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A REVIEW OF NEOGENE AND QUATERNARY SNAKES OF CENTRAL AND EASTERN EUROPE. PART II: NATRICINAE, ELAPIDAE, VIPERIDAE

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ABSTRACT

Remains of Neogene and Quaternary "natricine" colubrids, elapids and viperids, including snakes previously described and those undescribed yet, coming from Poland, Ukraine, Moldavia, Czechoslovakia, Austria, Hungary, Romania, Bulgaria, and Greece are discussed. The following taxa, including 11 extinct species, were recognized: "Natricinae": *Neonatrix nova, Neonatrix* sp., *Palaeonatrix silesiaca, Palaeonatrix lehmani, Natrix longivertebrata, Natrix* cf. *N. longivertebrata, Natrix natrix, Natrix tesselata, Natrix* cf. *N. tesselata, Natrix* sp., "Natricinae" indet.; Elapidae: *Naja romani, Naja* sp., cf. *Naja* sp.; Viperidae: *Vipera platyspondyla, Vipera sarmatica, Vipera burgenlandica, Vipera gedulyi, Vipera kuchurganica, Vipera antiqua, Vipera* cf. *V. ammodytes, Vipera berus, Vipera* sp. ('Oriental vipers' group), *Vipera* sp. (*'aspis'* group), *Vipera* sp. (*'berus'* group), *Vipera* sp. (status unknown). Taxonomic status of two other extinct species, *Natrix parva* and *Laophis crotaloides,* is uncertain. Modern species appeared first in Central and East Europe in the middle Pliocene (MN 15). Older snakes belonged to extinct species of either extinct or extant genera; taxonomic distinction of most extinct genera is, however, not fully demonstrated. Best recognized oldest snakes from the area (Elapidae, Viperidae, and some Colubridae) are clearly referable to modern genera and intrageneric subdivisions occurring today are observed in oldest (lower Miocene) remains; closest living relatives of these fossils are presently distributed in the Oriental Realm.

Key words: *Serpentes, Colubridae, Elapidae, Viperidae, Europe, Miocene, Pliocene, Pleistocene, Taxonomy, Paleofaunistics, Morphology.*

RESUMEN

Se revisan y estudian los restos neógenos y cuaternarios de colúbridos «natricinos», elápidos y vipéridos, incluyendo tanto serpientes previamente descritas como otras inéditas. Los materiales analizados proceden de Polonia, Ukrania, Moldavia, Checoslovaquia, Austria, Hungría, Rumania, Bulgaria y Grecia. Se reconocen los siguientes taxones, incluyendo 11 especies extinguidas: Natricinae: *Neonatrix nova, Neonatrix* sp., *Palaeonatrix silesiaca, Palaeonatrix lehmani, Natrix longivertebrata, Natrix* cf. *N. longivertebrata, Natrix natrix, Natrix tesselata, Natrix* cf. *N. tesselata, Natrix* sp., «Natricinae» indet.; Elapidae: *Naja romani, Naja* sp., cf. *Naja* sp.; Viperidae: *Vipera plastyspondyla, Vipera sarmatica, Vipera burgenlandica, Vipera gedulyi, Vipera kuchurganica, Vipera antiqua, Vipera* cf. *V. ammodytes, Vipera berus, Vipera* sp. («grupo Oriental»), *Vipera* sp. (grupo *«aspis»*), *Vipera* sp. (grupo *«berus»*), *Vipera* sp. (relaciones desconocidas). El estatus taxonómico de otras dos especies extintas, *Natrix parva* y *Laophis crotaloides,* es poco claro. Las especies actuales aparecen primero en Europa central y oriental durante el Plioceno medio (MN 15), mientras que las serpientes más antiguas pertenecen a especies extinguidas, incluidas tanto en géneros actuales como también en otros ya extinguidos. La validez taxonómica como entes independientes de muchos géneros extintos no está plenamente demostrada. Las serpientes bien conocidas más antiguas del área (Elapidae, Viperidae, algunos Colubridae) son claramente adscribibles a géneros actuales, y las subdivisiones intragenéricas actualmente existentes pueden ya observarse en los restos más antiguos (Mioceno inferior). Formas actuales cercanas a estos fósiles miocénicos se encuentran distribuidos en la Region Biogeográfica Oriental.

Palabras clave: *Serpentes, Colubridae, Elapidae, Viperidae, Europa, Mioceno, Plioceno, Pleistoceno, Taxonomía, Paleofaunística, Morfología.*

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Introduction

The present paper, devoted to Neogene and Quaternary "natricine" colubrids, elapids and viperids from Central and Eastern Europe, supplements Szyndlar's (1991) review of fossil scolecophidians, boids and "colubrine" colubrids coming from the same area. Table I lists all ophidian taxa described in both papers.

The arrangement of the information presented below in the chapter "Systematic account" follows exactly the system employed in my previous paper; see chapters "Localities" and "Systematic account" in Szyndlar (1991) for details.

The chapter "History of snakes in Central and East Europe" is based on the data presented in both papers and summarizes information about the composition and past distribution of the extinct snake fauna in the area, against the background of the recent fauna. The last chapter of the present paper, containing a critical review of methods used in ophidian paleontology, summarizes my ten-years experience with research on Neogene and Quaternary European snakes.

Systematic Account

Family COLUBRIDAE (s.l.) Oppel, 1811
"Natricines".

The basic feature differentiating natricine vertebrae from those of other members of the family Colubridae (s.l.) is the presence of hypapohyses throughout the precaudal region of the column; colubrines possess hypapophyses in the cervical region only, while in the remaining precaudal vertebrae this structure is replaced by the haemal keel. Natricine vertebrae can be easily distinguished from those belonging to other hypapophysis-bearing snakes. They differ from the Viperidae in having usually sigmoid (and not straight) hypapohyses, posteriorly vaulted (and not depressed) neural arches, shorter parapophyseal processes, and usually much longer centra (Szyndlar 1984, 1988). They differ from the Elapidae in having lightly built vertebrae, provided with much longer centra and strong subcentral ridges. In addition, the modern genus *Natrix* has relatively much higher neural spines than those of elapids.

Natricine snakes presently inhabiting Europe belong exclusively to the genus *Natrix* (see below). There are two valid extinct genera known from Europe, *Neonatrix* and *Palaeonatrix*.

Genus *Neonatrix* Holman, 1973.

Neonatrix is an extinct genus, widespread in the North American and European Miocene (Holman, 1979; Rage, 1984; Rage and Holman, 1984). The most important diagnostic feature of this genus are strongly reduced hypapophyses. One species was reported from East Europe.

Neonatrix nova Szyndlar, 1987 (fig. 1).

1987a *Neonatrix nova* Szyndlar, pp. 61-62, fig. 6.

Material: (37) Lower Miocene (MN 4) of Dolnice (type locality): one trunk vertebra (holotype, DPFNSP 5197), 62 precaudal vertebrae (DPFNSP 931, 932, 934-937, 1171, 1237, 1245, 1253, 1311, 1312, 1414, 1419, 1430, 1433, 1440, 1443, 1451, 1458, 3962, 3967, 3979, 3983, 3987, 3988, 4026, 4029, 4030, 4075, 4107, 4201, 4511, 4526, 4532, 5156-5159, 5162, 5164, 5169, 5171-5173, 5175, 5176, 5182, 5186-5188, 5192, 5194-5196, 5198, 5200, 5202, 5204, 5214, 5221, 5224).

Diagnostic vertebral characters: This extinct species, known only from the type locality, is most similar to its North American relative, *N. elongata*, but differs from the latter in much larger absolute size. The centrum length of the holotype vertebra is 4.33 mm and it is 1.54 times longer than wide. For detailed description see Szyndlar (1987a).

Neonatrix sp.

Material: (38) Middle Miocene (MN 6) of Děvínska Nová Ves: 3 precaudal vertebrae (DPFNSP 5835, 5837, 5843).

Remarks: The vertebrae, somewhat damaged, closely resemble those of *N. nova*, but differ from them by smaller absolute size and by having strongly reduced neural spines.

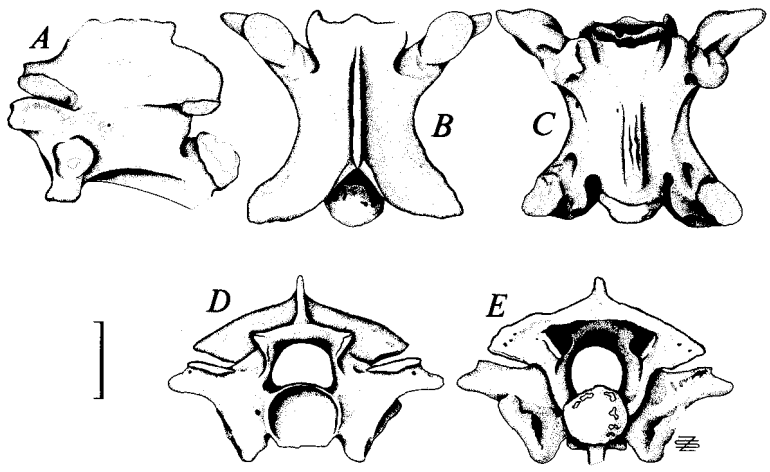

Fig. 1.—Trunk vertebra of *Neonatrix nova* from lower Miocene of Dolnice (holotype, DPFNSP 5197). A, left lateral view; B, dorsal view; C, ventral view; D, anterior view; E, posterior view. Scale equals 2 mm (From Szyndlar, 1987a. Copyright 1987 by the Society of Vertebrate Paleontology. Used with permission).

Genus *Palaeonatrix* Szyndlar, 1982.

This extinct genus consists of two species, *P. silesiaca* and *P. lehmani,* both from the East European Miocene. These snakes are known exclusively by vertebrae. The most important diagnostic features, differentiating *Palaeonatrix* from the living genus *Natrix* and some other related genera, are a prominent anterior keel accompanying the hypapophysis and a vestigial neural spine (Szyndlar 1987a).

Palaeonatrix silesiaca Szyndlar, 1982.

1982 *Palaeonatrix silesiaca* Szyndlar (in Młynarski et al.), pp. 114-116, fig. 10.
1984 *Palaeonatrix silesiaca* Szyndlar: Szyndlar, pp. 45-47, fig. 16.

Material: (2) Middle Miocene (MN 7) of Opole 2 (type locality): one trunk vertebra (holotype, ZPUW OP-86/24), 5 precaudal vertebrae (ZPUW OP-86/21-26), two caudal vertebrae (ZPUW OP-86/27, 28).

Diagnostic vertebral characters: This species, known only from the type locality, differs from *P. lehmani* in some minor features, among others, in lacking the epizygapophyseal process, in having postzygapohyses less expanded laterally, and a relatively larger condyle. The largest vertebra has the centrum length 5.77 mm. For detailed description see Szyndlar in Młynarski et al. (1982) and Szyndlar (1984).

Palaeonatrix lehmani (Rage et Roček, 1983) (fig. 2).

1983 *Dolniceophis lehmani* Rage et Roček, pp. 17-21, Pls. I, II.
1984 *Dolniceophis lehmani* Rage and Roček: Rage, p. 46.
1987a *Palaeonatrix lehmani* (Rage et Roček): Szyndlar, pp. 60-61, fig. 5.

Material: (37) Lower Miocene (MN 4) of Dolnice (type locality): one trunk vertebra (holotype, DPFNSP 3920), 13 precaudal vertebrae (DPFNSP 933, 1207, 1243, 1316, 1408, 1434, 1437, 3969, 4020, 4021, 4096, 4553, 4554).

Diagnostic vertebral characters: Vertebrae of this species are somewhat smaller than those of *P. silesiaca.* For differences between both species see above (*P. silesiaca*).

Remarks: This species, known exclusively from the type locality, was originally described by Rage and Roček (1983) as the only member of the extinct genus *Dolniceophis;* it was then synonymized with *Palaeonatrix* by Szyndlar (1987a). For detailed description see Rage and Roček (1983) and Szyndlar (1987a).

Genus *Natrix* Laurenti, 1768.

The genus *Natrix* consists of four living members presently inhabiting Europe and adjacent areas of the West Paleartic. In addition, four fossil species are known from Europe; their geological age ranges from the Oligocene to Upper Pliocene (Rage 1988). The most important feature differentiating *Natrix* from the extinct natricine genera is a distinctly higher neural spine.

Natrix longivertebrata Szyndlar, 1984 (fig. 3).

(6) 1984 *Natrix longivertebrata* Szyndlar, pp. 71-80, figs. 27, 29.
(34) 1985 *Natrix longivertebrata* Szyndl.: David et al., p. 73.
(6) 1986 *Natrix longivertebrata:* Rage and Szyndlar, *passim,* figs. 2, 4, 7, 8, 11, 12, 15, 16.
(31) (32) 1987 *Natrix longivertebrata:* Redkozubov, p. 71.
(34) 1989 *Natrix longivertebrata:* Redkozubov, p. 209.

Material: (31) Middle Pliocene (MN 15) of Musait: trunk vertebrae (not seen, fide Redkozubov 1987). (6) Upper Pliocene (MN 16) of Rębielice Królewskie 1A (type locality): 2 basioccipitals (ZZSiD RKI-10001-10002), 11 basiparasphenoids (ZZSiD RKI-10003-10013), 5 maxillary fragments (ZZSiD RKI-10014-10018), 2 pterygoid fragments (ZZSiD RKI-10019-10020), one ectopterygoid (ZZSiD RKI-10021), one quadrate (ZZSiD RKI-10022), 7 compounds (ZZSiD RKI-10023-10029), one trunk vertebra (holotype, ZZSiD RKI-10000), 598 precaudal vertebrae (ZZSiD RKI-10030-10093), 6 caudal vertebrae (ZZSiD RKI-10629-10635). (34) Upper Pliocene (MN 16) of Salchiya: trunk vertebrae (not seen, fide Redkozubov 1987).

Diagnostic vertebral characters: Trunk vertebrae of this extinct snake differ from other members of the genus *Natrix* by having stout and dorsoventrally flattened prezygapophyseal processes; a narrow centrum with the hypapophyseal basis continuing anteriorly by a salient ridge (Rage and Szyndlar 1986). The most distinct feature is an extreme elongation of vertebrae. The centrum length of 27 vertebrae from the type locality ranges between 4.27 and 5.58 mm and the centrum length/width ratio is 1.76-2.22 (mean 1.92 ± 0.12); in another vertebra it reaches 2.30.

Remarks: Most cranial bones of this snake closely resemble those of the living *N. natrix.* The maxilla, quadrate and parietal are practically identical in both snakes; the compound of *N. longivertebrata* differs from that of *N. natrix* by presence of a distinct concavity below the posterior end of the lateral flange. The main difference between both species is in the posteriormost area of the basiparasphenoid: in *N. longivertebrata* the posterior orifices of the Vidian canals are hidden inside bony recesses. This condition is also observable in basiparasphenoids from the French Miocene (described as *Natrix* aff. *longivertebrata* by Rage and Szyndlar 1986). In *N. natrix,* recesses housing the orifices are largely absent; of about 170 examined basiparasphenoids of (recent and Pleistocene) *N. natrix,* the pattern characteristic for *N. longivertebrata* occurred in three examples only.

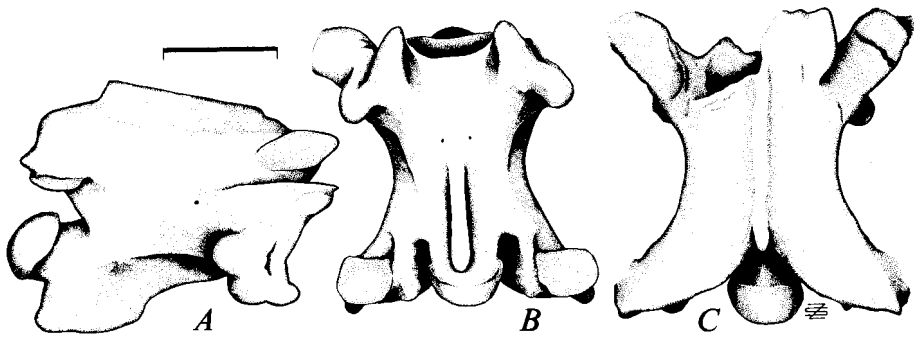

Fig. 2.—Trunk vertebrae of *Palaeonatrix lehmani* from lower Miocene of Dolnice (A, B, DPFNSP 4554; C, holotype, DPFNSP 3920). A, right lateral view; B, ventral view; C, dorsal view. Scale equals 2 mm.

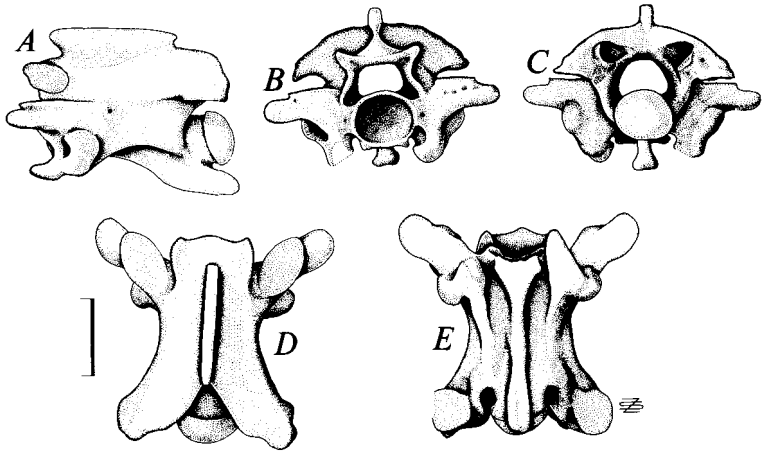

Fig. 3.—Trunk vertebra of *Natrix longivertebrata* from upper Pliocene of Rębielice Królewskie 1A (holotype, ZZSiD RKI-10000). A, left lateral view; B, anterior view; C, posterior view; D, dorsal view; E, ventral view. Scale equals 2 mm (From Szyndlar 1984).

