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Description of Miocene Snakes from Petersbuch 2 with Comments on the Lower and Middle Miocene Ophidian Faunas of Southern Germany

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With 10 figures

Summary

The snake fauna from the latest Lower Miocene (MN 4) of Petersbuch 2 in southern Germany consists of the following taxa: *Eoanilius* sp. (Aniliidae); *Bavarioboa hermi* n. g. n. sp., *Bransateryx septentrionalis* (Boidae); *Natrix* aff. *N. sansaniensis, Palaeonatrix lehmani,* cf. »*Neonatrix*« sp., a still unnamed natricine, *Coluber caspioides* n. sp. (Colubridae); *Naja romani, Micrurus gallicus,* an unnamed elapid (Elapidae); *Vipera antiqua* and *Vipera platyspondyla* (Viperidae). By its composition, the snake fauna from Petersbuch 2 closely resembles that from the coeval Dolnice in western Bohemia.

A comparison of snakes from Petersbuch 2 with those coming from several other Miocene localities of Germany indicates that greatest changes in the composition of ophidian faunas took place at the end of the Lower Miocene. Prior to that, snake assemblages inhabiting Germany were dominated by Oligocene survivors, including the extinct genera *Eoanilius* and *Bransateryx* as well as unnamed tiny Colubridae; an important novelty in the beginning of the Miocene was the appearance of the modern genus *Vipera*. At the Lower/Middle Miocene transition, the ancient fauna was largely replaced by new immigrants, including mostly living genera of the families Elapidae (*Naja* and *Micrurus*), Viperidae (so called 'Oriental vipers', i. e., large species of the genus *Vipera*), and Colubridae (*Coluber* and perhaps *Elaphe*); a few immigrants, considered temporarily members of extinct genera of the Colubridae (*Neonatrix, Palaeonatrix,* and *Texasophis*) did not survive beyond the Middle Miocene.

Zusammenfassung

Die Schlangenfauna des spätesten Untermiozäns (MN 4) von Petersbuch 2 in Süddeutschland besteht aus folgenden Taxa: *Eoanilius* sp. (Aniliidae), *Bavarioboa hermi* n. g. n. sp., *Bransateryx septentrionalis* (Boidae); *Natrix* aff. *N. sansaniensis, Palaeonatrix lehmani,* cf. »*Neonatrix*« sp., eine noch unbenannte Natricine, *Coluber caspioides* n. sp. (Colubridae); *Naja romani, Micrurus gallicus,* eine unbenannte Elapide (Elapidae); *Vipera antiqua* und *Vipera platyspondyla* (Viperidae). Durch ihre Zusammensetzung erinnert die Schlangenfauna von Petersbuch 2 sehr stark an die des zeitgleichen Fundortes Dolnice in Westböhmen.

Ein Vergleich der Schlangen von Petersbuch 2 mit denen einiger anderer miozäner Fundstätten Deutschlands zeigt an, daß die größten Veränderungen in der Zusammensetzung der

Schlangenfaunen am Ende des unteren Miozäns stattfanden. Vor dieser Zeit überwogen unter den deutschen Schlangengemeinschaften diejenigen Formen, die das Oligozän überlebt hatten, einschließlich der ausgestorbenen Gattungen *Eoanilius* und *Bransateryx*, wie auch einer sehr zarten, unbenannten Colubride; eine wichtige Neuheit zu Beginn des Miozäns war das Erscheinen der modernen Gattung *Vipera*. Am Übergang vom unteren zum mittleren Miozän war die Fauna überwiegend durch Neueinwanderer ersetzt von meist rezenten Gattungen der Familien Elapidae (*Naja* und *Micrurus*), Viperidae (die sogenannten 'Orientalischen Vipern', d. h. die großen Arten der Gattung *Vipera*), und Colubridae (*Coluber* und vielleicht *Elaphe*); einige wenige Einwanderer, zur Zeit als Angehörige ausgestorbener Colubridengattungen angesehen (*Neonatrix*, *Palaeonatrix* und *Texasophis*), haben das Ende des Mittelmiozäns nicht überlebt.

Contents

1. Introduction

The locality of Petersbuch 2 is situated near Eichstätt, Bavaria, southern Germany. The age of this site, based on the mammalian faunas (HEISSIG 1978; HEIZMANN 1983; ZIEGLER & FAHLBUSCH 1986; ZIEGLER 1989, 1990), was estimated as late Lower Miocene (middle Orleanian; biozone MN 4). Apart from mammals, Petersbuch 2 yielded also abundant remains of amphibians and reptiles; for details see SCHLEICH (1985) and references therein.

The snake remains described in the present paper consist of more than 4000 vertebrae and vertebral fragments belonging to the collection of the Bayerische Staatssammlung für Paläontologie und historische Geologie in München (BSP) and of above 900 vertebrae and vertebral fragments belonging to the collection of the Staatliches Museum für Naturkunde in Stuttgart (SMNS). Several fragmentary cranial bones and teeth, present in both collections, are of secondary importance.

The snake assemblage from Petersbuch 2 shows relations to other ophidian faunas inhabiting Europe in the period between the Lower Oligocene and Middle Miocene.

Nevertheless, it resembles most closely that reported previously from the coeval locality of Dolnice in western Bohemia (Szyndlar 1987). Several snake species described from the latter site were based, however, on very limited material. Much more abundant remains coming from Petersbuch 2, referred to the species previously described from Dolnice, enable to emend the diagnoses of these snakes and to define more precisely their taxonomic status.

During the last years our knowledge on the ophidian faunas occurring in the European Oligocene and Miocene has grown considerably, yet the systematic allocation of some of these snakes, based almost exclusively on isolated vertebrae, is still uncertain. Several snake species coming from this period were described as members of extinct genera. However, it is known now that at least one living ophidian genus (*Natrix*) occurred in Europe yet in the Lower Oligocene (Rage 1988a), while a number of other extant genera were recorded from Europe since the beginning of the Miocene. Recently it has been well evidenced that the oldest fossil members of these genera differed only to a little degree from their living relatives (Szyndlar 1991c; also this paper). It is therefore obvious that these genera must have evolved: 1) prior to the Miocene, and 2) most likely outside Europe. On account of that we cannot exclude the possibility that a number of European Miocene snakes, described as members of extinct genera, could actually belong to some living genera occurring presently outside Europe. This remark concerns principally the Colubridae and Elapidae (except for Bungarinae), because axial osteology of most living members of these families remains unknown. In consequence, in the following text we avoid describing new taxa based on remains of some colubrids and elapids (previously unknown in fossil state), because we are unable to compare them with all possible living relatives. On the other hand, we temporarily use some existing generic names (namely *Neonatrix* and *Palaeonatrix*), although their distinction from recent related snakes has not been satisfactorily demonstrated yet.

In the last chapter of this paper we attempt to summarize the up-to-date knowledge on changes in the German snake faunas that took place during the Miocene. This summary is based almost exclusively on previously unpublished materials, mainly belonging to the SMNS collection. Below we list all these Miocene sites as well as some Oligocene localities discussed later in this paper:

Herrlingen 7: Lower Oligocene (lower Suevian; MP 22);
Ehrenstein 12: Lower Oligocene (lower Suevian; MP 22);
Bernloch: Lower Oligocene (middle Suevian; MP 23);
Ehingen 1: Middle Oligocene (?upper Suevian; MP?);
Ehrenstein 7: Upper Oligocene (middle Arvernian; MP 27);
Gaimersheim: Upper Oligocene (middle Arvernian; MP 27);
Burgmagerbein: Upper Oligocene (middle Arvernian; MP 27);
Herrlingen 8: Upper Oligocene (middle Arvernian; MP 28);
Eggingen-Mittelhart: uppermost Oligocene (upper Arvernian; MP 30);
Rott: uppermost Oligocene (upper Arvernian; MP 30);
Weisenau: lowermost Miocene (lower Agenian; MN 1);
Ulm-Westtangente: Lower Miocene (upper Agenian; MN 2);
Schnaitheim: Lower Miocene (lower Orleanian; MN 3);
Stubersheim 3: Lower Miocene (lower Orleanian; MN 3);
Petersbuch 2: Lower Miocene (middle Orleanian; MN 4);
Langenau: Lower Miocene (middle Orleanian; MN 4);
Randecker Maar: Middle Miocene (upper Orleanian; MN 5);
Oggenhausen: Middle Miocene (upper Orleanian or lower Astaracian; MN 5 or 6);
Sandelzhausen: Middle Miocene (lower Astaracian; MN 6);

Rothenstein 13: Middle Miocene (lower Astaracian; MN 6);
Steinheim a. A.: Middle Miocene (upper Astaracian; MN 7+8).

The mammalian stages are employed after FAHLBUSCH (1976), while the use of the Paleogene (MP) and Neogene (MN) land mammalian biozones follows SCHMIDT-KITTLER (1987) and DE BRUIJN et al. (1992), respectively. The MN zonation for some Miocene German localities not included in the paper of DE BRUIJN et al. are given by SCHLEICH (1985). The age of Oggenhausen and Rothenstein 13 was estimated by Dr. E. P. J. HEIZMANN (pers. comm.).

