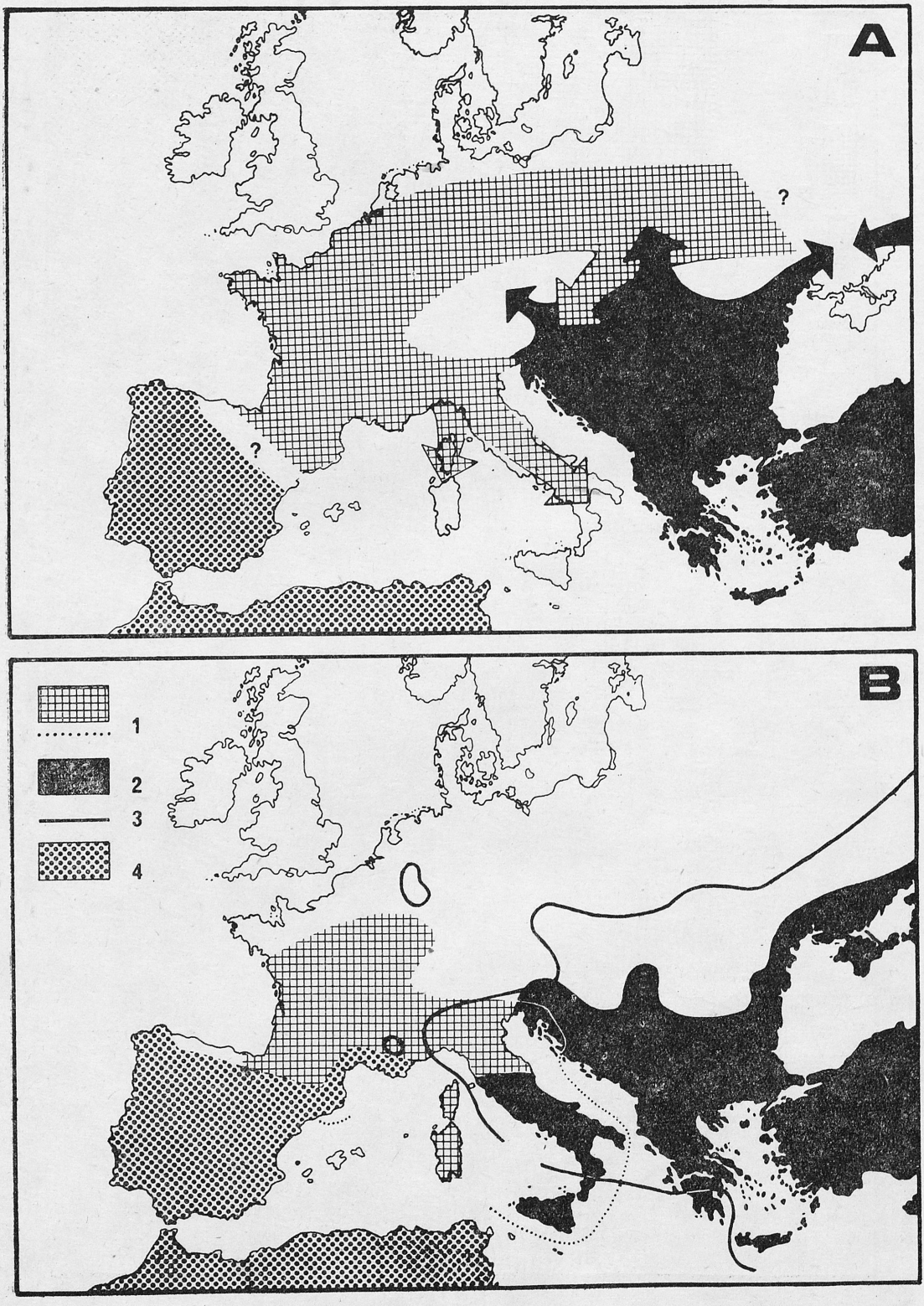


Fig. 61. Main hypothetical routes of migration of snakes in Europe during the Pliocene. 1 — North European route, 2 — South European route, 3 — North African route, 4 — areas covered by the sea (after POMEROL, 1973)


A
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4

are restricted to the Iberian Peninsula and (eventually) to a narrow land strip in southern France. These species, unless Iberian endemics, also inhabit northwestern Africa (cf. CRUSAFONT-PAIRÓ, 1958, with reference to endemism of Iberian mammalian faunas).