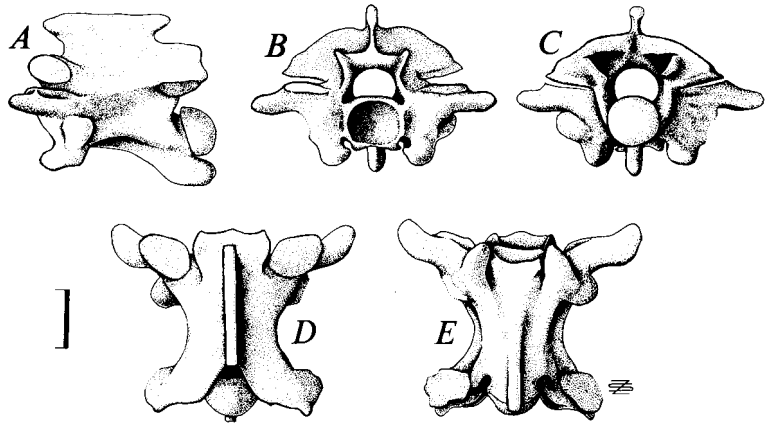

Fig. 4.—Trunk vertebra of *Natrix natrix* from Polish Pleistocene (ZZSiD GI-547). A, left lateral view; B, anterior view; C, posterior view; D, dorsal view; E, ventral view. Scale equals 2 mm (Fron Szyndlar 1984).

Natrix cf. *N. longivertebrata* Szyndlar, 1984.

(4) (5) (7) 1984 *Natrix* cf. *longivertebrata* Szyndlar, pp. 81-82, fig. 30.
(5) 1985 *Natrix* cf. *longivertebrata* Szyndlar: Szyndlar in MIynarski et al., pp. 222-224, fig. 7: 3, 4.
(40) 1985 *Natrix longivertebrata* Szyndlar: Bachmayer and Szyndlar, pp. 87-88, fig. 2.
(40) 1987 *Natrix longivertebrata* Szyndlar: Bachmayer and Szyndlar, pp. 30-31, fig. 3.

Material: (40) Upper Miocene (MN 11) of Kohfidisch: one parietal (NMW 1986/6), 15 precaudal vertebrae (NMW 1984/103/1, 2). (14) Upper Miocene (MN 12) of Cherevichnoie (lower layer): 67 precaudal vertebrae (IZAN 45-5027, 5028). (4) Middle Pliocene (MN 15) of Węże 1: 100 vertebrae (ZZSiD WEI-600-699). (5) Upper Pliocene (MN 16) of Węże 2: 78 precaudal vertebrae (ZPPAN R-III/15). (7) Upper Pliocene (MN 16) of Rębielice Królewskie 2: 59 vertebrae (ZZSiD RKII-61-120).

Remarks: The above listed materials do not differ essentially from the vertebrae of *N. longivertebrata* from the type locality. Considering, however, the close similarity between most skeletal elements of *N. longivertebrata* and the living *N. natrix*, proper identification based exclusively on vertebrae is problematic. In some rare cases, trunk vertebrae of *N. natrix* (like those of *N. longivertebrata*) display extreme elongation of the centrum, with the length/width ratio reaching even 2.07 (Szyndlar 1984).

Natrix parva Szyndlar, 1984.

1984 *Natrix parva* Szyndlar, pp. 47-50, fig. 17.

Material: (8) Mala Cave (type locality; geological age uncertain): one trunk vertebra (holotype, ZPUW IZ/6/R/4), 4 other precaudal vertebrae (ZPUW IZ/6/R/5-8).

Remarks: Description of this extinct species was based on very scarce material (exclusively vertebrae), partly belonging to juvenile specimens. The basic feature differentiating *N. parva* from other members of the genus *Natrix* is the straight (and not sigmoid-shaped) hypapophysis; for other details see Szyndlar (1984). Unfortunately, on account of deficiency in the available material, the scope of intraspecific variation cannot be observed; it is therefore not certain whether the recognized differentiating features

are representative of this taxon. Dating of the type locality, previously ascertained as the upper Miocene (Sulimski et al. 1979), was recently questioned by Glazek and Szynkiewicz (1987); according to the latter authors, the layer bearing *N. parva* is of late Pleistocene age. If this is the case, specific distinction of this fossil is doubtful; the vertebrae may have belonged to a recent member of the genus *Natrix*, perhaps *N. natrix*.

Natrix natrix (Linnaeus, 1758) (fig. 4).

(44) (52) (53)
1913 *Tropidonotus natrix* L.: Bolkay, p. 223.
(44) (46) (47) (48) (52) (53)
1932 *Natrix natrix* L.: von Szunyoghy, pp. 8 and 47.
(47) 1956 *Natrix natrix* (Linné): Kretzoi, p. 259.
(43) 1977 *Natrix natrix* L.: Rabeder, pp. 83-86, fig. 9: 5, Pl. 1: 3, 4, 6, 9, 13, Pl. 2: 14, 18, 19, 24.
(57) 1982 *Natrix* aff. *natrix* (Linnaeus) [part]: Młynarski, p. 31.
(9) 1984 *Natrix natrix* (Linnaeus): Szyndlar, pp. 106-122, figs. 44-49; [for full synonymy of *N. natrix* from Polish sites see Szyndlar 1984: 106].
(25) 1987 *Natrix natrix:* Zerova, p. 17.
(35) 1987 *Natrix* aff. *natrix:* Redkozubov, p. 71.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi: 3 parietals (not seen, fide von Szunyoghy 1932). (35) Upper Pliocene (MN 16) of Chishmikioy: trunk vertebrae (not seen, fide Redkozubov 1987). (46) Upper Pliocene (MN 16) of Beremend 1: parietals (not seen, fide von Szunyoghy 1932). (47) Uppermost Pliocene (MN 17) of Villány 3: 8 compounds (not seen, fide von Szunyoghy 1932). (48) Uppermost Pliocene (MN 17) of Nagyharsányhegy: one braincase, 7 compounds (not seen, fide von Szunyoghy, 1932). (9) Polish Pleistocene (13 sites altogether; for details see Szyndlar 1984: Table XVII): 5 frontals, 42 parietals, one supraoccipital, one exoccipital, 30 basioccipitals, 3 prootics, 153 basiparasphenoids, above 41 maxillae and maxillary fragments, above 6 pterygoids and pterygoid fragments, above 7 ectopterygoids and ectopterygoid fragments, above 8 palatines and palatine fragments, 3 squamosals, above 9 quadrates and quadrate fragments, 56 compounds, ca. 246 dentaries and dentary fragments, one vomer, 2 premaxillae, ca. 108500 vertebrae, above 110 ribs (ZZSiD ZA-311-313, KG-10000-10450, 12000-12101, 110000-110050, GI-547-608, JO-1000-1009; ZPPAN). (25) Ukrainian Pleistocene: vertebrae (IZAN). (52) Lower Pleistocene of Betfia: 2 parietals, one maxilla, one pterygoid (not seen, fide von Szunyoghy 1932). (43) Middle Pleistocene of St. Margarethen: 3 parietal fragments, 2 supraoccipitals, 2 basiparasphenoids, one basioccipital, 11 prootics, 3 exoccipitals, one frontal, one fragmentary ectopterygoid, one fragmentary compound, one quadrate (UWPI 2350/1/1-27; not seen, fide Rabeder 1977). (53) Middle Pleistocene of Braşov: 4 basiparasphenoids, one maxilla, 2 ectopterygoids, 7 compounds (not seen, fide von Szunyoghy 1932). (56) Late Pleistocene of Stoilovo: 8 precaudal vertebrae (IZBAN). (57) Late Pleistocene of Bacho Kiro: 5 precaudal vertebrae (ZZSiD).

Diagnostic vertebral characters: Trunk vertebrae of *N. natrix* differ from those of both *N. tesselata* and *N. maura* by having obtuse distal hypapophysis and parapophyseal processes. The homologous structures of the two latter species are characterized by pointed tips (Szyndlar 1984, fig. 7); it is to be noted, however, that these observations were based on few specimens. Skeletons of *N. megalocephala* were not available for study. The centrum length of the largest vertebrae of *N. natrix* from two Polish upper Pleistocene localities (90 bones altogether) was 3.81-5.90 mm and 4.17-5.60 mm; the centrum length/width ratio was 1.45-1.90 (mean 1.63 ± 0.11) and 1.57-2.07 (mean 1.74 ± 0.10), respectively (Szyndlar 1984).

Remarks: (9) (25) (56) (57) Vertebrae examined personally by me are usually well preserved and display clearly the diagnostic features characteristic for *N. natrix*. (35) No comment to his report of the presence of *Natrix* aff. *natrix* in the Moldavian Pliocene was given by Redkozubov (1987).

N. natrix was described on the basis of cranial bones from a number of localities. (9) Almost all kinds of skull elements were described and figured from the Polish Pleistocene (Szyndlar 1984); Rabeder's (1977) report of *N. natrix* from St. Margarethen is based exclusively on abundant cranial bones. Skull morphology of *N. natrix* was described in detail and figured by von Szunyoghy (1932: 16-17, 24-25, 29, figs. 13-15, 56, 68, 80, 86, 97, Pl. I: 1-4, Pl. VI: 4, Pl. VII: 6), differentiating features of some cranial elements were also discussed by Rabeder (1977, figs. 3: 1, 4: 2, 5: 1, 6: 5, 7: 2, 8: 6, 9: 2, 10: 2, 12: 5).

(44) Of special importance is the presumed presence of *N. natrix* in the Miocene of Polgárdi as reported by Bolkay (1913) and von Szunyoghy (1932). Bolkay (1913: 223) only mentioned "unmistakeable remains of this species (...) from Polgárdi" consisting of "an about complete and several fragmentary parietals, and a complete basioccipital». Von Szunyoghy (1932) discussed only three parietals coming from this locality; he differentiated these fossils from homologous bones of *N. tesselata* based on morphology of the parietal crests. Taking into consideration intraspecific variatrion within both *N. natrix* and *N. tesselata* (not considered by von Szunyoghy), specific determination based exclusively on parietals is uncertain. Moreover, it should be added that the parietal of the extinct species *N. longivertebrata* does not differ from that of *N. natrix*. The presence of the modern species *N. natrix* in Polgárdi is therefore not demonstrable and the discussed material needs prompt re-examination.

The entire fossil record comes from the area presently inhabited by *N. natrix*.

Natrix tesselata (Laurenti, 1768).

(44) (52) (53)
1913 *Tropidonotus tesselatus* Laur.: Bolkay, p. 223.
(44) (47) (48)
1932 *Natrix tesselata* Laur.: von Szunyoghy, pp. 9 and 47-48.
(49) (51)
1956 *Natrix tesselatus* Laurenti: Kretzoi, p. 259.
(25) 1987 *Natrix tesselata:* Zerova, p. 17.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi: 2 basiparasphenoids, 2 compounds (not seen, fide von Szunyoghy 1932). (47) Uppermost Pliocene (MN 17) of Villány 3: one basiparasphenoid, 16 compounds (not seen, fide von Szunyoghy 1932). (48) Uppermost Pliocene (MN 17) of Nagyharsány-hegy: 2 parietals, one ectopterygoid (not seen, fide von Szunyoghy 1932). (49) Uppermost Pliocene (MN 17) of Villány 6: ? (not seen, fide Kretzoi 1956). (25) Ukrainian Pleistocene: vertebrae (IZAN). (51) Lower Pleistocene of Beremend 4: ? (not seen, fide Kretzoi 1956). (52) Lower Pleistocene of Betfia: ? (not seen, fide Bolkay 1913). (53) Middle Pleistocene of Braşov: ? (not seen, fide Bolkay 1913).

Diagnostic vertebral characters: For differences between vertebrae of *N. tesselata* and *N. natrix* see the diagnosis of *N. natrix* (above).

Remarks: Almost the entire reported fossil record was based on cranial elements, but in most cases the remains were not described nor figured and therefore their allocation to the species is uncertain. The skull morphology of *N. tesselata* was described in detail by von Szunyoghy (1932: 16-17, 25, 29-30, figs. 16-22, 57, 69, 81, 85, 98, Pl. I: 5, 6, Pl. VI: 6, Pl. VII: 9).

(44) Regarding the presumed presence of *N. tesselata* in the Miocene of Polgárdi, no comments were given by Bolkay (1913) who first reported its presence in the above locality. Von Szunyoghy (1932) based his determination on parietals and compounds coming from Polgárdi. Although the parietals can be easily mistaken for those of *N. natrix*, there are clear differences between compounds belonging to the two species — *N. tesselata* is characterized by a much higher medial flange. Unfortunately, the fossils from Polgárdi were not figured by Bolkay (1913) nor by von Szunyoghy (1932).

The entire fossil record comes from the area presently inhabited by *N. tesselata*.

Natrix cf. *N. tesselata* (Laurenti, 1768) (fig. 5).

Material: (68) Middle Pleistocene of Tourkobounia 2: one trunk vertebra (UUGI). (71) Upper Pleistocene of Gerani 1: 3 precaudal vertebrae (UUGI).

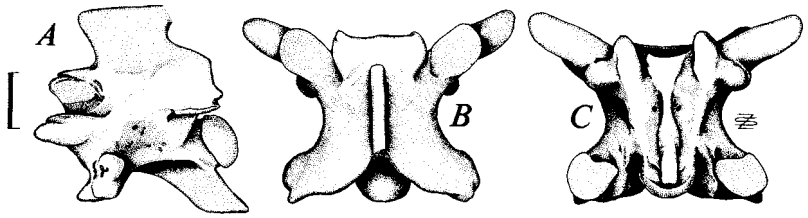

Fig. 5.—Trunk vertebra of *Natrix* cf. *N. tesselata* from upper Pleistocene of Gerani 1 (UUGI). A, left lateral view; B, dorsal view; C, ventral view. Scale equals 2 mm.

Remarks: The vertebrae are perfectly preserved and they clearly display distally pointed hypapophyses and parapophyseal processes. Considering both the scarcity of the material and the fact that the above features also occur sometimes (although rarely) in *Natrix natrix*, proper taxonomic allocation of the discussed fossils cannot be fully demonstrated. It should be noted that there are no significant differences between vertebrae of *N. tesselata* and *N. maura* from West Mediterranean; presence of the latter species in the Pleistocene of East Mediterranean is little probable. The two localities lie within the present range of both *N. tesselata* and *N. natrix* (Wettstein, 1953).

Natrix sp.

(27) 1984 *Natrix:* Chkhikvadze and Lungu, p. 82.
(54) 1986 *Natrix* sp.: Thomas et al., p. 1041.
(24) 1987 *Natrix* sp.: Zerova, p. 16.
(34) 1987 *Natrix* cf. *sansaniensis:* Redkozubov, p. 71.
(34) 1988 *Natrix* cf. *sansaniensis* (Lart.): David et al., p. 73.
(34) 1989 *Natrix* cf. *sansaniensis:* Redkozubov, p. 209.

Material: (27) Late Miocene (MN 9 or 10) of Buzhor: vertebrae (not seen, fide Chkhikvadze and Lungu 1984). (54) Lower Pliocene (MN 14) of Dorkovo: a vertebra (not seen, fide Thomas et al. 1986). (64) Middle Pliocene (MN 15) of Spilia 4: 21 precaudal vertebrae (UUGI). (24) Ukrainian Upper Pliocene: vertebrae (IZAN). (34) Upper Pliocene (MN 16) of Salchiya: trunk vertebrae (not seen, fide Redkozubov, 1987). (49) Uppermost Pliocene (MN 17) of Villány 6: 2 precaudal vertebrae (ZZSiD). (66) Lower Pleistocene of Laghada B: 2 fragmentary precaudal vertebrae (UUGI). (67) Pleistocene of Sitia 1: ca. 55 vertebrae and vertebral fragments (UUGI). (67) Pleistocene of Sitia 2: ca. 15 vertebral fragments (UUGI). (55) Middle Pleistocene of Varbeshnitsa: 7 precaudal vertebrae (IZBAN). (68) Middle Pleistocene of Tourkobounia 2: 14 precaudal vertebrae and one fragmentary compound (UUGI). (69) Middle Pleistocene of Tourkobounia 5: 3 precaudal vertebrae (UUGI). (73) Upper Quaternary of Pili B: 3 trunk vertebrae (UUGI).

Remarks: (27) The presumed oldest representative of the genus *Natrix* in East Europe (locality of Buzhor), was characterized by Chkhikvadze and Lungu (1984: 82) as "*Natrix,* a small snake with well-developed hypapophyses on the trunk vertebrae (...)"; unfortunately, this brief description is inadequate and does not demonstrate that the discussed fossil belonged indeed to the genus *Natrix.*

(34) Vertebrae from another Moldavian locality (Salchiya), compared by David et al. (1988) and Redkozubov (1987, 1989) with *N. sansaniensis* from the French Miocene, actually do not belong to the latter species (G. A. Zerova, pers. comm., 1989).

(64) (24) (66) (67) (49) (55) (68) (69) (73) Vertebrae examined personally by me are poorly preserved; morphology of the neural spines or their remnants indicates that the vertebrae belonged to the modern genus *Natrix.* Lack of other diagnostic structures, especially those diagnostic to species, makes identification below the generic level impossible.

"Natricinae" indet.

(10) 1987 *Natrix* sp.: Zerova, p. 13.
(17) (18) 1987 Natricinae: Zerova, p. 15.
(19) 1987 *Natrix:* Zerova, p. 15.

Material: (38) Middle Miocene (MN 6) of Děvínska Nová Ves: one fragmentary vertebra (DPFNSP 5844). (10) Late Miocene (MN 9) of Gritsev: vertebrae (IZAN). (12) Upper Miocene (MN 11) of Novoelizabetovka (lower layer): 3 precaudal vertebrae (IZAN). (13) Upper Miocene (MN 12) of Novaya Emetovka: 2 vertebrae (IZAN). (17) Uppermost Miocene (MN 13) of Novoukrainka 1: vertebrae (IZAN). (18) Uppermost Miocene (MN 13) of Andreievka: vertebrae (IZAN). (19) Uppermost Miocene (MN 13) of Frunzovka 2: precaudal vertebrae (IZAN). (60) Uppermost Miocene (MN 13) of Maramena 1: 16 fragmentary precaudal vertebrae (UUGI). (61) Uppermost Miocene (MN 13) of Ano Metochi 2: ca. 60 vertebral fragments.

Remarks: Taxonomic status of the above listed natricine vertebrae, on account of their poor preservation, especially the lack of any projecting structures, is uncertain. (10) (12) (13) (17) (18) (19): Most fossils coming from Ukrainian sites probably represented the living genus *Natrix.* (60) Of 16 very small vertebrae from Maramena 1, only one has retained its neural spine; this structure is extremely low, then probably the remains did not belong to *Natrix.*

Family ELAPIDAE Boie, 1827.

Vertebrae of cobras found in European fossil sites may be easily differentiated from those of other snakes; they closely resemble vertebrae of large-sized colubrine snakes, but contrary to the latter, they are provided with hypapophyses throughout the precloacal region of the column; moreover, they are characterized by very low neural spines. Apart from isolated vertebrae, elapid fossil finds also often offer numerous, well preserved cranial elements. On this account, diagnoses of the fossil species are based mainly on skull bones.