Acknowledgments

We are deeply grateful to Dr. Ronald Böttcher from the Staatliches Museum für Naturkunde in Stuttgart for the loan of the fossil materials under his care; Dr. Elmar P. J. Heizmann from the same institution kindly provided unpublished data on the age of the faunas from Oggenhausen and Rothenstein 13.

Special thanks are due to Dr. Marc Augé and Dr. Jean-Claude Rage (P. & M. Curie University in Paris) who allowed us to use and cite their unpublished paper on the squamate fauna from Sansan; Dr. J. C. Rage also kindly provided many unpublished data on the French Lower Miocene sites of viperid snakes as well as on the vertebral morphology of *Albaneryx depereti*.

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2. Systematic part

Family Aniliidae FITZINGER, 1826

Genus *Eoanilius* RAGE, 1974

Eoanilius sp.

Fig. 1

Material: 21 trunk vertebrae (BSP 1976 XXII 5843–5853), 22 trunk vertebrae (SMNS 57897/1, 57897/2, 57897/4), one caudal vertebra (SMNS 57897/3).

Description

Most trunk vertebrae belonged to the middle portion of the column (Fig. 1A–E). The feature characteristic of this snake are its very small dimensions; the centrum length of the midtrunk vertebrae ranges between 2.1 and 2.8 mm. The centrum is almost as wide as long, cylindrical, with a relatively broad but usually very indistinct haemal keel and shallow subcentral grooves. The neural arch is strongly depressed; the neural spine is very low and occupies one-third to one-fourth the neural arch length. The pre- and postzygapophyseal articular facets are relatively large and oval in shape; the prezygapophyseal processes are very short and hardly visible from above. The zygosphenal roof, delimited laterally with two small but distinct lobes, is slightly convex (rarely straight) in dorsal view, or provided with a central lobe. The cotyle and condyle are suborbicular (prevailing feature observed in the BSP material) or flattened dorso-ventrally. The paradiapophyses are relatively large, undivided into para- and diapophyseal portions. The lateral and subcentral foramina are distinct; paracotylar foramina are absent.

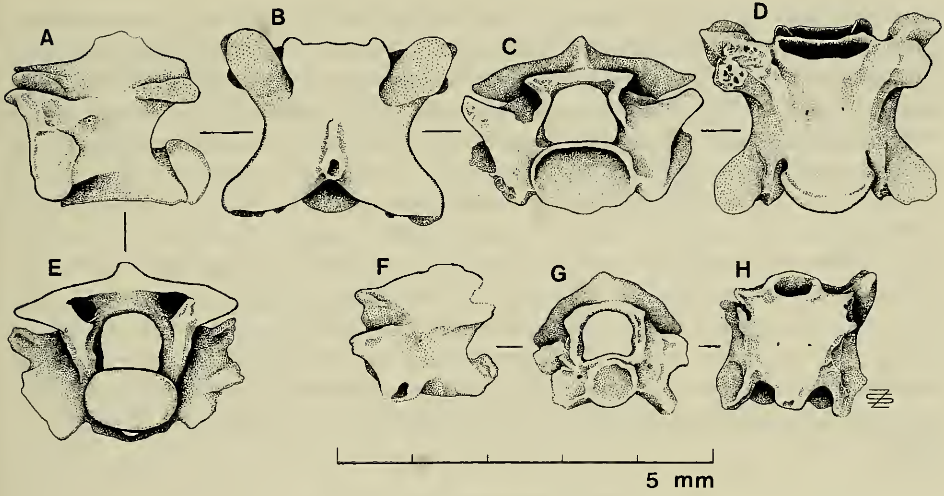


Fig. 1. *Eoanilius* sp. A–E: mid-trunk vertebra (SMNS 57897/2); F–H: caudal vertebra (SMNS 57897/3). – A, F: left lateral views; B: dorsal view; C, G: anterior views; D, H: ventral views; E: posterior view.

Posterior trunk vertebrae (e. g. BSP 1976 XXII 5844), are distinctly longer than those from the middle portion of the column and provided with more distinct haemal keel and subcentral grooves.

The caudal vertebra (Fig. 1 F–H), with a strongly reduced neural spine, is devoid of haemapophyses or hypapophysis below the centrum.

Discussion

Eoanilius europae, the type (and then the only known) species of the extinct genus *Eoanilius* was originally described from the Upper Eocene of Malpérié in France (Rage 1974); a single vertebra compared with this species (*Eoanilius* cf. *E. europae*) was also reported from the coeval Hordle Cliff in England (Milner et al. 1982).

Another, still unnamed member of the genus, differing little from the type-species, was described recently from the Upper Oligocene of Herrlingen 8; similar remains found in Herrlingen 7, Ehrenstein 12, and Ehrenstein 7, indicate that this snake was present in the entire German Oligocene (Szyndlar, in press). Vertebrae referable to the genus *Eoanilius* were also recorded from two German Lower Miocene localities, namely Ulm-Westtangente (SMNS 59114) and Stubersheim 3 (SMNS 57709/1) (Szyndlar, in press). The snake from Petersbuch 2, described above, closely resembles that from the German Oligocene, although a part of its vertebrae, by morphology of the zygosphenal roof (without a central lobe), approaches the condition characteristic of *E. europae*.

In France, *Eoanilius* apparently did not survive beyond the end of the Eocene; presumed occurrence of aniliids (named «?Aniliidae») in several Oligocene French localities (de Bonis et al. 1973) was not confirmed by later studies (Rage 1984 b). Possible presence of the family Aniliidae in other German Oligocene localities (Bernloch and Gaimersheim) was also reported by Schleich (1985), but these remains have not been described in detail yet.

Aniliid fossils have been usually referred to the family Aniliidae in its traditional broader context, i. e. including the living genera *Anilius* of South America as well as *Cylindrophis* and *Anomochilus* of Asia; it is known now, however, that *Anilius* is not closely related with the remaining two genera (McDowell 1987). Szyndlar (in press), based on some substantial differences observed in the axial morphology of *Anilius* and *Cylindrophis*, excluded possible relationships between *Eoanilius* and *Cylindrophis*, the latter approaching conditions characteristic of the uropeltines (osteology of *Anomochilus* remains, however, unknown). In consequence, *Eoanilius* was considered a member of the family Aniliidae s. s. (sensu McDowell 1987, i. e., containing only one living genus, *Anilius*). It should be added, however, that *Anilius* (unlike *Cylindrophis*) strongly differs from both *Eoanilius* and most other snakes by having peculiar square-shaped hypapophyses on ist cervical vertebrae (absent in the available material from Petersbuch 2); this difference proves that *Eoanilius* and *Anilius*, although considered members of the same family, are perhaps rather distantly related.

Family Boidae Gray, 1825

Subfamily Boinae Gray, 1825

Genus Bavarioboa n.g.

Type species (by monotypy): *Bavarioboa hermi* n. g. n. sp.

Derivatio nominis: from Bavaria, southern Germany.

Geographic and stratigraphical distribution: probably from Upper Oligocene (middle Arvernian; MP 28) to Middle Miocene (lower Astaracian; MN 6) of southern Germany; Lower Miocene (Middle Orleanian; MN 4) of western Bohemia; perhaps also Lower Miocene (lower Orleanian; MN 3) of Portugal.

Diagnosis. – A medium-sized member of the family Boidae, by its overall vertebral morphology displaying the generalized pattern characteristic for the subfamilies Boinae and Pythoninae; assigned to the Boinae due to the presence of paracotylar foramina observed in part of its trunk vertebrae.

Differs from the living Boinae except for *Boa, Candoia, Corallus* (part), *Sanzinia*, and *Xenoboa* by having paracotylar foramina in part of its trunk vertebrae. Differs from *Corallus* by having centrum of trunk vertebrae wider than long; differs from *Boa, Eunectes*, and *Xenoboa* by having relatively longer vertebral centrum. Differs from *Acrantophis, Boa, Eunectes*, and *Sanzinia* by having depressed and not vaulted neural arch; differs from the above named genera and from *Epicrates* by having distinctly lower and thicker neural spine. Differs from *Candoia* by not having hypapophysis on postcervical vertebrae. Differs from *Acrantophis* and *Sanzinia* by having well developed haemapophyses on caudal vertebrae.

Differs from the extinct Boinae (including presumed Boinae) except for *Pseudoepicrates* and *Waincophis* by having paracotylar foramina in part of its trunk vertebrae; differs from the extinct Boinae except for *Waincophis* by having prezygapophyses strongly tilted dorsally in anterior view. Differs from *Palaeopython* and *Paleryx* by having more depressed neural arch and by low and thick neural spine; differs from *Paleryx* by having zygosphene distinctly wider than cotyle and by having better marked indentation between pre- and postzygapophyses. Differs from *Plesiotortrix* by having depressed neural arch and much better marked indentation between pre- and postzygapophyses. Differs from *Cheilophis* by having relatively shorter vertebrae and straight zygosphene and by absence of posterior expansion of parapophyses. Differs from *Boavus* and *Pseudoepicrates* by having relatively longer vertebrae, more depressed neural arch and lower neural spine; differs from *Pseudoepicrates* by having shorter prezygapophyseal processes, and less expanded laterally pre- and postzygapophyses. Differs from *Waincophis* by having distinct haemal keel, much wider neural arch, and paradiapophyses projected beyond centrum.