It is notable that both exceptional species from West Europe, *Coronella girondica* and *Natrix maura* *, are supposed to be not immigrants but most likely are of European origin (cf. e. g. THORPE, 1975; SAINT GIRONS, 1980).

Presence of the North African *Vipera lebetina* in the Cyclades appears to be evidence of occasional migrations across the Tethys Sea. Presence of another African element in the Aegean area, namely *Naja* sp., reported from the Middle Pleistocene of Chios by SCHNEIDER (1975), remains dubious according to the statement of RAGE and ŞEN (1976) that distinguishing between *Naja* and *Palaeonaja* on the basis of vertebrae alone is uncertain.

During the Quaternary, owing to further deterioration of the European climate, ranges of a number of snake species contracted southwards. Northernmost distributed East European mediterranean snakes (e. g. *Vipera ammodytes*) and parameditерranean West European snakes *(Coluber viridiflavus)*, previously sympatrically present in Central Europe, retreated from the area. On the other hand, continentalization of European climate in consequence of decrease of temperature and humidity, and therefore development of climatic and vegetable zones, also exerted an important influence on distribution of snakes (cf. SAINT GIRONS, 1980, with reference to vipers). Although by the beginning of the Pleistocene the physical barrier in North Italy disappeared, no migrations of West and East European snakes followed by the route south from the Alps, most likely because ecological niches were occupied by local faunas which actually formed faunal barrier to one another. In postglacial (warm) periods ranges of mediterranean snakes again were shifting northwards, moreover, eastern species must have entered a little into Western Europe and vice versa, but never to the degree observed in the Pliocene. As is well known from paleontological evidence, at that time Eastern Europe was deeply penetrated by at least one western species, *Coluber viridiflavus* (cf. Fig. 25), how-

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* THORPE (1975, p. 181) accepts that speciation of the closely related snakes *Natrix tesselata* and *N. maura* took place in the Pleistocene when the ice caps split the ancestral species into western and eastern components. However, this differentiation must have appeared earlier as at least *N. tesselata* is known already in the Neogene. Range of the hypothetical ancestral species could have fragmented not because of the presence of a physiographic barrier, but owing to the occurrence of a competitive snake species in Central Europe, e. g. *N. longivertebrata* sp. n.

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Fig. 62. Hypothetical distribution of West and East European snake faunas at the end of the Pliocene (A) and at present (B). 1 — maximum range of West European parameditерranean species (except *Natrix maura*), 2 — maximum range of East European mediterranean species, 3 — maximum range of East European parameditерranean species, 4 — maximum range of West European mediterranean species (except *Coronella girondica*)

ever, because of the competition of the East European mediterranean fauna, those migrations presumably did not come from nearby Croatia, but must have rounded the Alps from the North.

The separation into western and eastern ophidian faunas must have been established during glaciations, when ranges of particular snake species were drastically reduced to refuge areas in mediterranean peninsulas. The same phenomena produced subspecific speciation of northern snake species (e. g. THORPE, 1975). At that time, eastern mediterranean snakes invaded, perhaps, the Appenine Peninsula, although there is no direct evidence in favour of this supposition. Presumably during the Pleistocene, as well, disconnection of ranges of mediterranean snakes took place in North Africa, in consequence of severe climatic changes (cf. MOREAU, 1963).

Contrary to the mediterranean ophidian fauna, boreal snakes succeeded in expanding throughout vast areas of Palearctica during the Glacial epoch. It is quite possible that changing ecological conditions of the Quaternary contributed to development of the eurythermic nature of these reptiles that enabled their extensive Recent distribution.

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STRESZCZENIE

Praca niniejsza stanowi monograficzne opracowanie kopalnych węży pochodzących z 27 polskich stanowisk, datowanych od środkowego miocenu po holocen. Część materiałów, pochodzących z 13 stanowisk, była poprzednio opisywana przez Młynarskiego (1961a, 1961b, 1962, 1964, 1977; Młynarski w Kowalski et al., 1963; Młynarski w Bałuk et al., 1979) i Szyndlara (1981, 1982); pozostałe są opisywane po raz pierwszy.