Morphological descriptions of skeletal elements of the genus *Naja* may be found in papers of Hoffstetter (1939), Bogert (1943), Rage (1976), Szyndlar (1985), and Szyndlar and Zerova (1990). The most comprehensive study, covering important diagnostic features found in braincases of most species of the genus *Naja,* is that of Szyndlar and Rage (1990).

Genus *Naja* Laurenti, 1768.

Naja romani (Hoffstetter, 1939) (fig. 6).

1939 *Palaeonaja Romani* Hoffstetter, pp. 57-65, Pl. I, Pl. II: 1-13.
1939 *Palaeonaja crassa* Hoffstetter, pp. 65-66, Pl. II: 14, 15.
1963 *Palaeonaja romani* Hoffstetter: Kuhn, p. 31.
1963 *Palaeonaja crassa* Hoffstetter: Kuhn, p. 31.
1984 *Palaeonaja romani* Hoffstetter: Rage, p. 54, fig. 32.
1984 *Palaeonaja crassa* Hoffstetter: Rage, p. 54.
(40) 1985 *Naja austriaca* Bachmayer et Szyndlar, pp. 88-96, figs. 3-5, Pl. 1: 7-9, Pl. 2.
(40) 1987 *Naja austriaca* Bachmayer et Szyndlar: Bachmayer and Szyndlar, pp. 31-33, fig. 4.
(10) (40) 1990 *Naja romani:* Szyndlar and Zerova, *passim,* figs. 1, 2, 3A-F.

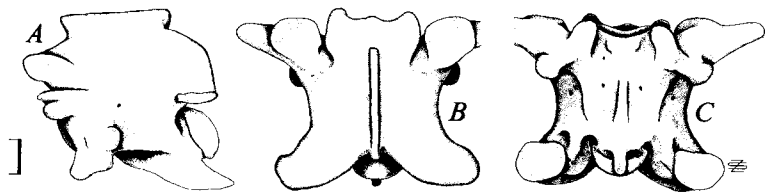

Fig. 6.—Trunk vertebra of *Naja romani* from Kohfidisch (NMW 1989/34/12). A, left lateral view; B, dorsal view; C, ventral view. Scale equals 2 mm (From Szyndlar and Zerova 1990).

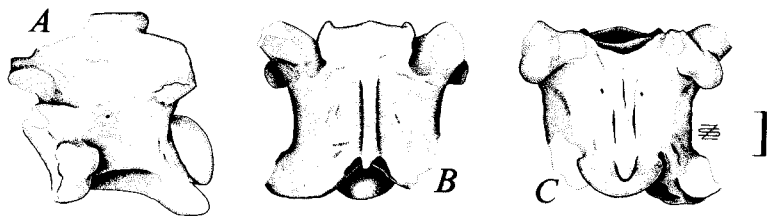

Fig. 7.—Trunk vertebra of *Naja* sp. from Tourkobounia 1 (UUGI). A, left lateral view; B, dorsal view; C, ventral view. Scale equals 2 mm (From Szyndlar and Zerova 1990).

Material: (10) Late Miocene (MN 9) of Gritsev: one basiparasphenoid (IZAN 22-1774), one compound (IZAN 22-1775), 10 precaudal vertebrae (IZAN 22-1776-1785). (40) Upper Miocene (MN 11) of Kohfidisch: 3 basiparasphenoids (NMW 1984/98, 1989/34/1, 2), 3 frontals (NMW 1984/104/4), one fragmentary parietal (NMW 1989/34/3), 2 prootics (NMW 1989/34/4, 5), one basioccipital (NMW 1989/34/6), 4 maxillae (NMW 1984/99, 100), 3 palatines (NMW 1986/7/5, 4), 6 pterygoid fragments (NMW 1984/104/1, 2), 2 squamosals (NMW 1989/34/7, 8), 2 quadrates (NMW 1989/34/9, 10), 4 dentaries (NHW 1984/104/3, 1986/7/5), 7 compounds (NMW 1986/7/1, 2), an axis (NMW 1984/105/3), 4 precaudal vertebrae (NMW 1984/105/1, 2, 4, 1989/34/12), a caudal vertebra (NMW 1984/105/5), above 1000 other vertebrae, ribs (NMW 1989/34/11).

Diagnostic vertebral characters: Differences between vertebrae of particular species of the genus *Naja* are usually indistinct; the most informative element is the braincase, especially the basicranium and temporal region (cf. below). Trunk vertebrae of *N. romani* most resemble those of the living Asiatic species *N. naja*, but differ from them by having much longer prezygapophyseal processes; the processes of *N. romani* are almost as long as the prezygapophyseal facets. Also the neural spine is relatively lower in *N. romani;* it is approximately three times longer than high. The zygosphene is provided with three distinct lobes in dorsal view; in very large specimens the median lobe disappears. There is a small difference between the populations from Gritsev and Kohfidisch, namely the parapophyseal processes of the former are directed anteriorly, while the processes of the latter face anteroventrally; the material from Gritsev is, however, very scarce; thus the variation within this population remains largely unrecognizable. Thirty of the largest trunk vertebrae from Kohfidisch have a centrum length ranging between 9.53 and 10.80 mm; the centrum length/width ratio is 0.82-0.99 (mean 0.90 ± 0.04) (Bachmayer and Szyndlar 1985). The centrum of smaller vertebrae is more elongate and it is longer than wide. Trunk vertebrae of *N. romani* from Central and East Europe do not differ significantly from those coming from the type locality; the only slight difference can be observed in the shape of the zygosphene, but only in the largest vertebrae. More differences are visible in the anteriormost vertebrae, including the atlas. For detailed morphological description of the remains from Kohfidisch and Gritsev see Bachmayer and Szyndlar (1985, 1987) and Szyndlar and Zerova (1990).

Remarks: The fossil cobra from Kohfidisch was originally described as a new extinct species, *N. austriaca*, by Bachmayer and Szyndlar (1985). Szyndlar and Zerova (1990), after examination of some new material from Kohfidisch, synonymized *N. austriaca* with *N. romani;* moreover, they also identified the remains from the Ukrainian locality of Gritsev as *N. romani. N. romani* was originally described as a member of the extinct genus *Palaeonaja* from the French Middle Miocene by Hoffstetter (1939); Szyndlar and Rage (1990) made *Palaeonaja* a junior synonym of the living *Naja*. Based on the morphology of its basisphenoid (especially considering Vidian canals opening extracranially), *N. romani* clearly displays features of the Asiatic complex of the genus; some conservative features of its skull (i.e., a groove for the facial nerve not covered from outside, presence of 2 solid maxillary teeth) demonstrate, however, that the snake represented an early offshoot of the Asiatic lineage (Szyndlar and Zerova, 1990; Szyndlar and Rage, 1990).

Naja sp. (fig. 7)

1990 *Naja* sp.: Szyndlar and Zerova, *passim*, fig. 3: G-I.

Material: (65) Upper Pliocene (MN 16) of Tourkobounia 1: 17 precaudal vertebrae (UUGI).

Remarks: In having relatively broad centra, relatively short and obtuse hypapophyses as well as a convex zygosphene in dorsal view the vertebrae differ significantly from those of *N. romani;* identification below the generic level, however, cannot be demonstrated (Szyndlar and Zerova, 1990).

cf. *Naja* sp.

Material: (60) Uppermost Miocene (MN 13) of Maramena 1: 2 vertebral fragments (UUGI).

Remarks: Two centra coming from large trunk vertebrae were identified as belonging to a cobra-like snake on the basis of flat and broad subcentral portions. Most likely they represented the genus *Naja,* but it cannot be fully demonstrated.

(?) *Naja* sp.

1975 *Naja* sp.: Schneider, p. 193, fig. 3B.

Material: (70) Middle Pleistocene of Chios: (?34) vertebrae (SMF; not seen, fide Schneider, 1975).

Remarks: Schneider's (1975) description of the discussed verte-

brae does not demonstrate they belonged to the genus *Naja;* ventral view of a trunk vertebra figured by Schneider (1975, fig. 3B) displays natricine rather than elapid morphology. The material needs to be revised.

Family VIPERIDAE Oppel, 1811.

Viperid vertebrae are provided with hypapophyses throughout the precloacal region as in elapids and natricines. Viperids differ from natricines in having straight (not sigmoid) hypapophyses, posteriorly depressed neural arches, distinctly longer and ventrally oriented parapophyseal processes and shorter vertebral centra; they differ from elapids (at least from the genus *Naja* and its allies) in having higher neural spines and longer hypapophyses, distinctly longer parapophyseal processes, posteriorly depressed neural arches and postzygapophyses strongly expanded laterally (Szyndlar, 1988). For differentiation between various viperine genera in vertebral morphology see also Szyndlar (1988).

Genus *Laophis* Owen, 1857.
Laophis crotaloides Owen, 1857.

1857 *Laophis crotaloïdes* Owen, p. 199; Pl. IV: 2-3.
1880 *Laophis crotaloides* R. Owen: de Rochebrune, p. 292.
1939 ? *Laophis crotaloides* Owen: Kuhn, p. 23.
1963 *Laophis crotaloides* Owen: Kuhn, p. 34.
1984 *Laophis crotaloides* Owen: Rage, p. 58.

Remarks: *Laophis crotaloides* was described by Owen (1857) on the basis of thirteen vertebrae coming from the Uppermost Miocene or Lowermost Pliocene of Karabournu in the Thessalonica area (Greek Macedonia) (62). Owen himself did not determine the exact taxanomic position of *Laophis,* although throughout the text he observed its close similarity to the North American pit-viper genus *Crotalus.* It has been later generally believed that Owen assigned *Laophis* to the subfamily Crotalinae, but this opinion was constituted under the influence of the specific name rather than Owen's writing.

Comments on the material described by Owen (which is probably lost) are only occasionally found in the literature. In his review of the fossil record of viperids, Hoffstetter (1955: 659) discussed *Laophis* in the section devoted to crotalines; nevertheless, he concluded that the available material was unfit for subfamilial identification. In his catalogue of fossil snakes, Kuhn (1939) placed *Laophis* within the family Crotalidae, but he used this name as a synonym of the Viperidae. However, in the second edition of the catalogue (Kuhn, 1963), *Laophis* is placed in the subfamily Crotalinae. Rage (1984), following Hoffstetter (1955), recognized that distinguishing the Crotalinae from the Viperinae is impossible on the basis of vertebrae. In conclusion, because "the characters mentioned by Owen are characteristic of a number of viperid genera, the figures are inadequate (...) and the syntypes are probably lost", Rage (supra cit.: 58) considered *Laophis* a *nomen dubium.*

The differentiation between crotaline and viperine vertebrae may be problematic indeed in many cases, as suggested by Rage; however, I agree only in part with his opinion. As an example, it may be very difficult or even impossible to distinguish vertebrae of smaller members of the genera *Vipera* and Asiatic *Agkistrodon* (= *Gloydius*) from each other, these difficulties, however, usually do not occur in the case of larger viperids. Considering *Laophis,* it most resembles largest members of the crotaline genera *Crotalus* and *Agkistrodon* from North America as well as *Deinagkistrodon* and *Calloselasma* from East Asia. Of the true vipers, the only snakes resembling *Laophis* in vertebral morphology is *Bitis.* Taking into consideration the absolute size of the vertebrae of *Laophis,* they undoubtedly come from the middle of the column. Mid-trunk vertebrae of the above-mentioned snakes, including *Laophis,* are strongly elongate dorso-ventrally in lateral view, owing to exceptionally long hypapophyses and neural spines together with relatively short centra (fig. 8). The vertebrae are more than twice the height (distance between the hypapophyseal tip and neural spine top) as long (centrum length). The same ratio observed in mid-trunk vertebrae of large viperines other than *Bitis,* i.e., *Vipera* in part ('Oriental vipers'), is distinctly lower. (In fact, the largest member of the Asiatic crotaline genus *Trimeresurus,* namely *T. flavoviridis,* displays in its vertebral morphology "typical" conditions of the 'Oriental vipers'). The above remarks are based exclusively on Owen's figures (1857, plate IV). The figures (according to Owen) display the lateral and anterior views of a single vertebra. The anterior view, as previously noticed by Rage (1984), is inaccurate. According to this figure, the zygosphenal roof is strongly convex, while in the lateral view its is distinctly concave. Moreover, the prezygapophyseal articular surfaces, as they are

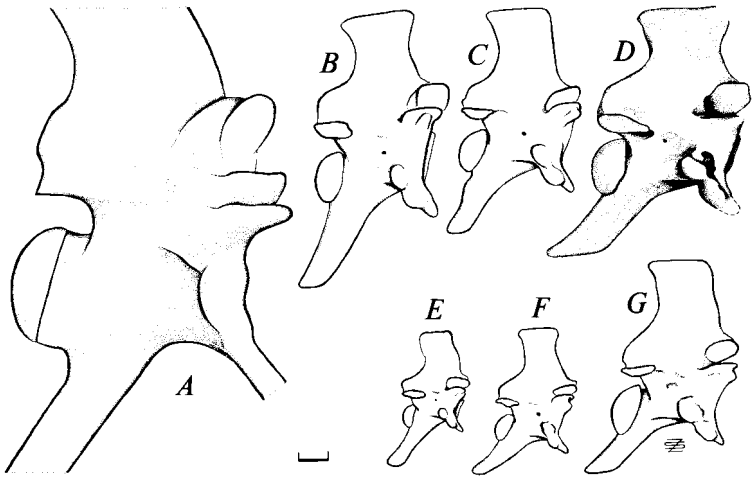

Fig. 8.—Trunk vertebra of *Laophis crotaloides* from uppermost Miocene of Karabournu (A) (redrawn from Owen 1857, Pl. IV: 2) and mid-trunk vertebrae of some recent viperid snakes, in right lateral views. B, *Crotalus atrox* (ZZSiD); C, *Agkistrodon piscivorus* (ZZSiD 233); D, *Trimeresurus flavoviridis* (subrecent fossil from Okinawa; ZZSiD); E, *Calloselasma rhodostoma* (ZZSiD 403); F, *Deinagkistrodon acutus* (ZZSiD 404); G, *Bitis gabonica* (IZAN). Scale equals 2 mm.

shown in the anterior view, have a thickness unparalleled in any snakes. It is to be noted that *Laophis,* according to the Owen's figure, was the largest viperid snake ever known; the centrum length of its vertebra is about 15 mm, while the same value for the largest reported pit viper is above 12 mm (*Crotalus adamanteus:* Christman, 1975, fig. 1) and for the largest true viper 12.37 mm (*Vipera maxima* from the Spanish Pliocene; Szyndlar, 1988: 700). Besides its absolute size, there are at least two distinct features distinguishing *Laophis* from other large viperids, namely very thin parapophyseal processes and, especially, a long condylar neck. It seems, however, that the latter as well as some other features, reflect fantasy of the lithographer rather than real morphology.

The problem of validity of this species remains then an open question. In light of current knowledge of past viperid distribution in the area, *Laophis* may have been a *Bitis*-like snake rather than a pit viper. The latter genus is unknown from European fossil sites: the only report of presumed *Bitis* remains from eastern Europe (Kormos, 1911) is most likely erroneous (Szyndlar, 1984; see also below).

Genus *Vipera* Laurenti, 1768.

The extant members of the genus *Vipera* form several separate complexes; this subgeneric diversity is also recognizable in fossil materials. The subdivision used in the present paper is generally consistent with that employed in my previous publications (Szyndlar, 1987a, 1987b): (1) 'Oriental vipers', including largest species of the genus, *V. lebetina, V. xanthina,* and others (= genus *Daboia* in part sensu Obst 1983; = complexes *'lebetina', 'xanthina-raddei',* and *'palaestinae-russelli'* sensu Groombridge, 1986); (2) *'aspis'* group (sensu Groombridge, 1986), including *V. ammodytes, V. latastei,* and *V. aspis* (= subgenus *Rhinaspis* of the genus *Vipera* sensu Obst, 1983); (3) *'berus'* group (sensu Grooombridge, 1986), including smallest members of the genus, *V. berus, V. ursinii,* and others (= subgenus *Vipera* [sensu stricto] of Obst 1983; = genus *Pelias* sensu Chkhikvadze and Zerova, 1983). The informal name 'European vipers' is used with reference to the two latter complexes in cases when their differentiation in fossil materials in unrealisable.

Identification of isolated vertebrae to particular complexes of the genus is usually an easy task. Vertebrae of the 'Oriental vipers' are characterized by much larger absolute size and less relative length (lower centrum length/width ratio) than those of the 'European vipers' (Szyndlar 1988). Of the latter group, the *'berus'* group may be differentiated from the *'aspis'* group on the basis of greater elongation of vertebrae and distinctly relatively lower neural spines and shorter hypapophyses (Szydlar 1984). Reliable allocation of fossils in the *'aspis'* group may, however, be problematic in the case of absence of cervical vertebrae; identification on the basis of mid-trunk vertebrae alone may be misleading because the latter are closely similar to those of the cervical region in the *'berus'* group. Cranial elements of viperids, especially those of smaller species, are seldom found in the fossil state.

Although differences among the above mentioned groups of the genus *Vipera* are usually very clear, skeletal morphology within each complex is usually highly homogenous. For instance, though *V. russelli* of the 'Oriental vipers' displays, both in its axial and cranial elements, an extremely distinct morphology, some other members of the same complex, as *V. lebetina, V. xanthina,* and *V. palestinae* are very similar to each other. Proper classification of isolated bones belonging to these species is thus always a hazard.

'Oriental vipers' group.

Vipera platyspondyla Szyndlar, 1987 (fig. 9).

1987a *Vipera platyspondyla* Szyndlar, pp. 67-68, fig. 10.

Material: (37) Lower Miocene (MN 4) of Dolnice (type locality): one trunk vertebra (holotype, DPFNSP 940), 7 other precaudal vertebrae (DPFNSP 939, 1421, 1431, 1435, 3926, 4004, 4008).

Diagnostic vertebral characters: This extinct species, known from the type locality only, differs from most of its living relatives in some minor features, among others by having sharp lateral lobes of the zygosphenal roof and elliptical shape of the prezygapophyseal articular facets. It most resembles the living *Vipera xanthina* but a close relationship between both species, considering scarcity of the fossil material, cannot be fully demonstrated. The centrum length of the holotype vertebra is 6.90 mm (Szyndlar 1987a); it is 1.18 times longer than wide.

Remarks: This is the oldest representative of the 'Oriental vipers' in East Europe. For more detailed morphological description see Szyndlar (1987a).

Vipera sarmatica Chkhikvadze et Lungu, 1987.