Bavarioboa hermi n. g. n. sp.

Fig. 2

1987 cf. *Gongylophis* sp. – Szyndlar, p. 59, fig. 4.

Holotype: One trunk vertebra, BSP 1976 XXII 5859 (Fig. 2 J-N).

Type locality: Petersbuch 2 near Eichstätt, Bayern, southern Germany.

Age: Lower Miocene (middle Orleanian; MN 4).

Derivatio nominis: Dedicated to Prof. Dr. D. Herm (Institute of Paleontology in Munich) who steadily promoted the paleontological investigations in Munich.

Referred material: 255 trunk vertebrae (BSP 1976 XXII 5854–5858, 5860–5864, 5868–6112), 11 trunk vertebrae (SMNS 57898/1), 8 caudal vertebrae (BSP 1976 XXII 5865–5867, 6113–6119).

Diagnosis. – As for the genus.

Description of the holotype

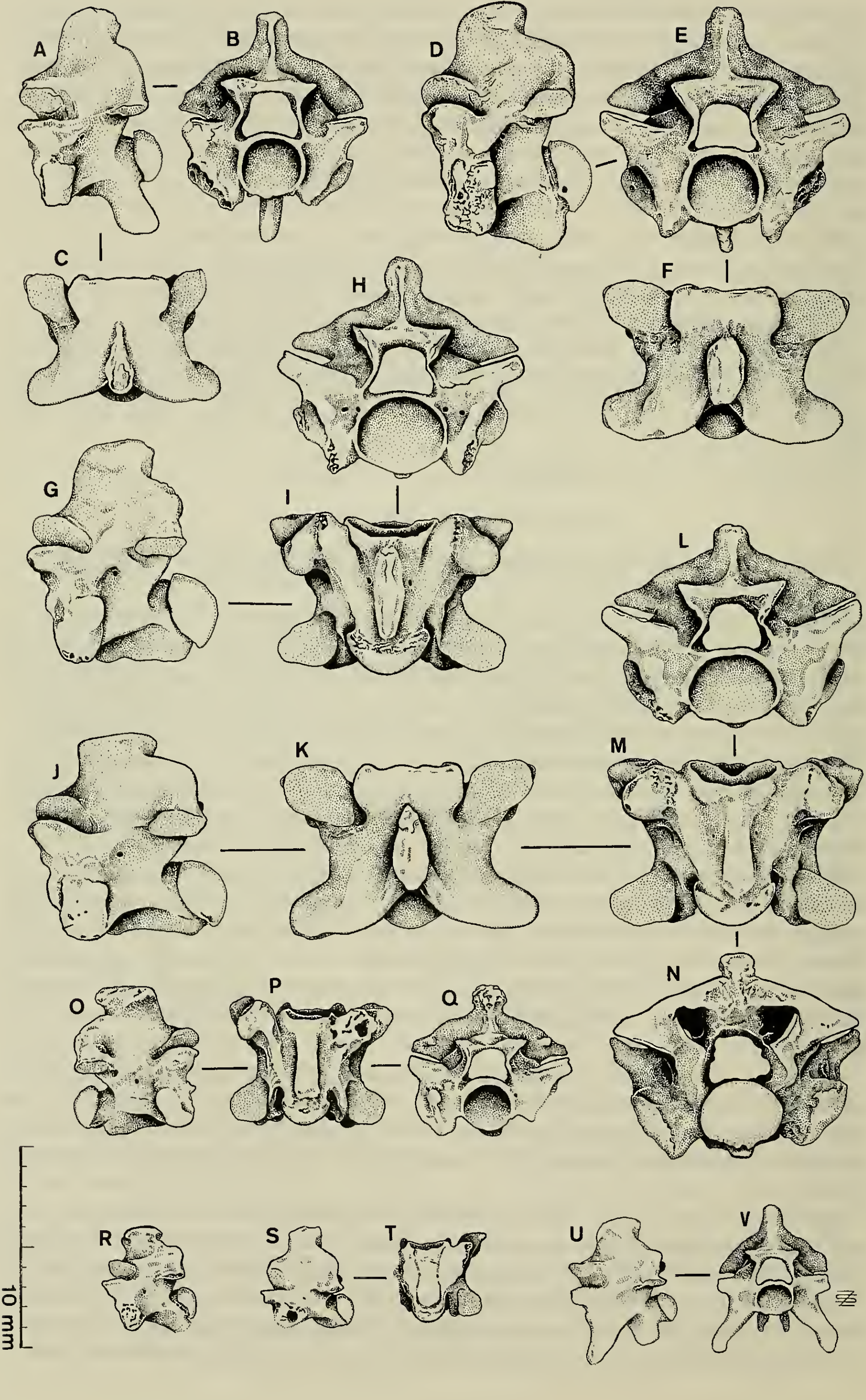
The completely preserved vertebra, massively built, comes from the middle portion of the column.

In lateral view, the vertebra is shorter than high. The neural arch is upswept above the zygantrum. The neural spine, approximately as high as long and being one-half of the length of the neural arch, begins immediately behind the zygosphenal base; its anterior margin is straight, while the posterior one is slightly overhanging posteriorly. The interzygapophyseal ridge (= margo lateralis) is thick and well developed. The lateral foramina are well visible. The paradiapophyses are subsquare in shape, and their division into parapophyseal and diapophyseal portions is weakly marked. The subcentral ridges are distinct, especially immediately behind the parapophyses, arched upwards, and extending posteriorly to near the base of the condyle.

In dorsal view, the vertebra is distinctly wider than long. The posterior border of the neural arch is moderately notched. The indentation between the pre- and postzygapophyses is well expressed. The dorsal border of the neural spine is strongly thickened, especially posteriorly. The zygosphene is delimited laterally by indistinct lobes; its anterior border is straight though uneven. The prezygapophyseal articular facets are oval, with prezygapophyseal processes barely visible from beneath the latter.

In ventral view, the centrum is distinctly wider than long, somewhat triangular in shape. The haemal keel is prominent, broad, and slightly widening posteriorly. The subcentral grooves, occurring lateral to the keel, are deepest at the level of two small but distinct subcentral foramina. The postzygapophyseal articular facets are ovaloid in shape.

In anterior view, the parts of the vertebral body located below the relatively thin and short prezygapophyses are especially massively built and strongly expanded laterally, but with weakly distinguishing paradiapophyses. The zygosphenal roof is slightly concave; it is distinctly wider than the cotyle, the latter slightly flattened dorso-ventrally. The neural canal is relatively small, trapezium-shaped. The areas located on both sides of the cotyle are deep, but devoid of paracotylar foramina.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In posterior view, the neural arch is rather flattened. The posterior border of the neural spine is very low and wide. The zygantrum is much wider than the slightly depressed condyle. No foramina are present on the areas located laterally to the zygantrum.

Basic measurements. – The holotype is the biggest complete vertebra found in the material from Petersbuch 2. Centrum length 6.8 mm; centrum width 8.0 mm; length between the outer edges of prezygapophyseal articular facets 12.0 mm; length between the outer edges of postzygapophyseal articular facets 12.1 mm; length from the anterior edge of prezygapophyseal articular facet to the posterior edge of postzygapophyseal articular facet 8.3 mm.

Description of the remaining material

The vertebrae referred to *Bavarioboa* represent all major parts of the vertebral column but the cloacal region.

The cervical (anterior trunk) vertebrae are distinctly higher and shorter (in lateral view) in comparison with the mid-trunk vertebrae; their neural spine is distinctly higher than long. They are provided with a thick (in anterior and posterior views) hypapophysis; in lateral aspect, in the anterior portion of the cervical region, this structure is slender and directed postero-ventrally, becoming stout and subsquare in shape in the posterior cervical vertebrae (Fig. 2 A-C). The indentation between the pre- and postzygapophyses is weakly marked in the cervical vertebrae. The vertebrae occupying the position between the cervical and mid-trunk portions of the column, in which the hypapophysis is strongly reduced in length and as such can be interpreted as a haemal keel, are strikingly short and high in lateral view (Fig. 2 D-F). The vertebrae from the cervical-/mid-trunk transition and those immediately following them (Fig. 2 G-I), are characterized by relatively higher neural spines and somewhat more vaulted neural arches than most mid-trunk vertebrae.