Na wstępie podano krótką charakterystykę wszystkich stanowisk kopal-

nych (Rozdział II; Ryc. 1, Tab. I i II), podając ich wiek geologiczny, korelację z innymi stanowiskami kopalnymi w kraju i za granicą, warunki środowiskowe (paleoklimat i szata roślinna), liczbę szczątków węży wraz ze składem gatunkowym oraz listę literatury zawierającej ich opis. Następnie przedstawiono szczegółowe metody badawcze, przy zastosowaniu osteologii porównawczej (Rozdział III) oraz biometrii i analizy statystycznej (Rozdział IV).

W części szczegółowej (Rozdział V) podano dokładny opis wszystkich szczątków kopalnych węży znalezionych do tej pory w Polsce; opis morfologiczny uzupełniają ryciny i tabele zawierające pomiary. W sumie rozpoznano 22 odrębne taksony, należące do trzech rodzin, *Boidae*, *Colubridae* i *Viperidae*; w tej liczbie opisano cztery nowe gatunki (*Zelceophis xenos* gen. sp. n., *Natrix parva* sp. n., *Natrix longivertebrata* sp. n., *Elaphe paralongissima* sp. n.) oraz redeskrybowano jeden gatunek (*Coluber robertmertensi* Młynarski, 1964). Pełną listę gatunkową z podaniem stanowisk zawiera Tab. IV. Do opisów poszczególnych taksonów dołączono pełny przegląd pokrewnych gatunków węży opisanych z kopalnych stanowisk Palearktyki wraz z ich współczesnym rozsiedleniem (Ryc. 25, 40, 51, 57 i 59).

W końcowej części opracowania przedstawiono analizę zmian ilościowych i jakościowych zachodzących w faunie węży z obszaru Polski od neogenu po dzień dzisiejszy (Rozdział VI). W omawianym przedziale czasowym można wyróżnić pięć kolejnych charakterystycznych etapów: (1) fauna środkowomioceńska, reprezentowana wyłącznie przez wymarłe rodzaje węży; (2) fauna przełomu miocenu i pliocenu, złożona z przedstawicieli zarówno wymarłych, jak i współczesnych rodzajów; współcześnie żyjących gatunków brak; (3) fauna młodszego pliocenu, złożona wyłącznie z przedstawicieli współczesnych rodzajów, skupiających zarówno wymarłe, jak i współcześnie żyjące gatunki; (4) fauna wczesnego plejstocenu, zawierająca wyłącznie współcześnie żyjące gatunki, aczkolwiek o nieco odmiennej budowie anatomicznej szkieletu; (5) fauna młodszego czwartorzędu, różniąca się od współczesnej fauny Polski tylko ilościowo na korzyść form termofilnych. Wzajemny stosunek ilościowy szczątków węża Eskulapa *(Elaphe longissima)* i zaskrońca *(Natrix natrix)* w materiałach z poszczególnych stanowisk posłużył do odtworzenia zmian klimatycznych zachodzących w trakcie czwartorzędu (Ryc. 58).

Na końcu, w oparciu o współczesne rozsiedlenie węży w Europie oraz o dane paleontologiczne z obszaru Polski i krajów ościennych, podjęto próbę odtworzenia historii migracji współczesnej fauny węży na naszym kontynencie (Rozdział VII). Przedstawione dowody wskazują, że większość europejskich gatunków węży pochodzi od azjatyckich imigrantów. Wskutek istnienia w pliocenie fizycznych barier (Morza Tetydy i Paratetydy) poszczególne gatunki węży posuwały się w głąb Europy trzema odrębnymi drogami: (1) północnoeuropejską, przez terytorium Polski, (2) południowoeuropejską, przez obszar Azji Mniejszej, oraz (3) północnoafrykańską, wzdłuż południowych wybrzeży Morza Śródziemnego (Tetydy) (por. ryc. 61). Od migrantów pierwszej grupy

(1) pochodzi współczesna ofiofauna przyśródziemnomorska, zamieszkująca obszar Francji i Włoch; migranci drugiej grupy (2) dali początek współczesnej faunie śródziemnomorskiej i przyśródziemnomorskiej, zamieszkującej obszar Europy południowo-wschodniej; wreszcie od migrantów trzeciej grupy (3) pochodzi współczesna ofiofauna śródziemnomorska Półwyspu Iberyjskiego (ryc. 62).

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