1984 *Vipera* sp.: Chkhikvadze and Lungu, p. 82;
1987 *Vipera sarmatica* Chkhikvadze et Lungu (in Zerova et al.), pp. 92-94, fig. 2, Pl. V;
1987 *Vipera sarmatica:* Zerova, p. 13;
1989 *Vipera sarmatica:* Zerova, p. 92.

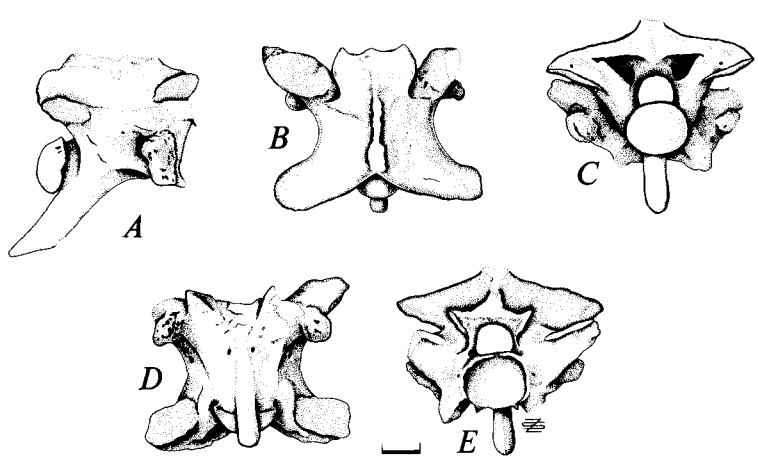

Fig. 9.—Trunk vertebra of *Vipera platyspondyla* from lower Miocene of Dolnice (holotype; DPFNSP 940). A, right lateral view; B, dorsal view; C, posterior view; D, ventral view; E, anterior view. Scale equals 2 mm (From Szyndlar 1987a. Copyright 1987 by the Society of Vertebrate Paleontology. Used with permission).

Material: (26) Late Miocene (MN 9) of Kalfa (type locality): one trunk vertebra (holotype, TGPI 18/72-1), 24 other precaudal vertebrae (TGPI 18/72-2 to 25) (not seen, fide Chkhikvadze and Lungu in Zerova et al. 1987).

Diagnostic vertebral characters: This extinct species, known from the type locality only, displays all the characteristic features of the 'Oriental vipers'. Comparisons of *V. sarmatica* with two living species of the 'Oriental vipers', provided by Chkhikvadze and Lungu (in Zerova et al. 1987), are not satisfactory because they are concentrated on features subjected to allometric variation: *V. sarmatica* differs from *V. xanthina* «...by larger absolute dimensions of the vertebrae, by a thicker cotyle, by more strongly developed subcentral ridges and a groove between the hypapophysis and subcentral ridges»; it differs from *V. lebetina* «...by a wider zygosphene the width of which is approximately equal to the centrum width» (ibid., p. 94). According to the figure of Chkhikvadze and Lungu (ibid., fig. 2v), the latter statement is untrue. The zygosphene is straight (or slightly concave or convex) in dorsal view. The centrum length of the holotype vertebra is 9.4 mm; in the entire sample, the centrum length/width ratio ranges between 1.25 and 1.62 (ibid., p. 94). (The centrum length/width ratio, originally given in the paper of Zerova et al., is 1.54-1.90; the data presented here come from a corrected reprint provided by the authors). For more detailed morphological description see Chkhikvadze and Lungu (in Zerova et al. 1987).

Vipera burgenlandica Bachmayer et Szyndlar, 1987 (figs. 10, 11).

1985 *Vipera* sp. (=*Daboia* sp.): Bachmayer and Szyndlar, pp. 96-97, fig. 6;
1987 *Vipera burgenlandica* Bachmayer et Szyndlar, pp. 33-39, figs. 5, 6, Pl. I:5-6.

Material: (40) Upper Miocene (MN 11) of Kohfidisch (type locality): one basiparasphenoid (holotype, NMW 1986/3), another basiparasphenoid (NMW 1989/35/1), one basioccipital (NMW 1984/106/5), one maxilla (NMW 1989/35/2, one pterygoid fragment, one compound (1986/8/1), one dentary (NMW 1986/8/2), 3 precaudal vertebrae (NMW 1984/106/1,2,3), more than 70 other precaudal vertebrae.

Diagnostic vertebral characters: Trunk vertebrae of this extinct snake, known exclusively from the type locality, closely resemble those of the living *V. lebetina* and *V. palaestinae;* differences between these three species are, however, clearly visible in cranial elements (see below). The zygosphene is provided with two distinct outer lobes and an indistinct median lobe; the prezygapophyseal processes are extremely short; the neural spine of the mid-trunk vertebrae is approximately as high as long; the parapophyseal processes are directed downwards. The centrum length of 11 trunk vertebrae is 5.59-7.18 mm (mean 6.40 ± 0.49); the centrum length/width ratio is 1.18-1.28 (mean 1.22 ± 0.05) (Bachmayer and Szyndlar 1987).

Remarks: This snake is at present the best documented fossil member of the 'Oriental vipers' group. Of several cranial bones available, the lower jaw elements are of lesser importance because they display the same morphological pattern as in most 'Oriental vipers'. The holotype basiparasphenoid was supposed to be closest to that of the living *V. xanthina* (Bachmayer and Szyndlar 1987); discovery of another basiparasphenoid (fig. 11A,B), most similar to *V. lebetina,* indicates a broad spectrum of intraspecific variation of this bone. Another recently discovered element, a maxilla (fig. 11C, D), by having a distinct ridge on the antero-inner wall of its ascending process, closely resembles that of the extinct *V. gedulyi* from the Hungarian Miocene. Both species can be, however, well differentiated on the basis of morphology of the basioccipital process; in *V. gedulyi* the process is exceptionally long and thick, unlike *V. burgenlandica* and their living relatives. For more detailed morphological description see Bachmayer and Szyndlar (1985, 1987).

Vipera gedulyi Bolkay, 1913.

1911 *Vipera* sp.; Kormos, p. 63 (187);
1911 [?] ?*Bitis:* Kormos, p. 63 (187);
1913 *Vipera Gedulyi* Bolkay, pp. 225-226, fig. 4, Pl. XII:9-12;
1932 †*Vipera Gedulyi* By. (an spec. ident. inc.?) [part]: von Szunyoghy, pp. 10 and 50-52, fig. 116);
1939 *Vipera gedulyi* Bolkay: Kuhn, p. 23;
1963 *Vipera gedulyi* Bolkay: Kuhn, p. 32;
1984 *Vipera gedulyi* Bolkay: Rage, p. 56, fig. 33C, D;
1988 *Vipera gedulyi:* Szyndlar, pp. 702, 704.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi (type locality): 15 basiparasphenoids, 2 frontals, 2 prefrontals, 2 fragmentary parietals, one prootic, one exoccipital, 8 basioccipitals, 19 fragmentary maxillae, 206 isolated venom fangs, 26 fragmenta-

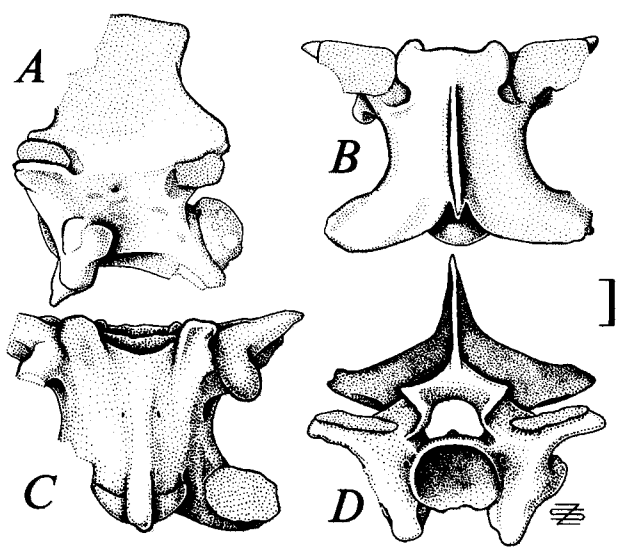

Fig. 10.—Trunk vertebrae of *Vipera burgenlandica* from upper Miocene of Kohfidisch (A, B, C, NMW 1984/106/1; D, NMW 1984/106/2). A, left lateral view; B, dorsal view; C, ventral view; D, anterior view. Scale equals 2 mm (From Bachmayer and Szyndlar 1987).

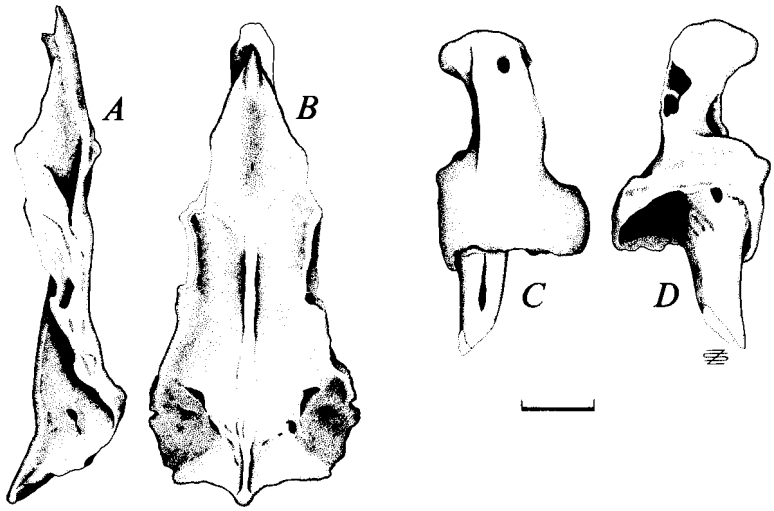

Fig. 11.—Basiparasphenoid (A, B, NMW 1989/35/1) and left maxilla (C, D, NMW 1989/35/2) of *Vipera burgenlandica* from upper Miocene of Kohfidisch. A, left lateral view; B, ventral view; C, anteroventral view; D, posterodorsal view. Scale equals 2 mm.

ry compound bones, 33 fragmentary ectopterygoids (syntypes, MHGI Ob-4467/Vt. 74; not seen, fide Bolkay 1913 and von Szunyoghy 1932).

Remarks: This snake, known from the type locality only, was described exclusively on the basis of cranial bones. Bolkay (1913:225) pointed out «...the great degree of agreement which this species shows with *Vipera ammodytes*»; at the same time he observed that the most important difference between both species is «...the considerably larger size of this Viper [i.e., of *V. gedulyi*]». Bolkay was largely correct in his statement because, in fact, most isolated cranial bones of both *V. ammodytes* and the 'Oriental vipers' display similar morphological patterns, apart from the different absolute size. Unfortunately, he neither described nor figured the bones of the temporal region, which have perhaps the greatest taxonomic importance in viperids; also, Bolkay did not consider vertebrae, which provide the best data in differentiating the 'Oriental vipers' from other members of the genus. Bolkay's opinion may have simply resulted from the fact that he did not have any skeletons of the 'Oriental vipers' at hand. Although von Szunyoghy (1932) observed some similarities between the Polgárdi fossil and the living *V. lebetina,* his observations were ignored by later students and *V. gedulyi* was then traditionally regarded a close relative of the living *Vipera ammodytes.*

Actually, the skeletal elements figured by Bolkay (1913, Pl. XII) clearly display features characteristic for the 'Oriental vipers' group; *V. gedulyi* seems closest to the living *V. lebetina* (Szyndlar 1987b, 1988), but differs clearly from the latter in having an extremely long basioccipital process and in the presence of a strong ridge on the ascending process of the maxilla (cf. Bolkay 1913, Pl. XII:9,12). Perhaps one of most important features showing close relationships between *V. gedulyi* and *V. lebetina* is the type of the ectopterygoid-maxillary articulation. In both species (as well as in *V. mauritanica*) the internal (i.e., smaller) ramus of the ectopterygoid is well produced anteriorly so that it protrudes distinctly outside the stem of the bone (cf. Bolkay 1913, Pl. XII:10); on the contrary, in *V. xanthina* (as well as in *V. raddei*) the ramus is shifted far posteriorly.

Kormos (1911), who first described briefly the Polgárdi herpetofauna, mentioned a fragmentary maxilla provided with a fang, supposedly belonging to a large venomous snake, perhaps of the genus *Bitis*. The supposition of Kormos was not commented on by Bolkay (1913) or von Szynyoghy (1932); most likely, the maxilla was included by Bolkay to the syntypes of *V. gedulyi.*

Vipera kuchurganica Zerova, 1987 (fig. 12).

1987 *Vipera kuchurganica* Zerova (in Zerova et al.), pp. 95-97, fig. 3, Pl. 6:a-d;
1987 *Vipera kuchurganica:* Zerova, p. 15.

Material: (20) Lower Pliocene (MN 14) of Kuchurgan (type locality): one precaudal vertebra (holotype, IZAN 37-2536), 2 other precaudal vertebrae (37-2537 and 2538).

Diagnostic vertebral characters: According to Zerova (in Zerova et al. 1987), this extinct species, known exclusively from the type locality, most closely resembles the living *V. lebetina.* It differs from *V. lebetina* «...in a wider and larger vertebral centrum, more laterally projected pre- and postzygapophyses, less developed parapophyseal processes.»; it differs from *V. xanthina* «...in the shape of the zygosphene (straight in *V. kuchurganica* (...) and undulating in *V. xanthina*), [and in] the degree of development of parapophyseal processes and subcentral ridges» (ibid., p. 96). The vertebrae of *V. kuchurganica* are also closely similar to those of *V. burgenlandica* from the Austrian Miocene (see above) and perhaps both snakes represented the same evolutionary lineage or even the same species; the only significant difference is the presence of two distinct outer lobes in the zygosphene of *V. burgenlandica,* structures that are absent in *V. kuchurganica.* For detailed morphological description of *V. kuchurganica* see Zerova (in Zerova et al. 1987).

Vipera sp. ('Oriental vipers') (fig. 13).

(70) 1975 *Vipera* sp.: Schneider, p. 193, fig. 3C;
(19) 1987 *Vipera kuchurganica:* Zerova, p. 15;
(10) 1989 *Daboia* of *xanthina*-type: Zerova, p. 92.

Material: (10) Late Miocene (MN 9) of Gritsev: vertebrae (IZAN). (19) Uppermost Miocene (MN 13) of Frunzovka 2: one fragmentary precaudal vertebra (IZAN). (65) Upper Pliocene (MN 16) of Tourkobounia 1: one fragmentary precaudal vertebra (UUGI). (55) Middle Pleistocene of Varbeshnitsa: one fragmentary precaudal vertebra (IZBAN 23-43/81/1). (70) Middle Pleistocene of Chios: (?26) vertebrae (SMF; not seen, fide Schneider 1975).

Remarks: Considering absolute size and centrum length/width ratios of all the examined vertebrae, they undoubtedly belong to the 'Oriental vipers'; unfortunately, because of the poor preservation of the material, no more precise identification is possible.

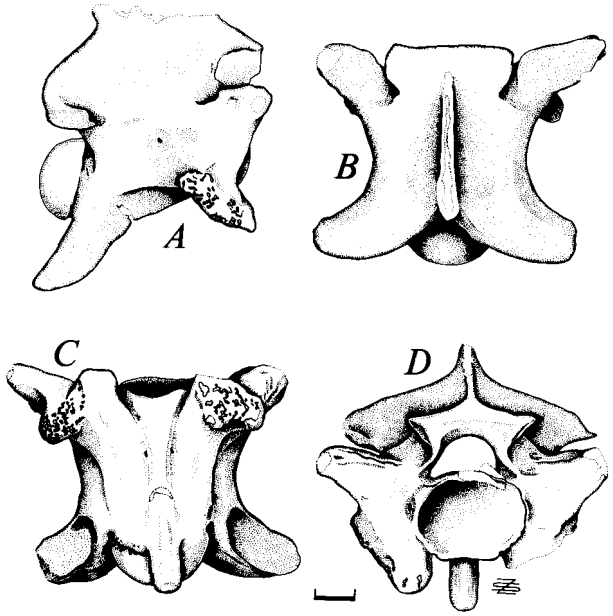

Fig. 12.—Trunk vertebra of *Vipera kuchurganica* from lower Pliocene of Kuchurgan (holotype; IZAN 37-2536). A, right lateral view; B, dorsal view; C, ventral view; D, anterior view. Scale equals 2 mm.

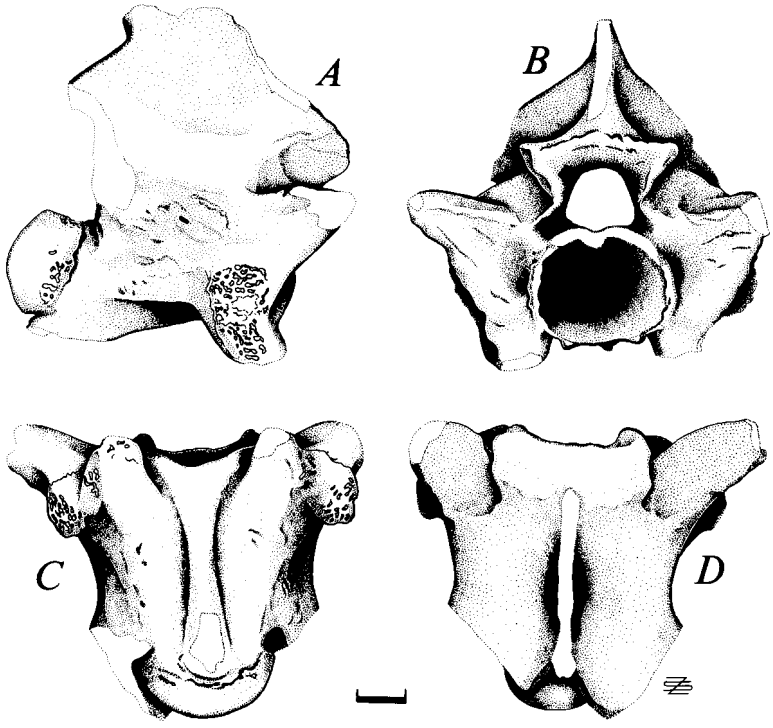

Fig. 13.—Trunk vertebra of *Vipera* sp. (Oriental viper) from upper Pliocene of Tourkobounia 1 (UUGI). A, right lateral view; B, anterior view; C, ventral view; D, dorsal view. Scale equals 2 mm.