The mid-trunk vertebrae closely resemble the holotype. The centrum length of 40 largest mid-trunk vertebrae ranges between 5.2 and 6.8 mm, their centrum width between 5.9 and 8.0 mm (although dimensions of some isolated neural arches indicate that they must have belonged to even larger vertebrae). The centrum length/centrum width ratio, showing the value (except for two cases) 0.8 or 0.9, seems very stable in these vertebrae. In the two exceptions, the ratio is 0.7 and 1.1; the latter is the only mid-trunk vertebra with the centrum longer than wide. Most mid-trunk vertebrae referred to *Bavarioboa* belonged to relatively large snakes. Mid-trunk vertebrae with the centrum shorter than 4 mm are rare in the available material; centrum length/width ratio of the smaller vertebrae is similar as in the largest ones.

A feature of particular interest is the occurrence of paracotylar foramina, small but distinct, in a part of the vertebrae referred to *Bavarioboa*. The foramina are present

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Fig. 2. *Bavarioboa hermi* n. g. n. sp. A–C: cervical vertebra (BSP 1976 XXII 5856); D–F: vertebra from the cervical/mid-trunk transition (BSP 1976 XXII 5857); G–I: mid-trunk vertebra (BSP 1976 XXII 5858); J–N: mid-trunk vertebra (holotype, BSP 1976 XXII 5859); O–Q: posterior trunk vertebra (BSP 1976 XXII 5862); R: last trunk vertebra (BSP 1976 XXII 5863); S–T: anterior caudal vertebra (BSP 1976 XXII 5866); U–V: more posterior caudal vertebra (BSP 1976 XXII 5864). – A, D, G, J, R, S, U: left lateral views; B, E, H, L, Q: anterior views; C, F, K: dorsal views; I, M, P, T: ventral views; N: posterior view; O: right lateral view.

on 25 cervical and mid-trunk vertebrae altogether. In 8 vertebrae they occur on both sides of the cotyle, while in the remaining ones asymmetrically on the left (8 vertebrae) or on the right side (9 vertebrae) of the cotyle. In a few cases the foramina are doubled on one or both sides (Fig. 2 H).

The posterior trunk vertebrae of *Bavarioboa* are characterized, as typical also for other snakes, by better developed haemal keels and strongly expanded latero-ventrally paradiapophyses (Fig. 2 O-Q). The feature often observed in the posterior trunk vertebrae is a prominent thickness surmounting the neural spine. The last trunk vertebra (or vertebrae) was provided with a prominent hypapophysis instead of a haemal keel (Fig. 2 R). It can be easily distinguished from the cervical vertebrae, also bearing hypapophyses, by a flattened neural arch as well as a low and thickened dorsally neural spine.

Cloacal vertebrae displaying features characteristic for boid snakes (cf. SZYNDLAR & BÖHME, in press a, for details) have not been found in the available material. Nevertheless, presence of a prominent hypapophysis in the last trunk vertebra indicates indirectly that the latter structure may have occurred at least in anterior cloacal vertebrae of *Bavarioboa*. Several caudal vertebrae referred to *Bavarioboa* bear, as generally characteristic of snakes, long (partly broken) pleurapophyses instead of paradiapophyses and paired haemapophyses; apart from these features, morphology of these vertebrae is reminiscent of that observed in the posterior trunk portion of the column (Fig. U-V). Most caudal vertebrae possess paracotylar foramina. Two caudal vertebrae do not possess paired haemapophyses below the centrum, but a tubercle-like haemal keel (Fig. S-T). Among snakes, this feature is observed exclusively in the first or a few anterior caudal vertebrae of several boids (SZYNDLAR & BÖHME, in press a), therefore the vertebrae of *Bavariophis* not bearing haemapophyses are also interpreted as anterior caudals. However, we cannot exclude the possibility that the first caudal vertebra of *Bavariophis* was provided with a hypapophysis (cf. below: Boidae indet.)

Discussion

Of several lineages forming the family Boidae (sensu lato), *Bavarioboa* displays clearly the generalized vertebral pattern characteristic for the subfamilies Boinae (= 'boines' sensu KLUGE 1991) and Pythoninae (sensu UNDERWOOD & STIMSON 1990); cf. SZYNDLAR & BÖHME (in press a) for differences between boine and pythonine vertebrae on one hand and those of the remaining Boidae on the other. As noted previously by various authors, there exist no substantial differences between the overall vertebral morphology of boines and pythonines. The only exception are paracotylar foramina, never occurring in pythonines but present in a few boine genera (UNDERWOOD 1976; UNDERWOOD & STIMSON 1990; KLUGE 1988, 1991; SZYNDLAR & BÖHME, in press a); occurrence of paracotylar foramina in a part of the vertebrae of *Bavarioboa* was the basis of referring this snake to the subfamily Boinae.

Vertebrae of boine snakes do not exhibit many diagnostic features; nevertheless, *Bavarioboa* displays a set of characteristic features enabling to distinguish it from other, extant and extinct, members of the Boinae. Paracotylar foramina of *Bavarioboa,* considered an apomorphy, are the only feature that can be interpreted on the phylogenetic ground. Regarding, however, that the overwhelming majority of vertebrae of *Bavarioboa* does not possess the foramina at all as well as that they appeared apparently independently in several boine lineages, this feature seems of little value for any phylogenetic considerations. Necessarily, the comparison of *Bavarioboa* with other boines was therefore based on the overall similarity. The differentiating features were summarized above in the diagnosis of the genus. We compared *Bavarioboa* with all genera of the living boine snakes (but not with all species); the differences described in the diagnosis refer to adult snakes.

Comparison with fossil boids was based principally on the literature. We compared *Bavarioboa* with all fossil boid genera that potentially could represent the Boinae; they are listed below. It should be stressed, however, that in most cases there exists no decisive proof whether the below named taxa belonged indeed to the Boinae or to another subfamily; of them, only *Palaeopython* and *Pseudoepicrates* are unanimously considered true boine snakes.

Comparing *Bavarioboa* with the genus *Palaeopython* DE ROCHEBRUNE (1880) from the European Eocene, we regarded only the French species *P. cadurcensis* (= *Python cadurcensis* FILHOL, 1877: pl. 26, figs. 439–444; cf. also RAGE 1988b: fig. 18 A) and *P. filholi* DE ROCHEBRUNE, 1880 (cf. RAGE 1974: fig. 3 A-B); the taxonomic status of *P. neglectus* DE ROCHEBRUNE (1884) from France and of *P. ceciliensis* BARNES (1927) from Germany is uncertain. The genus *Paleryx* is represented by *P. rhombifer* OWEN (1850: pl. 13, figs. 29–32) from the English Eocene (cf. RAGE 1984a: fig. 13 A); the other species described by OWEN, *P. depressus,* was synonymized with *P. rhombifer* by RAGE & FORD (1980); the taxonomic status of *P. spinifer* BARNES (1927) from the German Eocene is uncertain (RAGE 1984a). LYDEKKER (1888) synonymized *Palaeopython* and *Paleryx,* but both genera display different vertebral morphology; cf. RAGE & FORD (1980) and RAGE (1984a) for differences between *Palaeopython* and *Paleryx*. The other valid boid taxon from the European Paleogene is *Plesiotortrix edwardsi,* originally described as an aniliid from the French «Phosphorites du Quercy» (Eocene or Oligocene; DE ROCHEBRUNE 1884: pl. 2, Fig. 6); *Plesiotortrix* was actually a member of the Boidae (HOFFSTETTER 1939; RAGE 1984a). A number of other boid species, described (usually as non-boids) from the «Phosphorites du Quercy» by FILHOL (1877), DE ROCHEBRUNE (1880; 1884), and DE STEFANO (1905), were considered nomina dubia (RAGE 1984a). The only named Asiatic boid, not assigned to the genus *Python,* is *Daunophis langi* reported from the Pliocene of Burma by SWINTON (1926); unfortunately, no useful information about this fossil can be derived from the description provided by SWINTON; RAGE (1984a) misinterpreted the SWINTON's writing, reporting that hypapophyses were present on most trunk vertebrae of *Daunophis*. Of several extinct boid genera described from North America, the Eocene *Boavus* MARSH, 1871 (a tropidophiine according to McDOWELL 1987) and *Cheilophis* GILMORE (1938), and the Miocene *Pseudoepicrates* AUFFENBERG (1963) display the vertebral morphology characteristic for boines or pythons. A member of the latter genus, *P. stanolseni* (= *Neurodromicus stanolseni* VANZOLINI, 1952; = *Pseudoepicrates stanolseni,* part, AUFFENBERG, 1963), having vertebrae provided with large paracotylar foramina, was considered a sister taxon of the living genus *Boa* (Kluge 1988) [note that *Neurodromicus barbouri* VANZOLINI, 1952, synonymized with *Pseudoepicrates stanolseni* by AUFFENBERG (1963), was recognized a junior synonym of the living *Boa constrictor* by KLUGE (1988)]. The presumed Eocene boine *Paraepicrates brevispondylus* HECHT (1959) was recently recognized a member of the erycine genus *Lichanura* (KLUGE 1988). Cf. GILMORE (1938: figs. 2–3, 5–8, 34), VANZOLINI (1952: pl. 55, figs. 6–11, pl. 56, figs. 1–6), Holman (1979: figs. 16–18), and Rage (1984a: figs. 9–10) for illustrations of vertebrae of the above discussed North American snakes. *Waincophis australis* Albino (1987) from the South American Eocene is considered here a boine, owing to the presence of paracotylar foramina.