The remains most likely represented different species, but neither this nor any other opinion can be fully demonstrated. (65): The vertebral fragment from Tourkobounia 1, with the centrum length reaching 10.10 mm, represented the largest viper known from East European fossil sites. (70): The vertebra from Chios, according to the figure given by Schneider (1975, fig. 3C), displays clearly features characteristic for the 'Oriental vipers'. Nilson and Andrén (1986:77), who re-examined this material, stated that the fossils «...are very similar in size and form to vertebrae from large specimens of the recent *V. lebetina* from Cyprus.» No members of the genus *Vipera* presently occur on Chios (Wettstein 1953).

'Vipera aspis' group.

Vipera antiqua Szyndlar, 1987 (fig. 14).

1987a *Vipera antiqua* Szyndlar, pp. 68-69, fig. 11.

Material: (37) Lower Miocene (MN 4) of Dolnice (type locality): one trunk vertebra (holotype, DPFNSP 4538), five other precaudal vertebrae (DPFNSP 938, 1114, 1213, 4014, 4057).

Diagnostic vertebral characters: Owing to the presence of both cervical and trunk vertebrae in the material, it is clearly referable to the *'aspis'* group. It differs from the living members of the latter group in having vertebrae of the mid-trunk region characterized by relatively longer centra and a distinctly lower neural spine. The centrum length of the holotype vertebra is 3.75 mm; it is 1.54 times longer than wide. For more detailed morphological description see Szyndlar (1987a).

Remarks: This extinct species, known exclusively from the type locality, is the oldest known representative of the 'European vipers'.

Vipera cf. *V. ammodytes* (Linnaeus, 1758) (fig. 15).

(44) 1932 *Vipera* cfr. ? *ammodytes* L. (= *V. Gedulyi* By., part.): von Szunyoghy, pp. 10 and 53.

(4) (6) (7) 1984 *Vipera ammodytes* (Linnaeus): Szyndlar, pp. 82-84, figs. 31, 32.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi: one parietal (not seen, fide von Szunyoghy, 1932). (4) Middle Pliocene (MN 15) of Węże 1: 15 precaudal vertebrae (ZZSiD WI-701-715). (6) Upper Pliocene (MN 16) of Rębielice Królewskie 1A: 3 precaudal vertebrae (ZZSiD). (7) Upper Pliocene (MN 16) of Rębielice Królewskie 2: 15 precaudal vertebrae (ZZSiD RKII-121 to 135). (55) Middle Pleistocene of Varbeshnitsa: 2 precaudal vertebrae (IZBAN 23-43/81/2,3). (68) Middle Pleistocene of Tourkobounia 2: 4 precaudal vertebrae (UUGI). (56) Late Pleistocene of Stoilovo: 8 precaudal vertebrae (IZBAN).

Diagnostic vertebral characters: *V. ammodytes* can be easily differentiated from another living member of this complex, *V. aspis*, on the basis of cervical vertebrae, which in the former snake are provided with much longer hypapophyses and much higher neural spines (Szyndlar, 1984, fig. 8). It should be stressed, however, that trunk vertebrae immediately following the cervical region of the column in *V. ammodytes*, which have both reduced height of neural spines and reduced length of hypapophyses, can be easily mistaken for cervical vertebrae of *V. aspis*. In both *V. ammodytes* and *V. aspis*, the zygosphene is provided with three distinct lobes and the prezygapohyseal processes are extremely short. The centrum length of 60 trunk vertebrae of a large specimen of the living *V. ammodytes* (ZZSiD 292) ranges between 4.54 and 5.10 mm and it is 1.42-1.63 (mean 1.53 ± 0.06) times longer than wide; the largest fossil vertebra from Węże 1 has a centrum length of 4.22 mm (Szyndlar, 1984). For detailed morphological description of vertebrae of *V. ammodytes* see Szyndlar (1984).

Remarks: (4) (6) (7) The features characteristic for *V. ammodytes* are clearly visible in the material coming from three Polish Pliocene localities and this was the basis for identifying them as *V. ammodytes* without any reservation by Szyndlar (1984). There are no significant differences, however, in vertebral morphology between *V. ammodytes* and its close relative from Iberia and north-western Africa, *V. latastei*. Considering that in the Pliocene the differences between both species may have been lesser than today and that their geographical ranges may have been closer to each other, the taxomonic syntax used in the present paper was completed by the qualifier "cf.". (55) (68) (56) The same syntax was employed in reference to the remains from the Pleistocene Greek and Bulgarian sites, in this case, however, regarding the poor preservation of the fossils rather than other reasons.

(44) One parietal from Polgárdi, referred originally by Bolkay to the extinct *V. gedulyi*, was then compared by von Szunyoghy (1932) with the living species *V. ammodytes*. The discussed bone perhaps belonged indeed to *V. gedulyi*, but von Szunyoghy did not consider intraspecific variation. The material needs re-examination.

Except for Poland, the remaining fossil sites are located within the present range of *V. ammodytes*.

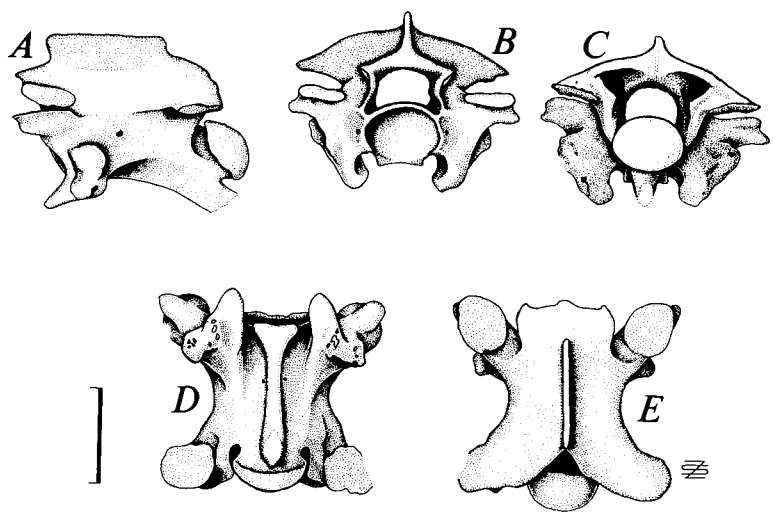

Fig. 14.—Trunk vertebra of *Vipera antiqua* from lower Miocene of Dolnice (holotype; DPFNSP 4538). A, left lateral view; B, anterior view; C, posterior view; D, ventral view; E, dorsal view. Scale equals 2 mm. (From Szyndlar 1987a. Copyright 1987 by the Society of Vertebrate Paleontology. Used with permission).

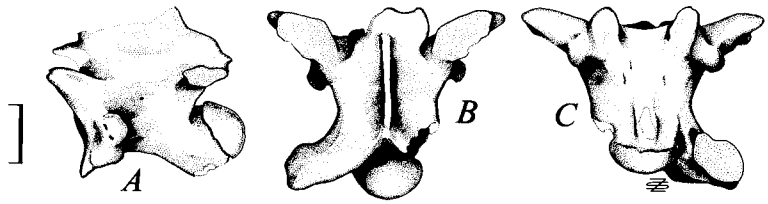

Fig. 15.—Trunk vertebra of *Vipera* cf. *V. ammodytes* from middle Pleistocene of Varbeshnitsa (IZBAN 23-43/81-2). A, left lateral view; B, dorsal view; C, ventral view. Scale equals 2 mm.

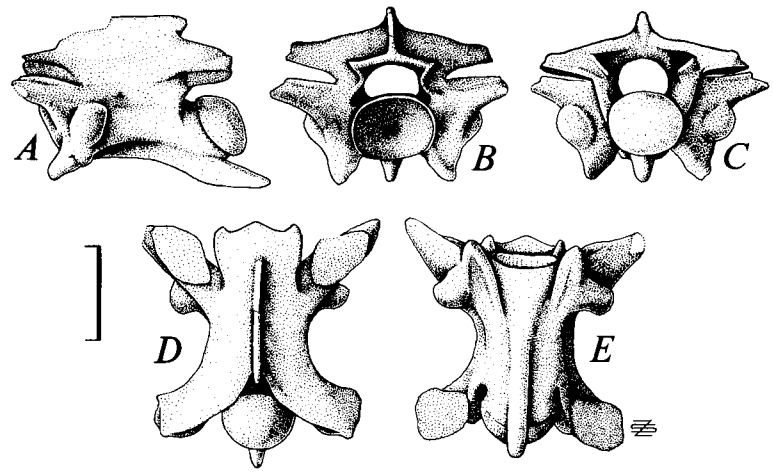

Fig. 16.—Trunk vertebra of *Vipera berus* from Polish Pleistocene (ZZSiD RA-13). A, left lateral view; B, anterior view; C, posterior view; D, dorsal view; E, ventral view. Scale equals 2 mm (From Szyndlar 1984).

Vipera cf. *V. aspis* (Linnaeus, 1758).

1932 *Vipera* cfr. *aspis* L.: von Szunyoghy, pp. 10 and 52-53.

Material: (44) Uppermost Miocene (MN 13) of Polgárdi (not seen, *fide* von Szunyoghy, 1932): 2 parietals.

Remarks: Taxonomic allocation of the parietals from Polgárdi is doubtful for the same reasons as discussed above with reference to *V. ammodytes* from the same locality. Von Szunyoghy (1932) did not consider intraspecific variation; the bone probably belonged to *V. gedulyi* as previously recognized by Bolkay (1913). The present range of *V. aspis* is restricted to West Europe; the only (uncertain) record from East Europe was reported by Buresch and Beškov (1965).

The osteology of *V. aspis,* including both cranial and axial elements, was described by Kramer (1980).

Vipera sp. (*'aspis'* group).

(2) 1982 Viperidae indet.: Szyndlar (in Młynarski et al.), p. 117, fig. 11.
(2) (3) 1984 Viperidae indet.: Szyndlar, pp. 50-5 2, fig. 18.
(11) (14) 1987 *Vipera* cf. *ammodytes:* Zerova, p. 13.
(14) 1987 *Vipera ammodytes:* Zerova, p. 17.
(16) 1989 *Daboia:* Zerova, p. 93.
(14) 1989 *Vipera:* Zerova, p. 93.

Material: (38) Middle Miocene (MN 6) of Děvínska Nová Ves: 2 precaudal vertebrae (DPFNSP 5855, 5857). (2) Middle Miocene (MN 7) of Opole 2: 2 fragmentary vertebrae (ZPUW OP 86/29, 30). (11) Upper Miocene (MN 11) of Krivoy Rog: one precaudal vertebra (IZAN). (12) Upper Miocene (MN 11) of Novoelizabetovka (lower layer): 4 precaudal vertebrae (IZAN). (14) Upper Miocene (MN 12) of Cherevichnoie (lower layer): one basiparasphenoid (IZAN 45-5023), 22 precaudal vertebrae (IZAN 45-5024). (16) Upper Miocene (MN 12) of Novoelizabetovka (upper layer): 8 precaudal vertebrae (IZAN). (44) Uppermost (MN 13) Miocene of Polgárdi: one fragmentary precaudal vertebra (MHGI). (3) Lower Pliocene (MN 14) of Podlesice: two fragmentary precaudal vertebrae (ZZSiD PO-2, 3). (25) Ukrainian Pleistocene: vertebrae (IZAN).

Remarks: The above materials were allocated to the *'aspis'* group on the basis of relatively long hypapophyses and/or neural spines retained on cervical vertebrae or on their fragments. Most vertebrae resemble those of *V. ammodytes-V. latastei;* most of them, however, probably belonged to different species. Considering the poor state of preservation of these materials, more precise identification cannot be demonstrated.

'Vipera berus' group.
Vipera berus (Linnaeus, 1758) (fig. 16).

(53) 1913 *Vipera berus* L.: Bolkay, p. 226, fig. 5.
(53) 1932 *Vipera berus* L.: von Szunyoghy, pp. 10 and 50.
(43) 1977 *Vipera berus* L.: Rabeder, pp. 92-93, Pl. 1: 3, Pl. 2: 21.
(9) 1984 *Vipera berus* (Linnaeus): Szyndlar, pp. 122-131, figs. 52-55. [For full synonymy of *V. berus* from Polish sites see Szyndlar, 1984: 122].

Material: (9) Polish Pleistocene (8 sites altogether; for details see Szyndlar: Table XX): 5 basiparasphenoids (ZZSiD ZA-2000,

KG-8500-8503), 2 maxillae (ZZSiD ZA-2002, KG-8504), ca.5740 vertebrae (ZZSiD ZA-2003, KG-8550, 8750, 8800, RA-13). (43) Middle Pleistocene of St. Margarethen: 2 prootics, one fragmentary compound (UWPI 2350/4/1-3; not seen, *fide* Rabeder, 1977). (53) Middle Pleistocene of Braşov: two basiparasphenoids (not seen, fide Bolkay, 1913).

Diagnostic vertebral characters: Precaudal vertebrae of two East European smallest vipers, *V. berus* and *V. ursinii,* are very similar to each other; some minor differentiating features were found in caudal vertebrae by Szyndlar (1984, fig. 8). The centrum length of 25 trunk vertebrae of a living example of *V. berus* (ZZSiD 22) is 3.40-3.95 mm and it is 1.70-1.88 (mean 1.80 ± 0.05) times longer than wide; the largest vertebra from the Polish Pleistocene has a centrum length of 5.51 mm (Szyndlar, 1984). The absolute size and proportions of vertebrae of *V. ursinii* are similar. For detailed morphological description of vertebrae of *V. berus* see Szyndlar (1984).

Remarks: Regarding cranial bones occurring in fossil sites, some differences between *V. berus* and *V. ursinii* are visible in basiparasphenoids and maxillae. In *V. berus,* the anterior orifices of the Vidian canals are located on the dorsal side of the basiparasphenoid, while in *V. ursinii* they lie on the lateral margin of the bone; the maxilla of *V. berus* is relatively much higher than that of *V. ursinii.* (9) (43) The fossil remains from both Polish and Austrian Pleistocene, containing well preserved cranial bones of taxonomic importance, are clearly referred to *V. berus.* (53) Based on Bolkay's drawing (Bolkay, 1913, fig. 5), allocation of the figured basiparasphenoid to *V. berus* is not demonstrable.

Al the discussed fossil sites are situated withing the present range of the species.

Vipera sp. ('*berus*' group).

(57)	1982	*Natrix* aff. *natrix* (Linnaeus) [part]: Mlynarski, p. 30.
(10)	1987	*Pelias* cf. *berus:* Zerova, p. 13.
(18) (19)	1987	*Pelias* sp.: Zerova, p. 15.
(24)	1987	*Pelias* sp.: Zerova, p. 16.
(25)	1987	*Pelias berus:* Zerova, p. 17.
(10)	1989	*Pelias* of *berus* type: Zerova, p. 92.
(18)	1989	*Pelias:* Zerova, p. 93.

Material: (10) Late Miocene (MN 9) of Gritsev: precaudal vertebrae (IZAN). (18) Uppermost Miocene (MN 13) of Andreievka: 4 precaudal vertebrae (IZAN). (19) Uppermost Miocene (MN 13) of Frunzovka 2: one precaudal vertebra (IZAN). (21) Middle Pliocene (MN 15) of Kotlovina (lower layer): one precaudal vertebra (IZAN). (24) Ukrainian Upper Pliocene: vertebrae (IZAN). (41) Upper Pliocene (MN 16) of Bad Deutsch Altenburg 20: one precaudal vertebra (UWPI). (65) Upper Pliocene (MN 16) of Tourkobounia 1: one fragmentary maxilla, one fragmentary parietal, one precaudal vertebra (UUGI). (25) Ukrainian Pleistocene: precaudal vertebrae (IZAN). (66) Pleistocene of Laghada B: one vertebra (UUGI). (68) Middle Pleistocene of Tourkobounia 2: 2 fragmentary precaudal vertebrae (UUGI). (57) Late Pleistocene of Bacho Kiro: 12 vertebrae (ZZSiD).

Remarks: The above vertebrae, belonging to very small snakes, have strongly reduced neural spines on their trunk vertebrae. Several species are probably represented, but, because of the poor state of preservation of the materials, more precise identification is impossible.

Vipera sp. (status uncertain).

(27)	1973	Viperidae: Chkhikvadze and Lungu, p. 84.
(37)	1987a	Viperidae indet.: Szyndlar, p. 69.

Material: (37) Lower Miocene (MN 4) of Dolnice: 4 vertebrae (DPFNSP 1158, 3929, 4023, 4529). (38) Middle Miocene (MN 6) of Děvínska Nová Ves: one fragmentary vertebra (DPFNSP 5858). (27) Late Miocene (MN 9 or 10) of Buzhor: a lower jaw (not seen, fide Chkhikvadze and Lungu, 1973). (28) Middle Pliocene (MN 15) of Etuliya: precaudal vertebrae (not seen, fide Redkozubov, 1987). (31) Middle Pliocene (MN 15) of Musait: precaudal vertebrae (not seen, *fide* Redkozubov, 1987). (33) Upper Pliocene (MN 16) of Novye Tanatary: precaudal vertebrae (not seen, *fide* Redkozubov, 1987). (35) Upper Pliocene (MN 16) of Chishmikioy: precaudal vertebrae (not seen, fide Redkozubov, 1987).

Remarks: (37) The unidentified viperines from Dolnice most likely belonged to either *V. platyspondyla* or *V. antiqua* described from this locality (Szyndlar, 1987a). (38) The vertebral fragment from Děvínska Nová Ves belonged to the 'European vipers' but lack of any protruding structures makes more precise identification impossible. (28) (31) (33) (35) Redkozubov (1987) neither described nor figured the material from Moldavia; he only stated that trunk vertebrae of *Vipera* were found in four fossil sites.

History of snakes in Central and East Europe

A scenario of the distributional history of the European snake fauna, outlined by Szyndlar (1984), was mainly based on the present distribution of particular snake species rather than on the fossil record. This hypothesis is confronted below with paleontological evidence. Szyndlar (1984) pointed out that the recent European snakes (except for a few species of northernmost ranges) may be grouped into three separate geographical units, restricted to southeastern Europe, western Europe exclusive of Iberia, and the Iberian Peninsula. It was then supposed that these regions were settled by modern snakes as a result of migrations via three different corridors, i.e., from western Asia through the Asia Minor, from western Asia through Central Europe, and from northwestern Africa through the Gibraltar Strait, respectively. Later studies (Szyndlar, 1985, 1988) confirmed the supposition that in the past Iberia was invaded by African snakes. At the same time, there is no evidence that African snakes entered the remaining parts of the European continent, at least with reference to post-Paleogene times; thus, the non-Iberian European snakes are supposed descendants of invaders from Asia.

Considering that the above supposition is demonstrable, traces of any faunal exchanges between Asia and West Europe are to be found in the area covered by the present study. Although this is largely true, unfortunately the Miocene history of East European snakes may be demonstrated in the northern part of the area only. Regarding the southernmost part of Eastern Europe, no snake fossils coming from localities older than uppermost Miocene were available for study. The oldest examined remains from the Greek locality of Pikermi 4 are so damaged that identification even to familial level was impossible; those from two other Greek Miocene localities (Maramena 1 and Ano Metochi 2) are also poorly preserved and (except for a presumed *Naja* from Maramena 1) they were not identified below the subfamilial level.

Review of families

Scolecophidians

The oldest scolecophidians are known from the lower Eocene of Belgium (Rage, 1984). In the Miocene, they occupied a considerable part of the European continent; a full list of the fossil record reported from the entire Europe prior to 1985 can be found in Szyndlar (1985). In West Europe, scolecophidians survived until at least the Pliocene (S. Bailon, pers. comm., 1989).

In East Europe, scolecophidians probably occupied most of the area during almost entire Miocene; the youngest East European site yielding remains of these snakes and lying outside the present range of scolecophidians, Cherevichnoie (lower layer), is of upper Miocene age. Younger localities are located exclusively within the area occupied presently by *Typhlops vermicularis*. This species, the only representative of the family Typhlopidae in Europe, occurs in the south-eastern part of the continent.

As stated in the previous paper (Szyndlar, 1991), identification of scolecophidian vertebrae to the familial level is not possible. Therefore, it cannot be demonstrated whether the European fossils belonged to the family Typhlopidae or to the Leptotyphlopidae: at present, members of the latter family live in the close vicinity of Europe, occupying among other areas the entire south Mediterranean coast and southwestern Asia.

Boidae

Except for a doubtful record of *Python euboicus*, non-erycine boids have never been reported from Eastern Europe. The subfamily Erycinae, recorded since the Paleocene, underwent a great radiation in West Europe and North America in the Eocene (Rage, 1987). Erycine snakes were also widespread in the end of the Paleogene and in the Neogene of Europe (Hoffstetter and Rage, 1972). They probably inhabited a considerable part of Western Europe until the end of the Pliocene (Szyndlar, 1985). All pre-Miocene finds represent extinct genera; during the Miocene, they were being gradually replaced by members of the living genus *Eryx*. At present, species belonging to this genus occur in west and southern Asia and in a part of Africa; the only species presently inhabiting Europe, *Eryx jaculus*, occupies the southeastern part of the continent (fig. 17).

The Miocene erycine fauna of East Europe is re-

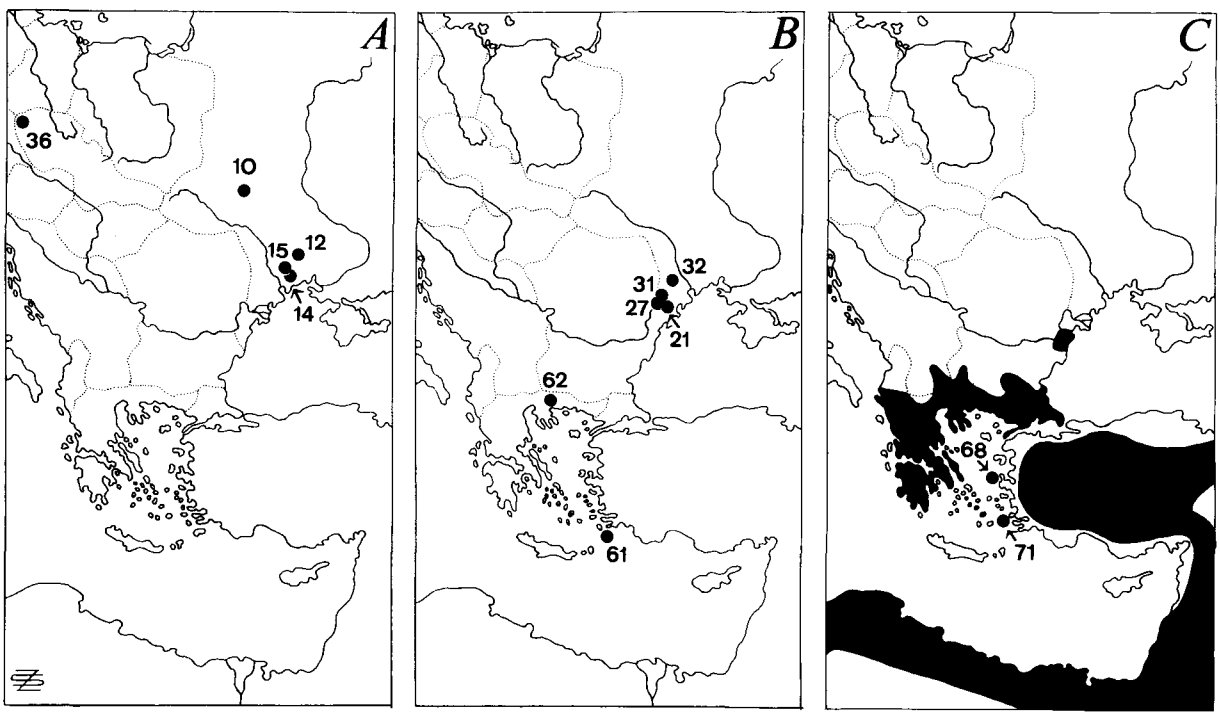

Fig. 17.—Past and present distribution of Erycinae in Central and East Europe. A, Miocene; B, Pliocene; C, Pleistocene. Fossil localities: 10, Gritsev; 12, Novoelizabetovka, lower layer; 14, Cherevichnoie, lower layer; 15, Bielka; 21, Kotlovina, lower layer; 27, Etuliya; 31, Dermendzhi; 32, Novye Tanatary; 36, Dolnice; 61, Maritsa; 62, Spilia 4; 68, Chios; 71, Pili B. Present distribution (black areas) of *Eryx jaculus* after Engelmann et al. (1985) and Le Berre (1989). For further details see text.

presented by both extinct (*Bransateryx* and *Albaneryx*) and extant (*Gongylophis* and *Eryx*) genera. It should be noted that the finds of *Bransateryx* and *Albaneryx* from the Ukrainian locality of Gritsev are the youngest European records of these genera. On the other hand, first appearance of the living genera antedated disappearance of the archaic elements in the area.

According to Rage (1977), the oldest European erycines were replaced by *Bransateryx* and *Albaneryx* in post-Eocene times, i.e., after disappearance of the Turgai Strait, which separated Asia from Europe. Szyndlar (1987a) suggested an opposite direction of these migrations. Unfortunately, there is no direct evidence supporting either hypothesis. The only record of a presumed *Bransateryx* from Central Asia (Zaisan locality near the Kazakhstan-Chinese frontier) is of middle Oligocene age; middle Eocene and early Oligocene erycines from the same locality are represented by primitive *Calamagras*-like snakes and by "... a small, apparently new genus of the Erycinae" (Chkhikvadze, 1985: 234). The pre-Oligocene presence of *Bransateryx* to the east of the Turgai Strait is thus not demonstrable; nevertheless, the Zaisan remains (if indeed they belonged to *Bransateryx*) indicate that the genus was widely distributed by the end of the Paleogene. *Bransateryx* is not found in post-Oligocene materials from Zaisan; since the early Miocene, the only erycine remains recorded from this locality are referable to the modern genus *Eryx* (Chkhikvadze, 1985).

As noted in the previous paper (Szyndlar, 1991), *Bransateryx* and *Albaneryx* closely resemble the living North American *Charina* and *Lichanura,* respectively, at least with reference to the axial skeleton (Rage, 1984; Szyndlar, 1987a). It is quite probable that the European extinct genera are synonymous with their American counterparts.

Bransateryx and *Albaneryx* disappeared in West Europe in the lower and middle Miocene, respectively (Rage, 1984). Finds of these genera in the late Miocene of Ukraine provide new evidence that extinction of archaic European snake faunas proceeded gradually from West to East. The available fossil record demonstrates that in the Miocene the Old World and New World ranges of *Bransateryx-Charina* and *Albaneryx-Lichanura* lineages were disjunct (only *Charina* is known from the North American Miocene; Holman, 1979). It is quite probable that Eastern Europe was a last refugium of these snakes in Old World.

A similar phenomenon, i.e., a gradual extinction from West to East, took place later in the case of the living genera, *Gongylophis* and *Eryx*. The oldest European find of *Eryx* comes from the Spanish lower Miocene (Szyndlar, 1987a); the oldest (and the only) European record of its close relative, *Gongylophis* from Czechoslovakia, represents the same age. In the Miocene, *Eryx* was widely distributed in the southern half of Europe; in West Europe it gradually disappeared during the Pliocene (Szyndlar, 1985). Also, no post-Neogene find is available from the Black Sea area where *Eryx* was common until the end of the Pliocene (Zerova, 1987). The only Pleistocene records come from the area inhabited by this snake today, i.e., southeasternmost Europe.

Colubridae

A few of the oldest European finds of the Colubridae come from the Oligocene of France and Germany; they are represented exclusively by vertebrae displaying morphology consistent with those characteristic for both modern "natricines" *(Natrix)* and "colubrines" (tentatively placed in the genus *Coluber*) (Rage, 1988).

Although most described extinct species represent only this family, perhaps an overwhelming majority of these descriptions does not reflect the true taxonomic position of the fossils. This situation derives from the fact that the family Colubridae includes an enormous number of species that are largely characterized by homogenous morphology of vertebrae. Since most ophidian paleontologists use a subdivision of the family Colubridae into Colubrinae and Natricinae, it generates widespread opinions that only members of these two subfamilies were found in fossil state in Europe (e.g., Cadle, 1987). However, this subdivision has only a symbolic meaning and is used for differentiating hypapophyses-bearing colubrids from those devoid of hypapophyses (cf. the previous chapter). In fact, with reference to most fossil "colubrines", it is impossible to demonstrate whether they represented the Colubrinae (s.s.) or another subfamily. Regarding "natricines", neither all members of the Natricinae (s.s.) possess hypapohyses throughout the column nor are they the only colubrids having them.

It is symptomatic that the best recognized fossils of the family Colubridae are clearly referable to modern genera and the particular extinct species are in many aspects closely similar to their living relatives. On the other hand, all fossil genera reported from the area (including those originally described from remote regions) were erected on the basis of very scarce material.

No extinct colubrid genus was compared with all or even with a considerable part of living genera. Such a comparison seems to be physically impossible and that is why disregard of large scale comparisons is a normal practice among ophidian paleontologists.

In particular, regarding widespread fossil genera, e.g., those described from the Miocene of North America and then recorded also from the European Miocene, their taxonomic status leaves much to be desired. Considering sympatric occurrence of these fossils along with other snakes presently distributed, for example, in the Oriental Realm (as in the case of Dolnice), it is possible that the presumed extinct genera may have actually represented some modern genera with the present range of distribution remote from the fossil sites.

In conclusion, the taxonomic status of all of the discussed fossil colubrid genera is then either doubtful or not fully demonstrated.

The taxonomic status of extinct members of modern genera is usually more credible but (in most cases) only when their descriptions are based on both cranial elements and vertebrae. It seems demonstrable that European Miocene colubrids did not belong to living species, thus proper taxonomic description of these snakes may be realized, but only on the condition (usually) that cranial elements make satisfactory generic allocation possible. Regarding the Pliocene, when both extinct and extant species occurred, proper taxonomic allocation of given fossils needs comparison with all related taxa presently inhabiting both the close vicinity of the fossil site as well as some adjacent areas (in the case of Eastern Europe, more or less the West Palearctic).

The oldest unquestionable member of the genus *Coluber* in Eastern Europe is the lower Miocene *C. dolnicensis,* while the oldest member of *Elaphe* (still undescribed) comes from the late Miocene of Gritsev in the Ukraine; at the same time these taxa are also probably the oldest certain representatives of both genera in the whole of Europe. The oldest European remains of *Natrix* were recorded from the French (probably) lower Oligocene (Rage, 1988); the oldest (uncertain) record from East Europe comes from the late Miocene.

Elapidae

The entire available fossil record of these snakes from the West Palearctic was recently reviewed by Szyndlar and Rage (1990). All but one find from the area, coming from eighteen localities, belong to the modern genus *Naja;* the oldest European remains of *Naja* (at the same time the oldest known elapid remains) come from the lower French Miocene. In the Miocene, members of this genus occupied a major part of Europe. The last unquestionable members of the genus *Naja* survived in the Mediterranean area of the both West and East Europe at least until the upper Pliocene (Bailon, 1989; Szyndlar and Zerova, 1990).

At present, members of the genus *Naja* occur in most of Africa and southern Asia. Living members of the genus *Naja* represent two separate evolutionary lineages, confined to Asia and Africa respectively; it should be stressed that this subgeneric split can be observed in the oldest fossils. Most likely, all fossil cobras from Central and East Europe belonged to the former group (Szyndlar and Rage, 1990). It demonstrates, along with the fossil record of large vipers, that in the Miocene the discussed area was inhabited by snake faunas similar to those occurring at present in the Middle East and/or the Oriental Realm. It is also noteworthy that the oldest fossil cobras (at least those known from abundant remains), apart from some primitive features, are morphologically very similar to living species.

Viperidae

The oldest vipers were reported from the West European lowermost Miocene (Agenian) by Kinkelin (1892, 1896) and by Hoffstetter, (1962). The former find, an isolated fang named *Provipera boettgeri* by Kinkelin (1892), was then referred to the subfamily Crotalinae (Kinkelin, 1896). Taxonomic status of this fossil was rightly criticized by Cope (1892: 224) who stated that "neither species nor genus can be possibly described from the specimen in Dr. Kinkelin's possession"; Rage (1984) considered *Provipera boettgeri* as a *nomem dubium.* Hoffstetter (1962) only mentioned that the Viperidae appeared in Europe in the Aquitanian (= Agenian), unfortunately, no more lengthy information about his find has ever been published. Hoffstetter's report may have been based on a collection presently housed at P. & M. Curie University in Paris; it comes from the lowermost French Miocene (Agenian) and consists of vertebrae of small vipers (J.C. Rage, pers. comm., 1989). The same collection includes also numerous well preserved large vertebrae belonging apparently to the 'Oriental viper' group (pers. obs., 1989), coming from the lower Miocene (Orleanian) of France.

Fossil members of the family Viperidae found in Europe probably belonged exclusively (perhaps with exception of the enigmatic *Laophis*) to the modern genus *Vipera* (Szyndlar, 1987b).

As noted in the previous chapter, extant members of the genus *Vipera* form several separate complexes and this subgeneric diversity is usually also recognizable in fossil materials. The largest members of the genus, 'Oriental vipers' , presently inhabit southern Asia and northwestern Africa. The European distribution of the 'Oriental viper' group is restricted to

the Cyclades *(Vipera lebetina),* easthernmost Greece, European Turkey, and Greek islands in the vicinity of west Anatolian coasts (*V. xanthina*). In the Miocene, 'Oriental vipers' were widely distributed in the entire southern half of the continent; in Western Europe, they survived until the end of the Pliocene in the Mediterranean area (Szyndlar, 1987b, 1988). In Eastern Europe, they probably inhabited vast areas until at least the middle Pleistocene (fig. 18).

Smaller members of the genus *Vipera* ('European vipers') presently inhabit the southern part of the West Palaearctic (*'aspis'* group) and the northern part of the Palaearctic (*'berus'* group). A representative of the 'European vipers', *V. antiqua,* is present in the oldest site of Central and Eastern Europe, i.e., in the lower Miocene of Dolnice. It should be noted that all fossil species of *Vipera,* including the oldest forms, were closely similar to the living members of the genus.

Sympatric occurrence of two separate groups of *Vipera* was also reported from the early Miocene of Central Asia (Zaisan basin) by Chkhikvadze (1985: 234) who recorded "... *Pelias* (a small species) [i.e., a 'European viper'] and a much larger viper of size [comparable with] *V. xanthina*".

These facts suggest that the split of *Vipera* into the complexes characteristic for living members of the genus is an old phenomenon, undoubtedly antedating the early Miocene. According to Groombridge (1986), who based his supposition on morphological analysis, the 'European vipers' are members of early sidebranches, whereas the 'Oriental vipers' are regarded as recent radiations. On the contrary, Herrmann et al. (1987) considered that the *'xanthina'* and *'lebetina'* groups were early offsprings of the *Vipera* stem, whereas the 'European vipers' resulted from a comparatively modern radiation; the biochemically based reconstruction of the phylogeny of *Vipera* presented by the latter authors, which considers the first branching within the genus at ca. 17-18 million years ago (Herrmann et al. 1987, fig. 3), cannot be accepted. Palaeontological evidence cannot support any of these opposing hypotheses; however, the available fossil record indicates that irrefutably the main split within the genus *Vipera* must have taken place much earlier than suggested by the latter authors.