Remains referable to *Bavarioboa hermi* come also from two other Miocene localities, namely from Rothenstein 13 in Germany (13 trunk vertebrae; SMNS 59091) and from Dolnice in western Bohemia, the latter coeval with Petersbuch 2. The remains from Dolnice, consisting of 14 trunk vertebrae, were originally identified as cf. *Gongylophis* sp. (Szyndlar 1987). The best preserved trunk vertebra of the presumed cf. *Gongylophis,* illustrated by Szyndlar (1987: fig. 4 B-F), came (as we can conclude now) either from the cervical/mid-trunk transition or from the anteriormost mid-trunk portion of the column. Vertebrae belonging to this region are very similar indeed to each other in large specimens of the living erycine *Gongylophis* and in *Bavarioboa*: they have distinctly vaulted neural arches with neural spines emerging above rather than behind the zygosphene and their centra are distinctly wider than long. Distinct differences, however, can be observed in more posterior trunk vertebrae (poorly preserved in the material from Dolnice): among others, in *Gongylophis* the neural spine is relatively long, while the vertebral centra are longer than wide, unlike in *Bavarioboa.*

Other boid remains referred, although with some reservation, to the genus *Bavarioboa* are those reported from the Upper Oligocene of Ehrenstein 7 (Szyndlar, in press). These poorly preserved vertebrae were considered to represent two different morphological patterns and were temporarily classified as 'Boinae B' and 'Boinae C' (cf. Szyndlar, in press: fig. 2 G-K and L-P). Comparison with the type material of *Bavarioboa* demonstrates that the vertebrae from Ehrenstein 7 most likely represent the anterior ('Boinae C') and posterior ('Boinae B') mid-trunk vertebrae of probably the same species. Because of poor preservation of the material, we consider the status of the 'Boinae B & C' as cf. *Bavarioboa* sp. Another snake similar to *Bavarioboa,* as visible from the illustration of Antunes & Rage (1974: fig. 4), is the boine (sensu Hoffstetter & Rage 1972: = Boinae + Pythoninae) reported from the Lower Miocene of Lisboa; unfortunately, this fossil is known from a single vertebra only.

The existing fossil record does not enable to explain possible relationships of *Bavarioboa* nor its origin. The available material of *Bavarioboa* itself is little informative, while on the other hand even a subfamilial allocation of most non-erycine boids from Europe remains unknown or uncertain. This is also the case of several Oligocene boids reported from Bernloch, Burgmagerbein, Ehingen 1, Gaimersheim (Schleich 1985), and Ehrenstein 12 (Szyndlar, in press), as well as of a presumed Miocene boid from Schnaitheim 1 (Schleich 1985). The only snake from the German Oligocene that can be referred to the subfamily Boinae (on the basis of cranial remains) is the unnamed 'Boinae D' from the Upper Oligocene of Herrlingen 8 (Szyndlar, in press).

Of a few non-erycine boids reported from the European Lower and Middle Miocene, *Python euboicus* from Kimi in Greece (Roemer 1870) and *Botrophis gaudryi* from Pontlevoy in France (de Rochebrune 1880) were considered nomina dubia (Rage 1984a; the latter may have actually not belonged to the Boidae), while the taxonomic status of *Palaeopython sardus* from Monte Albu in Sardinia (Portis 1901; perhaps *Python* according to Rage 1984a) and of an unnamed boine from Córcoles in Spain (Szyndlar 1987) remains unknown. There exists, however, at least one certain record of an unnamed species of *Python* from the French locality of Vieux Collonges (Rage in Thomas et al. 1982; = «un assez gros Boïné» of Rage in Demarcq et al. 1983). But presence of pythons in the European Miocene is easily explained; these snakes, today occurring in most of Africa, southern Asia, and the Australasian region, were able to reach Europe in result of either trans-Tethyan or eastern migrations; Rage (in Demarcq et al. 1983) expected that arrival of these snakes was correlated with the thermal maximum observed in the European climate around the Lower/Middle Miocene transition.

On the contrary, occurrence of boine snakes in the European Miocene, as evidenced by *Bavarioboa*, is astonishing, considering that the present-day distribution of this family is restricted to remote regions in the tropical America, Madagascar, and some West Pacific islands. However, the family Boinae, as evidenced by cranial morphology of *Palaeopython* (Underwood 1976; McDowell 1987; Rage 1987a), occurred in Europe in the Eocene, therefore derivation of *Bavarioboa* from a hypothetical Eocene ancestor would be the simplest explanation of its presence in the European Miocene; similarities between the Eocene *Palaeopython filholi* and *Bavarioboa* could evidence their possible relationships. On the other hand, the available fossil record indicates that *Palaeopython*, one of the largest European constrictors, did not survive beyond the Eocene/Oligocene boundary (Rage 1987a). So far, we do not know whether some presumed Eocene boines could survive throughout the severe climatic conditions of the Oligocene; it seems, however, that potential survivors belonged exclusively to very small burrowing snakes (Szyndlar & Böhme, in press a). In this context, survival of *Bavarioboa*, a relatively large and apparently not fossorial snake, seems little probable.

In consequence, we prefer to consider *Bavarioboa* an eastern immigrant that appeared in Europe perhaps yet in the Upper Oligocene immediately after improvement of the climatic conditions. Unfortunately, there is again no fossil record supporting presence of boines in the Old World beyond Europe, in particular in Asia, but on the other hand our knowledge on Asiatic fossil snakes as a whole is still highly limited. Although non-erycine boids were reported from the Eocene of Pakistan (Rage 1987c) and Oligocene of Kazakhstan (Chkhikvadze 1985), their taxonomic status have not been explained. At the same time, the entire available Miocene record is restricted to pythonine snakes found in the area of the present distribution of this subfamily in Asia, Africa, and Australia (Hoffstetter 1964; Rage 1976; Rage in Thomas et al. 1982; Smith & Plane 1985).

The ultimate possibility is the North American origin of *Bavarioboa* and its arrival to Europe via the Beringian land bridge, although again this concept is not supported by the fossil record coming from the New World.

Subfamily Erycinae Bonaparte, 1831

Genus *Bransateryx* Hoffstetter & Rage, 1972

Bransateryx septentrionalis Szyndlar, 1987

Fig. 3

Material: 398 trunk vertebrae (BSP 1976 XXII 6120–6517), 36 trunk vertebrae (SMNS 57898/2).