Conclusions

The oldest record from Central and East Europe indicates that during the Miocene the entire snake fauna was probably represented exclusively by ex-

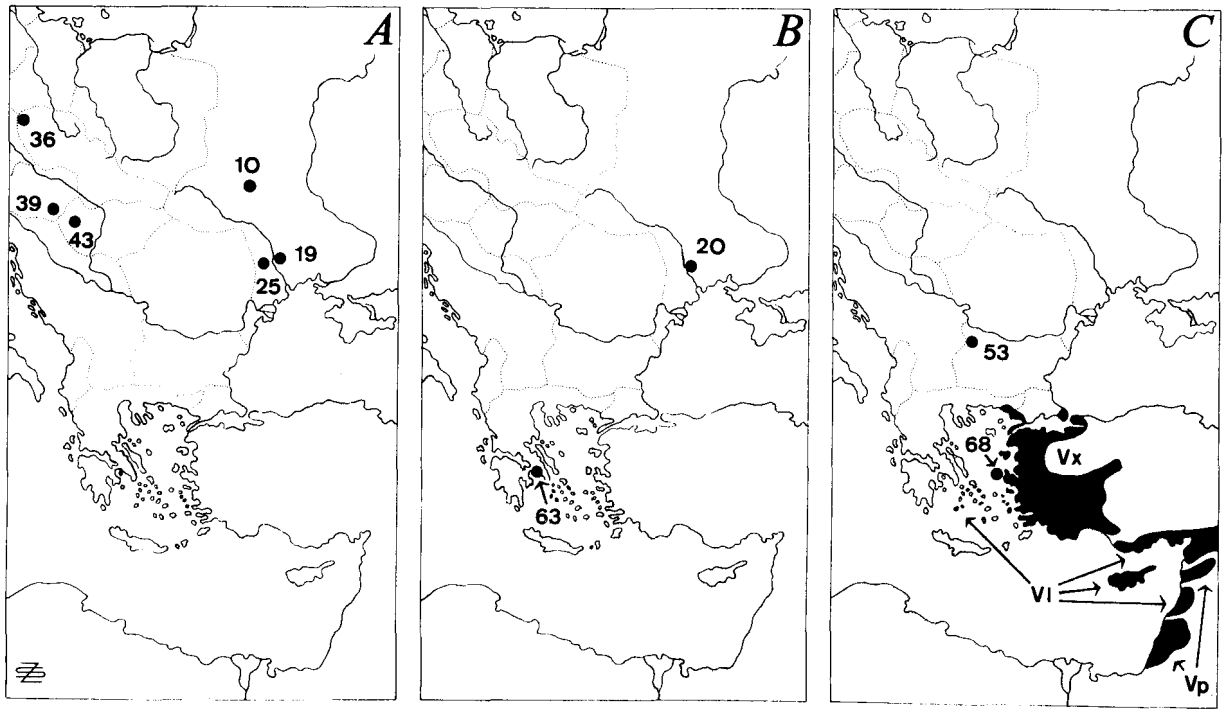

Fig. 18.—Past and present distribution of the 'Oriental vipers' in Central and East Europe. A, Miocene; B, Pliocene, C, Pleistocene. Fossil localities: 10, Gritsev; 19, Frunzovka 2; 20, Kuchurgan; 25, Kalfa; 36, Dolnice; 39, Kohfidisch; 43, Polgárdi; 53, Varbeshnitsa; 63, Tourkobounia 1; 68, Chios. Present distribution (black areas) of *Vipera lebetina* (Vl), *Vipera palaestinae* (Vp), and *Vipera xanthina* (Vx) after Joger (1984), Nilson and Andrén (1986) and Nilson et al. (1988). For further details see text.

tinct taxa, i.e., either by members of extinct genera or by extinct species belonging to extant genera. The taxonomic status of some presumed living species reported from the uppermost Miocene of Polgárdi by Bolkay (1913) and von Szunyoghy (1932) is doubtful; unfortunately, this opinion is not derived from re-examination of the discussed fossils. The Miocene fossils represented exclusively modern snake families. Except for the Elapidae, members of these families are present in the area until now; nevertheless, present ranges of a considerable number of the widespread Miocene snakes (Scolecophidia, Boidae, 'Oriental vipers') are of relict character.

It should be stressed once again that all well recognized fossil snakes from the Central and East European Miocene belonged exclusively to modern genera and were very similar to related living species. Regarding extinct genera, they are either closely related to modern genera (as in the case of *Bransateryx-Charina* and *Albaneryx-Lichanura* lineages), and perhaps they ought to be synonymized with the latter or their generic status is not demonstrated in a satisfactory manner, and therefore their distinction is uncertain. These facts suggest that the ophidian faunas (or at least the majority of snakes) inhabiting Central and East Europe since the beginning of the Miocene closely resembled those of living faunas, although not necessarily those occurring presently in Europe.

It is quite probable that the modern pattern of European snake faunas was characteristic also for the times immediately preceding the Miocene; presence of colubrid remains resembling living species in the West European Oligocene (Rage, 1988) may support this opinion. Unfortunately, the Oligocene is characterized by impoverished faunas, both in West Europe and anywhere, which contrasts sharply with the rich assemblages of the Eocene; the European ophidian fauna of the latter epoch was represented exclusively by representatives of archaic snake families (Rage, 1987).

A considerable part of the Miocene snakes of Eastern and Central Europe represent modern genera the distribution of which is located in the Middle East and the Oriental Realm. Connections between Europe and North America are also well demonstrated, at least with reference to erycine genera. Possible migrations between both continents seem, however, to antedate the Miocene; ranges of snake taxa, common for both Europe and North America, were perhaps disrupted in the Miocene. It is probable that at least a part of the colubrid snakes occurring in both the European and North American Miocene actually re-

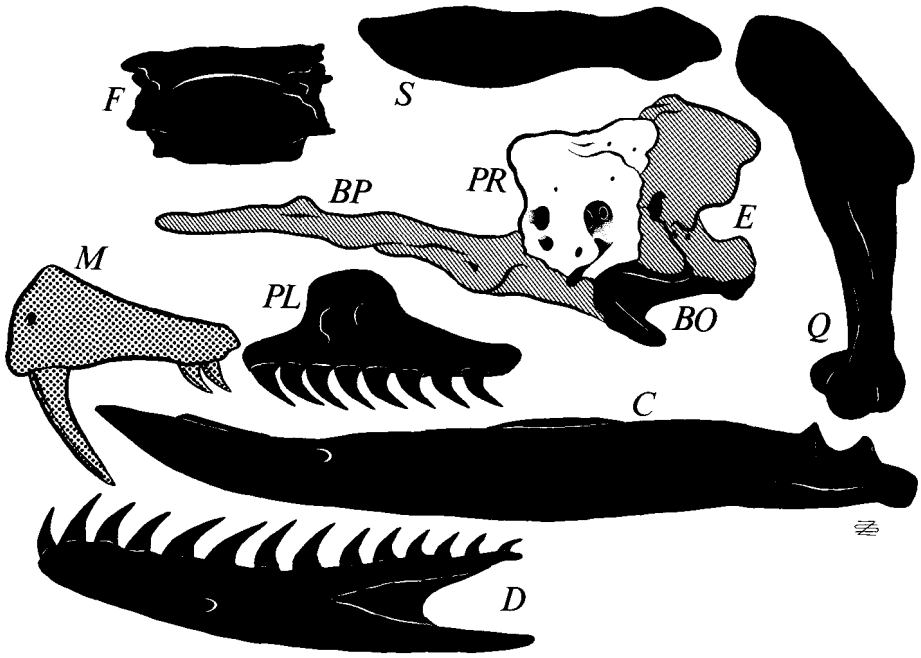

Fig. 19.—Cranial bones of *Naja romani*, in left lateral views. Not to scale. Black colour: elements identical with those of all or majority of living species of the genus *Naja;* slanting lines: elements identical with those of Asiatic members of the genus; dots: element identical with those of African members of the genus; white colour: element differing from those of all members of the genus. Abbreviations: BO, basioccipital; BP, basiparasphenoid; C, compound; D, dentary; E, exoccipital; F, frontal; M, maxilla; PL, palatine; PR, prootic; Q, quadrate; S, squamosal.

presented living genera presently restricted to the Oriental Realm.

A striking feature observed in the European Miocene is the longevity of ophidian species; it was well documented with reference to two Miocene snakes, *Natrix longivertebrata* and *Naja romani.* The former survived for about ten million years and only slight morphological differences can be observed between the oldest and youngest records (Rage and Szyndlar, 1986). The latter persisted in invariable form for at least six million years (Szyndlar and Zerova, 1990; Szyndlar and Rage, 1990). These long spans, apparently correlated with prolonged favourite climatic conditions, sharply contrast with the short longevities characteristic of living ophidian species; perhaps they were typical for most Miocene snakes. Indirectly it can suggest that snake species inhabiting presently tropical zones may have been established in remote epochs, perhaps in the Miocene.

Lack of an appropriate fossil record hinders the recording of any possible changes in the character of snake faunas in the Mediterranean area of Eastern Europe during the time of the Messinian crisis. In the northern part of the discussed area, no sudden changes occurred at the turn of Miocene (MN 13). The following phase of the Neogene, namely the lower Pliocene (MN 14) seems to be of special importance as a "transitional epoch" preceding immediately first appearance of modern snake species. Unfortunately, except for viper remains, the entire fossil record from the lower Pliocene is very scarce.

First living species (Colubridae) were recorded from the middle Pliocene (MN 15); in the upper Pliocene (MN 16), living species predominate over the Central and East European snake assemblage. It is noteworthy that the upper Pliocene fauna, apart from some relicts (Elapidae, 'Oriental vipers'), does not differ significantly from that inhabiting the area presently. The only apparent difference in comparison with the recent fauna is that the ranges of particular living species were more northern in the past.

In conclusion, snakes inhabiting Europe since the beginning of the Miocene do not differ significantly from the living relatives occurring presently in various regions of Eurasia and, although to much lesser degree, of North America: close similarities can be observed in the morphology of particular species as well as in intrageneric diversification. Considering these facts, divergence of advanced snakes (for which pre-Miocene fossil record, except for the Colubridae, is unknown) must have taken place long before the Miocene. This assumption is not concordant with the opinions of many authors that most lineages of advanced snakes emerged around the Paleogene/Neogene boundary. For instance, Dowling et al. (1983) suggested the origin of most colubrine genera as late as the Miocene, while Herrmann et al. (1987) hinted a similar opinion with reference to the genus *Vipera.* These hypotheses, however, when confronted with the fossil record, are little probable because they would suggest an extremely transient radiation leading to modern genera and, then, a surprising long evolutionary stasis in post-Paleogene times.

Contrary to interpretations of the above cited authors, Cadle (1988: 48) postulated that "... separation of the elapid and colubrid lineages was most likely a late Cretaceous-early Tertiary event, and the divergence of the viperids even earlier" and his opinion is clearly concordant with data provided by the available fossil record. These events, however, must have occurred in areas remote from Europe, presumably in tropical zones.

Methods in ophidian paleontology: a critique

Description of methods used in this study is brief and does not require additional comments. The fossil remains were identified on the basis of their similarity or dissimilarity with homologous skeletal elements of living snakes and of other fossils, while the use of numerical methods was of secondary utility. This essay is then intentionally placed at the end instead at the beginning of the present paper and aims at a critical appreciation of methodologies employed by students of snake fossils.

Writing the following remarks was inspired in part by recently published criticisms addressed to ophidian paleontology (e.g. McDowell, 1987; Cadle, 1987, 1988; Hecht and LaDuke, 1988). McDowell (1987) expressed the opinion that the fossil record of snakes is extremely difficult to interpret because it is based almost entirely on vertebrae, while considerable evolution may produce no detectable change in vertebrae; on the other hand, closely related forms may sometimes have quite different vertebrae. McDowell concluded that no use was made of the fossil record in snake classification until the twentieth century. Cadle (1987) pointed out that a lack of adequate survey of vertebral morphology and variation of extant snake lineages has hindered fully effective use of the fossil record. Hecht and LaDuke (1988) demonstrated that vertebrae of two closely related genera can display divergent morphology, implying that allocation of extinct forms to family or subfamily based on isolated vertebrae may be questionable.

Rage (1987) refuted a part of the above arguments, stating that the usefulness of vertebrae for purposes of identification is well established, but at the same time he observed that their significance in phyletic reconstruction is sometimes questioned on account of conservative vertebral morphology; this is awkward

TABLE I

MYBP	MN	Age	Localities	Scol.	Boidae	'Colubrinae'	'Natricin!'	Elap.	Viperidae
18	a	ORLEANIAN	58:Kimi	....	!+Pe ...	.....	.....	....	.....
	4		37:Dolnice	in.S	+Bs,cf.G	+Tb,+Cd,in.C	+Nn,+Pl .	....	+Vp,+Va,V
17	b								
	5								
16									
15	6	ASTARACIAN	1:Przeworno 2	....	.....	in.C	.....	....	.....
			38:Děvínska Nová Ves	....	.....	in.C	+N,in.N .	....	V2,V
14	7		2:Opole 2	....	.....	in.C	+Ps	....	V2
13	8								
12									
11	9	VALLESIAN	10:Gritsev	in.S	+B,+Av .	C,E,in.C	in.N	+Nr.	V1,V3
			26:Kalfa	....	.....	.....	.....	....	+Vs
10			27:Buzhor	....	.....	in.C	?N	....	V
	10		39:Vösendorf	....	.....	in.C	.....	....	.....

TABLE I /continued/

9										
	11	TUROLIAN	11:Krivoy Rog	....	.....	in.C	.....	....	V2	
			12:Novoelizabetovka/lower/	....	cf.E ...	in.C	in.N'....	....	V2	
8			40:Kohfidisch	....	.....	+Cp1,+Ekh	cf.+Nl ..	+Nr.	+Vb	
	12		13:Novaya Emetovka	....	.....	.....	in.N	....	.....	
7			14:Cherevichnoie/lower/ ..	in.S	E	cf.+Ekh	cf.+Nl ..	....	V2	
			15:Bielka	....	cf.E ...	.....	.....	....	.....	
			16:Novoelizabetovka/upper/	....	.....	.....	.....	....	V2	
			59:Pikermi 4	....	.....	.....	.....	....	.....	
6	13		17:Novoukrainka 1	....	.....	in.C	in.N	....	.....	
			18:Andreievka	....	.....	in.C	in.N	....	V3	
			19:Frunzovka 2	....	.....	in.C	in.N	....	V1,V3	
			44:Polgárdi	....	.....	!+Ch,?Cc,!+Ekr,!M,in.C	?Nn,?Nt .	....	+Vg,?cf.Va,?cf.Vas,V2	
			60:Maramena 1	....	.....	in.C	in.N	cf.N	.....	
			61:Ano Metochi 2	....	.....	.....	in.N	....	.....	
			62:Karabournu	....	.....	.....	.....	....	!+Lc	
5	14	RUSCINIAN	3:Podlesice	....	.....	in.C	.....	....	V2	
			20:Kuchurgan	....	.....	.....	.....	....	+Vk	
			54:Dorkovo	....	.....	.....	N	....	.....	
			63:Maritsa	in.S	cf.E ...	in.C	.....	....	.....	
4	15		4:Węże 1	....	.....	cf.Cv	cf.+Nl ..	....	cf.Va	
			21:Kotlovina/lower/	....	E	in.C	.....	....	V3	
			28:Etuliya	....	in.E ...	?Cv,?Cg,?C,?cf.El,?E,in.C	.....	....	V	
			29:Lucheshty	....	.....	?Cg,?C,in.C	.....	....	.....	
			30:Valeny	....	.....	?Cv,?C,?cf.El,in.C	.....	....	.....	
			31:Musait	....	.....	?Cv,?Cg,?C,?E	?+Nl	....	V	
			32:Dermendzhi	....	in.E ...	?C,?cf.El	.....	....	.....	
			64:Spilia 4	....	cf.E ...	in.C	N	....	.....	

TABLE I /continued/

Rec											
	16	V	5:Węże 2	....	.....	+Ep	cf.+Nl	..	....	.....
3		I	6:Rębielice Królewskie 1A	....	.....	Cv	+Nl	.....	....	cf.Va
		L	7:Rębielice Królewskie 2	....	.....	cf.Cv	cf.+Nl	..	....	cf.Va
		L	22:Kotlovina/middle/upper/	....	E	.....	.....		....	.....
		A	24:Ukrainian Upper Pliocene	....	.....	C,E,in.C	N	.....	....	V3
		N.	33:Novyie Tanatary	....	in.E ...	?Cg,?C,?cf.El	.....		....	V
		Y.	34:Salchiya	....	.....	?Cg,?C	?+Nl,?N	.	....	.....
		I.	35:Chishmikioy	....	.....	?Cv,?Cg,?C,?Coa,?Co,?cf.El,?E	?Nn	.....	....	V
		A.	36:Bachoy	....	.....	?Cv,?C,?Co,?cf.El,?E	.....		....	.....
		N.	41:Bad Deutsch Altenburg 20	....	.....	cf.Cv,Cc,cf.Cg,Eq	.....		....	V3
		.	45:Csarnóta 2	....	.....	?Cc	.....		....	.....
		.	46:Beremend 1	....	.....	Cv,Cc,El	?Nn	.....	....	.....
		.	65:Tourkobounia 1	in.S	.....	cf.M,in.C	.....		N ..	V1,V3
2	17		47:Villány 3	....	.....	?Cc,cf.Eq	Nn,Nt	...	....	.....
		.	48:Nagyharsány-hegy	....	.....	?Cc	Nn,Nt	...	....	.....
		.	49:Villány 6	....	.....	Cc	?Nt,N	...	....	.....
			9:Polish Pleistocene	....	.....	Coa,El	Nn	.....	....	Vb
		.	25:Ukrainian Pleistocene	. ....	.....	Cc,E	Nn,Nt	...	....	V2,V3
		.	50:Csarnóta 4	....	.....	Eq	.....		....	.....
		.	51:Beremend 4	....	.....	.....	?Nt	.....	....	.....
		.	52:Betfia	....	.....	?Cc,El	Nn,?Nt	..	....	.....
		.	66:Laghada A,B	....	.....	.....	N	.....	....	V3
		.	67:Sitia 1,2	....	.....	.....	N	.....	....	.....
1		B								
		I	42:Bad Deutsch Altenburg 2	....	.....	?cf.Cv,?Cc,cf.Cg,cf.El,Eq	.....		....	.....
		H	43:St.Margarethen	....	.....	Cv,Cg,El	Nn	.....	....	Vb
		A	53:Braşov	....	.....	?Cc,Coa,El	Nn,?Nt	..	....	?Vb
		R	55:Varbeshnitsa	....	.....	Cv,Cc,cf.Cg,cf.Co,El,Eq,cf.Es,T	N	.....	....	V1,cf.Va
		I.	68:Tourkobounia 2	in.S	.....	cf.Co,cf.El,Eq,cf.Es,in.C	cf.Nt,N	.	....	cf.Va,V3
		A.	69:Tourkobounia 5	in.S	.....	El,Eq,in.C	N	.....	....	.....
		N.	70:Chios	....	Ej	in.C	.....		?N .	V1
		.	56:Stoilovo	....	.....	Cc,cf.Cg,Eq	Nn	.....	....	cf.Va
		.	57:Bacho Kiro	....	.....	cf.Co,cf.Es	Nn	.....	....	V3
		.	71:Gerani 1,4	....	.....	cf.El,cf.Es	cf.Nt	...	....	.....
		.	72:Rethymnon	....	.....	cf.Es	.....		....	.....
		.	73:Pili B	....	Ej	cf.Co,cf.El,cf.Es,in.C	N	.....	....	.....
?		.	8:Mała Cave	....	.....	!+Zx,in.C	!+Np	....	....	.....
?		.	23:Bolurubince	....	.....	!+Cpo	.....		....	.....

for phyletic analyses at a low taxonomic level but favorable for phyletic analyses at a higher phyletic level.

The above opinions concern, however, rather older snake fossils that require somewhat different methodologies when studied. Perhaps it will be useful to summarize briefly some basic problems arising during examination of post-Paleogene snakes. Special attention is paid below to methods leading to false interpretations of studied snake fossils.