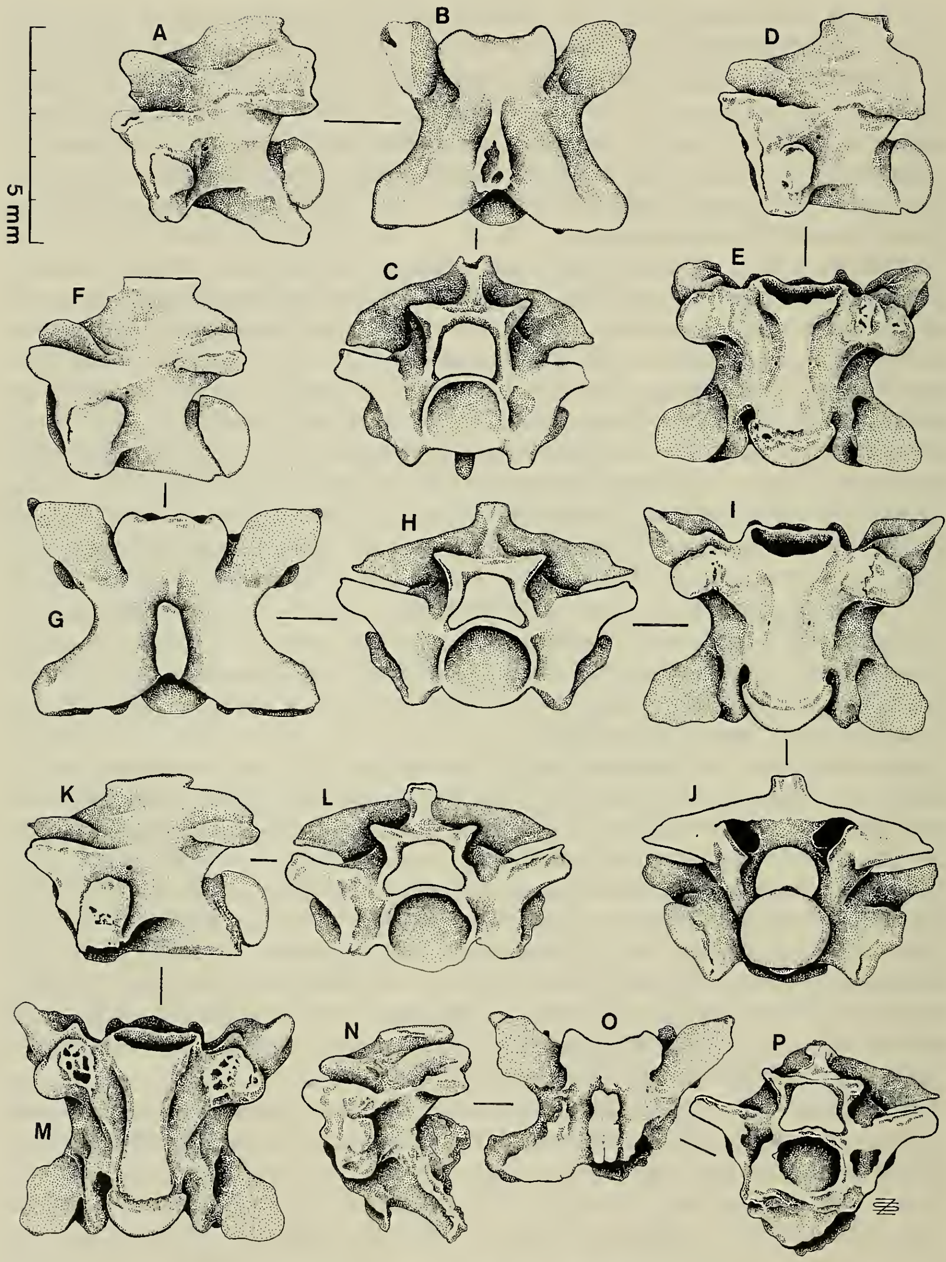


Fig. 3. *Bransateryx septentrionalis.* A–C: cervical vertebra (BSP 1976 XXII 6121); D–E: mid-trunk vertebra (BSP 1976 XXII 6125); F–J: mid-trunk vertebra (BSP 1976 XXII 6124); K–M: posterior trunk vertebra (BSP 1976 XXII 6127); N–P: last trunk vertebra (BSP 1976 XXII 6129). – A, D, F, N: left lateral views; B, G, O: dorsal views; C, H, L, P: anterior views; E, I, M: ventral views; J: posterior view.

Description

Bransateryx was a relatively small snake. The centrum length of 40 largest mid-trunk vertebrae ranges between 3.4 and 4.5 mm, the centrum width between 3.0 and 4.1 mm; the centrum length/centrum width ratio is 1.0 to 1.3, mean 1.1. Centra of other trunk vertebrae are rarely shorter than 3.0 mm. Dimensions of cervical and posterior trunk vertebrae do not differ much from those of the mid-trunk region.

Cervical vertebrae (Fig. 3 A-C) differ from those from the mid-trunk portion of the column by having, among others, vaulted neural arches, distinctly higher neural spines, and hypapophyses (relatively thin in anterior view) instead of haemal keels. The zygosphenal roof of the cervical vertebrae is usually concave in dorsal view.

Mid-trunk vertebrae (Fig. 3 D-J) are massively built, short and with well marked indentation between the pre- and postzygapophyses. The centrum is slightly longer than wide, with a relatively broad haemal keel, strongly widening and becoming flattened posteriorly; in some vertebrae the keel is weakly developed. The neural arch is strongly depressed. The neural spine, beginning far behind the zygosphene, is very low and occupies usually one-third the neural arch length; it is often thickened dorsally. The pre- and postzygapophyses are relatively large and elongate (rarely oval) in shape; the prezygapophyseal processes are very short and usually acute. The zygosphenal roof is provided with three distinct lobes in dorsal view. The cotyle and condyle are orbicular. The paradiapophyses are relatively very large, rectangular, weakly divided into para- and diapophyseal portions. The lateral and subcentral foramina are distinct; in a few vertebrae the latter are characterized by an exceptionally enormous size. Paracotylar foramina are lacking.

Posterior trunk vertebrae (Fig. 3 K-M) are more depressed than the mid-trunk ones and are characterized by a better developed haemal keel; the keel is usually uniform in width throughout its length. Two vertebrae belong undoubtedly to the last ones in the trunk portion of the column (Fig. 3 N-P). By the morphology of the neural spine and neural arch they closely resemble the preceding trunk vertebrae, but apart from the above features these vertebrae possess strongly shortened bodies. The zygosphene is deeply concave in dorsal view, similarly as in most cervical vertebrae. The haemal keel is replaced by a long and strongly expanded laterally hypapophysis-like projection, while the cotyle rim is produced ventrally into a prominent plate; exactly the same subcentral structures were observed in the last trunk vertebra of a large specimen of the living erycine *Gongylophis conicus*.

Discussion

Bransateryx septentrionalis was originally described from the Bohemian locality of Dolnice, coeval with Petersbuch 2 (SZYNDLAR 1987). Comparing *B. septentrionalis* with the type species, *B. vireti* from the Upper Oligocene of Coderet in France (HOFFSTETTER & RAGE 1972), SZYNDLAR based his diagnosis exclusively on differences observed in caudal vertebrae of both snakes. Differences between trunk vertebrae of both forms were described as «minor». In fact, the material from Dolnice contained only five mostly incomplete trunk vertebrae and a proper comparison could not be undertaken on such a basis. The above described material from Petersbuch 2 does not differ from the few trunk vertebrae of *Bransateryx septentrionalis* coming from the type locality and is therefore identified as belonging to the same species.

The abundant material from Petersbuch 2 extends our knowledge on the intracolumnar variation in *Bransateryx septentrionalis.* It is now obvious that the only perfectly preserved trunk vertebra of *Bransateryx* from Dolnice, with a vaulted neural arch (cf. SZYNDLAR 1987: fig. 2 C-D) did not come from the mid-trunk region but from the cervical/mid-trunk transition. It is also possible now to define better the basic differences in the morphology of mid-trunk vertebrae between *B. vireti* and *B. septentrionalis.* Thus, the latter differed from the type species by: 1) relatively shorter vertebral centra; 2) longer neural spine; 3) more depressed neural arch.

As demonstrated by an analysis of intervertebral joints in the caudal portion of its column, *Bransateryx* cannot be considered an ancestor of the living erycine genera (SZYNDLAR, in press). Possible ancestors of the genus *Bransateryx* itself remain, however, unknown; among others, it was considered an Oligocene invader of North American origin (RAGE 1977), but its presumed remains (cf. *Bransateryx*) found in the Upper Eocene of England (MILNER 1986) can suggest European ancestry.

Bransateryx belonged to commonest snakes in the French and German Oligocene and Lower Miocene. The oldest remains of the type species, *B. vireti,* come from the German Lower Oligocene localities of Herrlingen 7 and Ehrenstein 12 (SZYNDLAR, in press). As evidenced by the fossil record from France (HOFFSTETTER & RAGE 1972), it became especially common at the end of the Oligocene, the phenomenon correlated with the growing cooling and aridization observed in Europe; improvement of climatic conditions in the beginning of the Miocene caused that *B. vireti* decreased in number (RAGE 1987b).

Remains of *Bransateryx* coming from the lowermost Miocene of Weisenau (SMNS) are clearly referable to the type species, *B. vireti.* Appearance of the other species, *B. septentrionalis* in the late Lower Miocene may have been connected with climatic and environmental changes in southern Germany; relative abundance of *B. septentrionalis* observed in Petersbuch 2 may indicate that it was well adapted to the warm and humid climate characteristic for this phase of the Miocene. On the other hand, *B. septentrionalis* is unknown from beyond the latest Lower Miocene, while the Middle Miocene remains of *Bransateryx,* coming from Steinheim a. A. (SMNS 51152), resemble closely *B. vireti* and not *B. septentrionalis* (RAGE in SZYNDLAR, in press; pers. obs.). It is difficult to ascertain whether both species may have occurred sympatrically in southern Germany around the Lower/Middle Miocene or simply the ranges of their distribution fluctuated in the past.

Boidae indet.

Material: 2 caudal vertebrae (BSP 1976 XXII 6518, 6519), one caudal vertebra (SMNS 57898/3).

These vertebrae, massively built, relatively short, and with strongly reduced prezygapophyseal processes, are clearly referable to the Boidae, perhaps to *Bavarioboa,* but their taxonomic allocation is somewhat unclear.

The vertebra SMNS 57898/3 closely resembles the caudal vertebrae referred to *Bavarioboa,* but it differs from the latter by having a lower neural spine; below its centrum, the vertebra bears a prominent hypapophysis. The presence of hypapophyses below the first (and only the first) caudal vertebrae can be observed in a few pythonines and boines (e. g. *Eunectes*). The vertebra SMNS 57898/3 is therefore considered to be the first caudal one. It should be mentioned, however, that a few caudal vertebrae referred above to *Bavarioboa* did not possess hypapophyses nor haemapophyses at all (but a haemal keel) and as such they must have also represented anterior caudals. In the living boids possessing a hypapophysis on the first caudal vertebra, the second caudal vertebra is always provided with well developed haemapophyses. It cannot be evidenced, based on isolated bones, whether in *Bavarioboa* (unlike living boids) the anteriormost part of the caudal portion of the column contained both vertebrae bearing a hypapophysis and those devoid of a hypapophysis or haemapophyses, but we cannot exclude such a possibility. Possible allocation of the discussed vertebra to *Bransateryx* (anteriormost caudal vertebrae of this genus are unknown) is less probable, considering that the living erycine snakes never possess hypapophyses nor haemapophyses at the cloacal/caudal transition.

The most striking feature of the caudal vertebrae BSP 1976 XXII 6518 and 6519 are their neural spines, with thickened and expanded laterally dorsal portions. This peculiar morphology is concordant with that observed in the anterior caudal vertebrae of *Albaneryx depereti*, an extinct erycine known from the Middle Miocene of France (HOFFSTETTER & RAGE 1972: fig. 9 B). However, absence of any trunk vertebrae that could be referred to *Albaneryx* in the material from Petersbuch 2 makes such a possibility little probable. On the other hand, a somewhat similar morphology of the neural spine can be observed in a few posterior trunk vertebrae of *Bavarioboa* (Fig. 2 Q); it suggests indirectly that the same morphological pattern could be also characteristic of caudal vertebrae in some specimens of *Bavarioboa*.

Family Colubridae OPPEL, 1811 [s. l.]
Subfamily Natricinae BONAPARTE, 1838

Genus *Natrix* LAURENTI, 1768

Natrix aff. *N. sansaniensis* (LARTET, 1851)
Fig. 4

Material: 149 trunk vertebrae (BSP 1976 XXII 6520–6768), 8 trunk vertebrae (SMNS 57899/7), one maxillary fragment (SMNS 57903).

Description

Contrary to other colubrids having hypapophyses restricted to the cervical (anterior trunk) vertebrae, in natricine snakes the hypapophysis occurs throughout the trunk portion of the column. Owing to that it is not easy to differentiate from amongst isolated vertebrae those representing the cervical and more posterior parts of the column; moreover, vertebrae of natricine snakes (except for anteriormost and posteriormost elements) usually display highly homogenous morphology throughout the trunk portion of the column.

The vertebrae interpreted here as cervical (Fig. 4 A-C) differ from those located more posteriorly in the column by having their neural spines relatively higher (even higher than long) and weakly overhanging anteriorly, moreover, by wider and directed more ventrally hypapophyses (in lateral view) as well as by more slender and looking anteroventrally parapophyseal processes.

In the mid-trunk vertebrae (Fig. 4 D-J), the centra are elongate (in few cases approximately twice longer than wide), with flat ventral surface delimited laterally with usually strongly developed subcentral ridges. The hypapophysis (broken off in most vertebrae) is of variable shape in lateral aspect; the anterior edge is slightly curved in lateral view, while the distal tip can be either obtuse or (rarely) acute; in

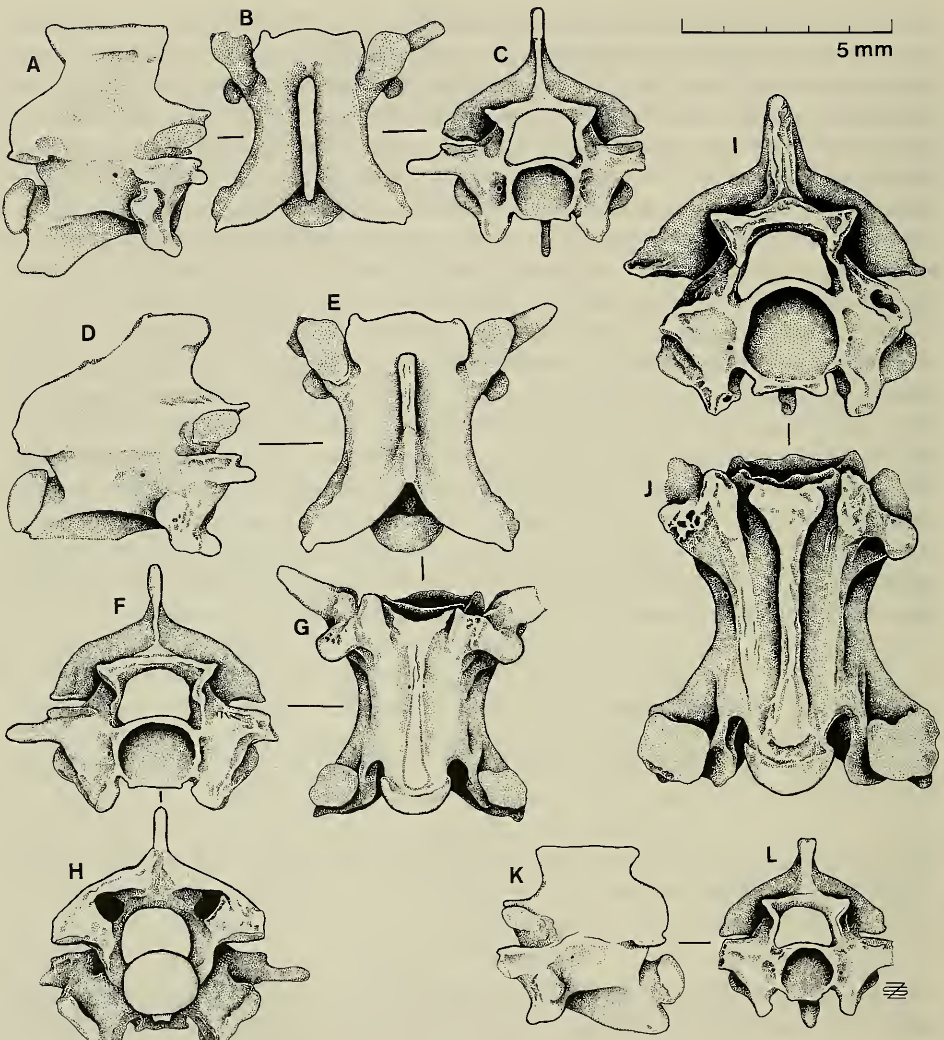


Fig. 4. *Natrix* aff. *N. sansaniensis*. A–C: cervical vertebra (BSP 1976 XXII 6521); D–H: mid-trunk vertebra (BSP 1976 XXII 6527); I–J: mid-trunk vertebra (BSP 1976 XXII 6524); K–L: posterior trunk vertebra (BSP 1976 XXII 6528). – A, D: right lateral views; B, E: dorsal views; C, F, I, L: anterior views; G, J: ventral views; H: posterior view.

ventral view it is of uniform width throughout the length, but it widens anteriorly immediately before reaching the cotyle rim. The neural arch is weakly vaulted. The neural spine is almost as high as long (higher than in recent members of *Natrix*), distinctly overhanging both anteriorly and posteriorly; antero-dorsal part of the spine is often thickened, especially in largest vertebrae. The paradiapophyses are strongly built, provided with prominent parapophyseal processes, obtuse in shape and directed anteriorly; the diapophyses are variable in size, usually as long as parapophyses but in some cases distinctly shorter. The zygosphenal roof is usually convex in dorsal view, with two relatively small lateral lobes; in a few vertebrae it is, however, straight or weakly notched medially. The prezygapophyseal articular facets are oval in shape and elongate in most vertebrae, while the postzygapophyseal articular facets are usually subsquare. The prezygapophyseal processes (broken off in most vertebrae) are of highly variable length and shape; they can be half as long as the prezygapophyseal articular facets and sometimes strongly flattened dorso-ventrally or as long as the facets and relatively slender. The cotyle and condyle are usually orbicular or slightly flattened dorso-ventrally; they are of a similar width as the neural canal. The subcentral, lateral, and paracotylar foramina are distinct; small parazygantral foramina occur in most vertebrae.

The posterior trunk vertebrae (allocated with some doubt in this species) possess a stout and short hypapophysis (Fig. 4 K-L).

A number of the trunk vertebrae belonged to relatively large snakes. The centrum length of 28 largest vertebrae ranges between 4.3 mm and 7.3 mm; the centrum width between 2.4 and 4.4 mm. The centrum length/width ratio is 1.4 to 2.0, mean 1.6. Most vertebrae belonged, however, to smaller individuals, with the centrum length fluctuating usually around the value of 4 mm.

The fragmentary left maxilla consists of a toothless posterior portion of the bone, provided with a subquadrate and elongate (antero-posteriorly) ectopterygoid process; the size of the tooth sockets indicate that a few posteriormost teeth were distinctly larger than the preceding ones, a feature characteristic for natricine snakes. Based on its relatively large size, the maxilla seems referable to either *Natrix* aff. *N. sansaniensis* or *Palaeonatrix lehmani*, although cranial bones of these two snakes have never been reported before. Considering its morphological similarity to maxillae of the living members of *Natrix*, the maxillary fragment is referred, although with some doubts, to *N.* aff. *N. sansanienis*.