Main difficulties

It is largely true that examination of geologically relatively young snake fossils is a more complex task than in the case of older materials. As pointed out in the previous chapter, even early Miocene snakes closely resemble their living relatives; obviously, this resemblance is more striking in the case of Pliocene and, especially, Pleistocene fossils. Paleogene snakes resemble modern snakes to a lesser degree and therefore examination of their remains does not require such detailed comparisons with related living taxa as in the case of geologically younger fossils. Proper examination of the latter requires not only access to large skeletal collections including related living species, but it also requires a knowledge of intraspecific variability. Unfortunately, intraspecific variation in skeletons of living snakes is poorly recognized in reference to most ophidian taxa. It is noteworthy that in rare cases where the variation was recognized its spectrum may be unexpectedly broad (as in members of the genus *Naja;* cf. Szyndlar and Rage (1990)).

Problems concerning taxonomic validity of extinct genera were widely discussed in the previous chapter. I have stated that satisfactory pros or cons of distinction of any fossil genera do not exist, especially in regard to colubrids. On account of that I have temporarily retained these genera valid. A possible fruitful systematic revision of these extinct genera would be perhaps possible after assignment of patterns of vertebral morphology for basic lineages of living snakes, as suggested by Cadle (1987). Unfortunately, so far nobody has undertaken such a study.

Another important problem is the proper recognition of whether given fossils belonged to a living or extinct species. As pointed out in the previous chapter even early Miocene European snakes are very similar to their living relatives. It means that some bones display distinct morphology, but most skeletal elements (usually an overwhelming part!) are morphologically concordant with homologous elements of recent species. It was well demonstrated in reference to two Miocene species, known on the basis of abundant cranial elements, namely *Natrix longivertebrata* and *Naja romani* (Rage and Szyndlar, 1986; Szyndlar and Rage, 1990; cf. also chapter "Systematic account").

For example, as shown on fig. 19, there are no significant differences between most cranial bones (frontal, basioccipital, squamosal, quadrate, palatine, dentary, compound) of the Miocene *Naja romani* and homologous elements belonging to majority or even all living members of the genus *Naja;* two other kinds of bones of *N. romani* do not differ significantly from those belonging to the living Asiatic members of the genus, while maxillae of *N. romani* are identical with those characteristic for living African species. The only cranial element of *N. romani* clearly differing from those of other members of the genus *Naja,* is the prootic.

Regarding *Natrix longivertebrata,* a presumed ancestor of the living *N. natrix,* it differs from the latter in frequency of two patterns of the basisphenoid morphology, while remaining available cranial elements are very similar or identical in both species. These examples are shown here in order to indicate that isolated cranial bones found in fossil sites, although identical with homologous elements of some living species, did not necessarily belong to the same species.

A classical example of doubtful identification, resulting from treatment of particular fossil remains independently, are descriptions of presumed living species from the Miocene of Polgárdi by Bolkay (1913) and von Szunyoghy (1932). In order to avoid such errors (or at least to lessen the probability of the errors) it is usually necessary to "fit" cranial elements to vertebrae coming from the same locality (cf. below).

Vertebrae

Most fossil snake collections consist exclusively of isolated vertebrae, therefore most fossil records are based exclusively (or mainly) just on these elements. Usefulness of vertebrae (usually trunk vertebrae) for identifying snake taxa differs for various families. Identification of scolecophidians based on vertebrae alone is impossible even to familial level; regarding viperids, vertebrae make it possible to identify most genera and even subgeneric units but identifications to specific level are hazardous in most cases; vertebrae of colubrids may be a sufficient basis for identifying species, but on the other hand it is often difficult to recognize the generic allocation (see Szyndlar, 1991, for details).

Although somewhat surprising, vertebrae are of especially great importance in studying materials containing also cranial elements. In many cases, consi-

deration of vertebrae alone enables proper estimation of the number and kind of taxa occurring in a given material. Szyndlar (1984) pointed out that disregard of vertebrae (often along with unawareness of intraspecific variation of skull bones) repeatedly has led to false identification of snake fossils. For example, particular isolated cranial bones that actually belonged to a single species may be identified as belonging to a few living species (if they are identical with comparative materials in hand). In such a case, proper number of species will be revealed when vertebrae are considered.

The basis of proper identification of snake vertebrae is mainly their morphology, while the use of numerical data is at most of secondary significance. Although presentation of measurements and ratios as a part of morphological description is desirable, satisfactory methods of identification based on numerical data have not been demonstrated yet (cf. Szyndlar, 1984). The difficulties result from the fact that ratios are strongly distorted by at least three kinds of considerable variation, i.e., intraspecific, allometric, and intracolumnar variations. It should be stressed that numerical differences, sometimes pointed out in differentiating diagnoses (especially in cases when morphological differences are unclear), are based both on limited fossil material and on limited comparative material. Such diagnoses are of doubtful value. Unfortunately, detailed studies of numerical variation of snake vertebrae, based on large number of specimens representing various age classes and considering all kinds of variation are not yet available in the literature.

It should be also stressed that vertebrae of Miocene and younger snakes cannot be a basis for any phylogenetic considerations. The only useful information available from vertebrae alone, apart from their systematic allocation, is the past distribution of the taxon considered.

Geographic and stratigraphic location

Difficulties connected with proper identification of snake fossils are closely correlated with latitudinal location of a given fossil site and with its geological age. In the case of localities of, let us say, middle Pleistocene age, containing exclusively modern snake species, the more northern locality the easier the identification of fossils. For example, northernmost sites (e.g., the Polish Pleistocene) always contain only a few snake species that are easily differentiated from each other even in the case when they are not abundant and strongly damaged.

The situation may change radically in reference to more southern and geologically older sites, e.g. Bad Deutsch Altenburg 20 in Austria (Szyndlar and Rabeder, in prep.). This upper Pliocene locality yielded exceptionally abundant snake material, consisting of thousands of vertebrae and hundreds of cranial bones, belonging to several ophidian species; an additional difficulty is the fact that upper Pliocene localities may contain both extant and extinct species. It perhaps seems paradoxical, but the remains from Bad Deutsch Altenburg 20 cannot be identified with full confidence, although they contain extremely abundant skull bones. On account of overlapping intraspecific variation of some cranial elements belonging to members of the genera *Coluber* and *Elaphe,* correct specific (and even generic) identification is impossible. Considering the high intraspecific variation of vertebrae coming from the same locality, proper taxonomic allocation of many fossil elements cannot be demonstrated.

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Distribution of fossil snake taxa in Central and East European localities

First column (MYPB): million years before present. Second column (MN); European Neogene Mammal Zones (after Mein 1975, and other sources). Third column (Age): European Land Mammal Zones (after Fahlbusch 1976).

Abbreviations:

(+), extinct taxon; (!), status doubtful; (?), status not demonstrated.

Column «Scolecophidia»: in. S, Scolecophidia indet.

Column «Boidae»: +Av, *Albaneryx volynicus;* +B, *Bransateryx* sp.; +Bs, *Bransateryx septentrionalis;* E, *Eryx* sp.; cf. E, cf. *Eryx* sp.; in. E, Erycinae indet.; Ej, *Eryx jaculus;* cf. G, cf. *Gongylophis* sp.; +Pe, *Python euboicus.*

Column «Colubrinae»: C, *Coluber* sp.; in. C, «Colubrinae» indet.; Cc, *Coluber caspius;* +Cd, *Coluber dolnicensis;* Cg, *Coluber gemonensis;* cf. Cg, cf. *Coluber gemonensis;* +Ch, *Coluber hungaricus;* Co, *Coronella* sp.; cf. Co, cf. *Coronella* sp.; Coa, *Coronella austriaca;* +Cpl, *Coluber planicarinatus;* +Cpo, *Coluber podolicus;* Cv, *Coluber viridiflavus;* cf. Cv, cf. *Coluber viridiflavus;* E, *Elaphe* sp.; +Ekh, *Elaphe kohfidischi;* cf. +Ekh, cf. *Elaphe kohfidischi;* +Ekr, *Elaphe kormosi;* El, *Elaphe longissima;* cf. El, cf. *Elaphe longissima;* +Ep, *Elaphe paralongissima;* Eq, *Elaphe quatuorlineata;* cf. Eq, *Elaphe quatuorlineata;* cf. Es, cf. *Elaphe situla;* M, *Malpolon* sp.; cf. M, cf. *Malpolon* sp.; T, *Telescopus* sp.; +Tb, *Texasophis bohemiacus;* +Zx, *Zelceophis xenos.*

Column «Natricinae»: N, *Natrix* sp.; +N, *Neonatrix* sp.; in. N, «Natricinae» indet.: +Nl, *Natrix longivertebrata;* cf. +Nl, *Natrix* cf. *N. longivertebrata;* Nn, *Natrix natrix;* +Nn, *Neonatrix nova;* +Np, *Natrix parva;* Nt, *Natrix tesselata;* cf. Nt, *Natrix* cf. *N. tesselata;* +Pl, *Palaeonatrix lehmani;* +Ps, *Palaeonatrix silesiaca.*

Column «Elapidae»: N, *naja* sp.; cf. N, cf. *Naja* sp.; +Nr, *Naja romani.*

Column «Viperidae»: +Lc, *Laophis crotaloides;* V, *Vipera* sp. (status uncertain); V1, *Vipera* sp. («Oriental viper»); V2, *Vipera* sp. (*'aspis'* group); V3, *Vipera* sp. (*'berus'* group); cf. Va, *Vipera* cf. *V. ammodytes;* +Va, *Vipera antiqua;* cf. Vas, *Vipera* cf. *V. aspis;* Vb, *Vipera berus;* +Vb, *Vipera burgenlandica;* +Vg, *Vipera gedulyi;* +Vk, *Vipera kuchurganica;* +Vp, *Vipera platyspondyla;* +Vs, *Vipera sarmatica.*

I suggest here that *N. longivertebrata,* morphologically closer to *N. natrix* than any other living members of the genus are (Rage and Szyndlar 1986), was a direct ancestor of *N. natrix.* The available skeletal material clearly demonstrates progressibe replacement of the sphenoid pattern characteristic for *N. longivertebrata* (supposed to be ancestral) by that prevailing in the living *N. natrix.* The few basiparasphenoids of *Natrix natrix,* displaying the ancestral pattern, are almost identical with all basiparasphenoids of *N. longivertebrata* coming from the French Miocene. The bones from France (including newly discovered materials, not yet described) are characterized by highly homogenous overall morphology unlike those from the type locality. The latter, although all possessing the 'typical' *longivertebrata* pattern in the posteriormost sphenoid area, differ much from one another in the shape of the basipterygoid processes and suborbital flanges (cf. Szyndlar 1984, Fig. 27:1-5). Such a broad spectrum of variation indicates high polymorphy in the hypothetical lineage leading to the recent *N. natrix* still in the Upper Pliocene; most features observed in the basiparasphenoid of the living *N. natrix* very little.

For more detailed description of skeletal elements of *N. longivertebrata* see Szyndlar (1984) and Rage and Szyndlar (1986).

(31) (34): David *et al.* (1988) and Redkozubov (1987), who recorded *N. longivertebrata* from two Pliocene Moldavian sites, neither described nor figured these fossils.

Notes Added in the Proof

Note 1

This note summarizes data included in several articles issued after submitting the present paper and the preceding one (Szyndlar, 1991) for publication.

Lungu et al. (1989) listed snake taxa from Gritsev in the Ukraine (labelled number 10 in this paper) as follows: «*Eryx* sp., Colubridae (a number of species, among them *Elaphe* sp.), Elapidae, *Vipera, Pelias*» (ibid.: 60), as well as those from Kalfa in Moldavia (labelled number 26 in this paper) as follows: «*Natrix* sp., *Coluber* sp., *Vipera sarmatica*» (ibid.: 59). They also repeated literally the description of *Vipera sarmatica* (ibid.: 64-66, Fig. 3) that was previously published by the same authors (Chkhikvadze and Lungu in Zerova et al., 1987).

Ratnikov (1988:120) reported *Natrix tesselata* and *Natrix* sp. from the new upper Pleistocene locality of Zmeevka in Russia (Belgorod oblast', near the town Staryy Oskol, ca. 100 km north of the frontier between Russia and the Ukraine).

Venczel (1987, 1989) described and figured abundant ophidian remains from the newly discovered upper Pleistocene locality Burzău-Rîpa in Romania (Bihor county; ca. 20 km south of the locality of Betfia, labelled number 52 in this paper). The material (property of the Muzeul Ţării Crişurilor) contains cranial and axial elements belonging to the following species: *Coluber* cf. *viridiflavus* (Venczel 1989: 765, Fig.3a; cat. no. 13770), *Elaphe longissima* (Venczel 1987: 580-581; 1989: 765-768, Figs 2j, 3b, 4a-k, 5a-c; cat. no. 13665-13671, 13673-13677, 13762, 13765, 13768), *Natrix tesselata* (Venczel 1987: 581; 1989: 768-770, Figs 3c, 41-q, 5d-f; cat. no. 13692-13701, 13705), and *Vipera* sp. (Venczel 1987: 581; 1989: 770, Fig. 5g-i; cat. no. 13720).

The same author (Venczel, 1991) also mentioned some new colubrid and viperid materials coming from the early Pleistocene of Betfia and Subpiatra (Bihor county); these remains have not been described in detail yet.

Note 2

The remarks concerning *Coluber podolicus* (cf. Szyndlar, 1991: 115) are unprecise and erroneous in part. The following explanation comes from Szyndlar and Böhme (in prep.):

The proper name of the type locality of this snake is either Holuzubiniec (Pusch 1837: 168) or Hotozubince (Pusch 1842: 179), and not Bolurubince as given by Mlynarski (1961: 36) and Rage (1984: 52).

In the opinion of Pusch (1837: 168), who first reported and figured the discussed fossil, it was similar to vertebrae of some small lizards and also to those of the living North American salamander *Siren lacertina.* The illustration of this vertebra (ibid.: Pl. XV: 5a-c) indicates with no doubt that it belonged to a member of the ophidian genus *Natrix.* The original erroneous systematic allocation of the vertebra was emended in a later paper of Pusch (1842. 180), who compared it correctly with *Coluber natrix* (i.e., *Natrix natrix*).

Then, in order to distinguish the vertebra from some related fossil snakes of the German Neogene, von Meyer (1844: 565) named it *Coluber (Tropidonotus?) Podolicus.* It should be noted that von Meyer considered the fossil a member of the genus *Natrix* (in the present sense of this name). The use of the nomenclatural combination *'Coluber (Tropidonotus?)'* reflected only von Meyer's uncertainty what was the proper generic allocation of the snakes presently included in the genus *Natrix.*

Note 3

The following remarks concern the classical material from the Hungarian locality of Polgárdi (labelled number 44 in this paper), examined recently by the author.

Of the snake remains from Polgárdi described by Bolkay (1913) and von Szunyoghy (1932), only types of *Coluber hungaricus,*

Elaphe kormosi and *Vipera gedulyi* are available, while the remaining material is lost.

Coluber hungaricus (Bolkay, 1913) (cf. remarks in Szyndlar, 1991: 115). The only element referred to this snake (right quadrate, holotype, MHGI Ob-4464) is most similar (but not identical with) to quadrates of the living *Coluber gemonensis* and to a lesser degree to those of *C. najadum* and *C. rubriceps*. I maintain my previous opinion that a single quadrate is insufficient for establishing a new colubrine species; *C. hungaricus* is considered here a *nomen dubium*.

Elaphe kormosi (Bolkay, 1913) (cf. remarks in Szyndlar, 1991: 120). The syntypes of this snake (MHGI Ob-4465) actually belonged to several ophidian species. Of the two ectopterygoids, that figured by Bolkay (1913, pl. XII: 6) most resembles ectopterygoids of the living *E. longissima,* but the other bone, with a distinctly bent stem and a very short internal ramus, is similar to those of the living *E. quatuorlineata;* the difference may result, however, from intraspecific variation. The premaxilla, weakly pointed anteriorly and with indistinct processes on the lateral arms, is similar (but not identical with) to that of *E. longissima*. The basioccipital and the three quadrates display features found in both *E. longissima* and *E. quatuorlineata*. The anterior portion of a palatine, identified by Bolkay as a fragmentary maxilla, characterized by the maxillary process almost parallel to the stem of the bone, is clearly referable to *Elaphe*. Based on the above-mentioned elements, I recognize *E. kormosi* a valid taxon, although it cannot be demonstrated with confidence that all these elements belonged indeed to a single species. Generic allocation of the fragmentary palatine figured by Bolkay (1913, pl. XII: 5) is uncertain; it belonged either to *Elaphe* or to *Natrix*. The parasphenoid fragment provides no information. Of the four maxillary fragments, no one can be referred to the genus *Elaphe;* two posterior fragments, with relatively short ectopterygoid processes and well defined dorsal constrictions for reception of the ectopterygoid, are clearly referable to *Coluber;* of two anterior fragments, one may have belonged to *Natrix,* while taxonomic allocation of the other cannot be demonstrated.

Vipera gedulyi Bolkay, 1913 (cf. remarks above, p.). The syntypes (MHGI Ob-4467) are clearly referable to a single species, although in some kinds of bones a broad spectrum of intraspecific variation can be observed. The ectopterygoids (30 anterior fragments), prefrontals (6 specimens), frontals (2 specimens, one left and one right), and compound bones (25 fragments) display, however, homogenous morphology; all these elements as well as a single left exoccipital do not differ from homologous bones of the living *V. lebetina*. Two small parietal fragments provide no useful information. In one right prootic, the constrictor internus dorsalis (cid) nerve pierced the laterospheroid bar and continued antero-ventrally within a deep and narrow furrow, the condition not observed in several available specimens of *V. lebetina;* considering high polymorphy of this feature in the genus *Vipera,* the observation derived from a single bone cannot provide any decisive evidence of taxonomic distinction. The basiparasphenoids (16 fragments) differ slightly from one another in location of the posterior orifice of the Vidian canal (either it is distinctly separated off the cerebral foramen or both foramina are located together in a shallow common recess) and in the course o the palatine and cid nerves on the inner side of the bone; this variation is concordant with that observed within *V. lebetina* (Zerova and Chikin, in press). Of 8 basioccipitals, only one bone (figured by Bolkay, 1913, pl. XII: 12), apparently belonging to a very large snake, possesses an exceptionally long and broad basioccipital process; the remaining basioccipitals are usually provided with distinctly shorter and thinner processes. The maxillae (16 specimens of various sizes) differ from one another in presence or absence of foramina at the top of the ascending process; all of them, however, are characterized jointly by a strong ridge on the inner side of the process, developed to the degree not observed in other «Oriental vipers».