Discussion

The striking feature of the fossil material described above is polymorphic morphology of the vertebral elements, therefore its allocation to a single species may be questioned; in particular, a few vertebrae characterized by strongly elongated centra, prominent subcentral ridges, and anterior keels produced into prominent subcotylar tubercles could be referable to *N. longivertebrata* (Fig. 4 I-J). We consider, however, this broad spectrum of polymorphy observed in the *Natrix* from Petersbuch 2 as an individual variation. Moreover, as demonstrated by AUGÉ & RAGE (in press), variable morphology, especially in the length of its prezygapophyseal processes, was characteristic also of *Natrix sansaniensis*, to which we affiliate the discussed fossil snake.

The snake from Petersbuch 2 is clearly referable to the modern genus *Natrix* on the basis of its overall vertebral morphology, in particular after the shape of the neural spine, provided with prominent anterior and posterior overhangs. It differs, however, from the living members of the genus *Natrix* by having its neural spine distinctly higher. So far, four extinct species of the genus *Natrix* were described from Europe: *N. sansaniensis* from the Middle Miocene of Sansan in France (RAGE 1981; originally described as *Coluber sansaniensis*, part, by LARTET 1851); *N. mlynarskii* from the Oligocene of the «Phosphorites du Quercy» in France (RAGE 1988a); *N. longivertebrata* from the Upper Pliocene of Rębielice Królewskie 1A in Poland

(Szyndlar 1984; later reported from many Miocene and Pliocene localities of Europe; cf. Szyndlar 1991b, 1991c); and *N. parva* from the alleged Miocene of Poland (Szyndlar 1984). The latter snake, based on a few vertebrae only, comes actually from the Upper Pleistocene and may have represented a living species (Szyndlar 1991b). See Augé & Rage (in press) for differentiating features observed in vertebrae of the living and extinct species of *Natrix*.

The basis for the affiliation of the *Natrix* from Petersbuch 2 to *N. sansaniensis* is its high neural spine. There are, however, a few features differentiating both snakes: in *N. sansaniensis* the vertebrae are somewhat smaller, the hypapophysis is pointed distally, the prezygapophyseal articular facets are not elongate, and the zygosphenal roof is trilobate rather than convex (cf. Rage 1981: fig. 1A, and 1984a: fig. 30A, for illustrations of *N. sansaniensis*). Among natricine snakes, in particular in the genus *Natrix*, the relative height of the neural spine seems a crucial feature in the specific identification, while the remaining above-listed characters, often subject to intraspecific variation, are of secondary meaning. On account of that we prefer to affiliate the natricine from Petersbuch 2 to *N. sansaniensis* rather than consider it a distinct species. The *Natrix* from Petersbuch 2 resembles also to some degree the Oligocene *N. mlynarskii* (cf. Rage 1988a: fig. 1), among others by its relatively large size and the shape of the zygosphene and prezygapophyseal articular facets; it differs, however, from the latter by not having a broad and flattened keel before the hypapophyses. Considering, however, that *N. mlynarskii* was based on merely three fragmentary vertebrae, no ultimate conclusions about possible relationships between these two snakes can be drawn.

We cannot exclude a possibility that *Natrix mlynarskii, N. sansaniensis,* and *N. longivertebrata* belonged to a single lineage inhabiting Europe since the Oligocene. Whether these taxa formed indeed a morphocline or they represented different waves of eastern immigrants, it is impossible to conclude on the basis of the existing material.

Genus *Palaeonatrix* Szyndlar, 1982

Palaeonatrix lehmani (Rage & Roček, 1983)
Fig. 5

Material: 19 trunk vertebrae (BSP 1976 XXII 6769–6785).

Description

These vertebrae (Fig. 5 A-E) are heavily built (when compared with those of *Natrix*). The centrum length is 4.3–5.1 mm, centrum width 2.6–3.2 mm; the centrum length/width ratio 1.4–1.8, average 1.6. The elongate centrum is delimited laterally by especially strongly built subcentral ridges. The neural spine is approximately three times longer than high, slightly overhanging posteriorly (anterior portions of the spines have not been preserved). The neural arch is produced posteriorly into prominent (sometimes very long) epizygapopyseal spines. The hypapophysis is thick and somewhat plate-shaped in lateral view; it is longer in the presumed cervical vertebrae, while in the posterior trunk vertebrae (Fig. 5 F-G) it resembles rather a prominent haemal keel with a long and strongly flattened ventral egde. Anteriorly, the hypapophysis continues into a strong high keel reaching the cotyle rim. The paradiapophyses are destroyed in most vertebrae; the preserved remnants indicate that these

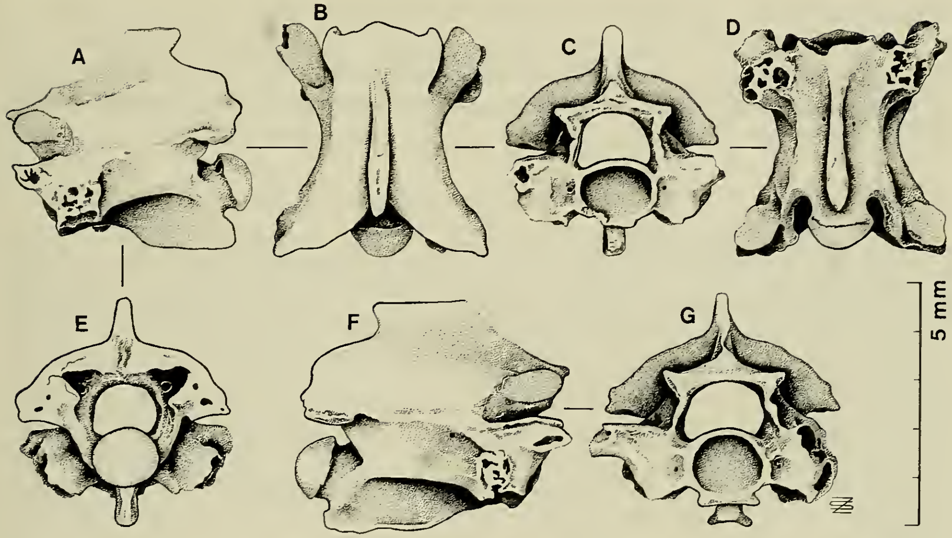


Fig. 5. *Palaeonatrix lehmani.* A–E: mid-trunk vertebra (BSP 1976 XXII 6769); F–G: posterior trunk vertebra (BSP 1976 XXII 6770). – A: left lateral view; B: dorsal view; C, G: anterior views; D: ventral view; E: posterior view; F: right lateral view.

structures were strongly built. The zygosphenal roof is usually triangular or convex in dorsal view, with two lateral lobes. The prezygapophyseal articular facets are usually well elongate; the postzygapophyseal articular facets are subsquare. The prezygapophyseal processes are broken off in all vertebrae; their bases are strongly built. The cotyle and condyle are orbicular and narrower than the neural canal. The subcentral, lateral, and paracotylar foramina are well marked; parazygantral foramina, usually relatively large and doubled on both sides of the zygantrum, occur in all vertebrae.

Discussion

The fossil species *Dolniceophis lehmani* was originally described from the Bohemian locality of Dolnice, coeval with Petersbuch 2, by Rage & Roček (1983). *Dolniceophis* was later synonymized (Szyndlar 1987) with the genus *Palaeonatrix* described earlier from the Middle Miocene of Opole in Poland (Szyndlar in Młynarski et al. 1982; type species *P. silesiaca*). *Palaeonatrix* substantially differs from the living *Natrix* by a number of features observed in the vertebral morphology, especially by its peculiarly shaped hypapophysis produced anteriorly into a prominent keel; unfortunately, as in the case of other fossil colubrids, *Palaeonatrix* was not compared with most living natricine genera (Szyndlar in Młynarski et al. 1982) and thus its taxonomic distinctiveness as an extinct genus is uncertain.

The vetebrae from Petersbuch 2 do not differ from those from the type locality. Moreover, as described above, they provide some new information about the intracolumnar variation, especially regarding the shape of the hypapophyses in different parts of the trunk portion of the column. Additionally, the material from Petersbuch 2 proves that the neural spine, although relatively low, was not vestigial as suspected by Szyndlar (1987, 1991b).

Genus *Neonatrix* Holman, 1973

cf. «*Neonatrix*» sp.

Material: 58 trunk vertebrae (BSP 1976 XXII 6791–6843), 5 trunk vertebrae (SMNS 57899/4).

Description

These small (centrum length 3.0 to 3.4 mm), largely incomplete vertebrae, are collectively characterized by relatively low neural spines and short hypapophyses; they possess parapophyseal processes directed anteriorly as typical for natricine snakes. Owing to the presence of reduced (but not vestigial!) neural spines and hypapophyses probably throughout most of the column, it is extremely difficult to recognize from which parts of the column the particular vertebrae are derived. Moreover, it is not certain whether these vertebrae belonged to one or more species. The vertebrae are most similar to those of the extinct species *Neonatrix europaea* and *N. nova,* but the fragmentary nature of most bones does not enable more exact identification.

Discussion

Neonatrix elongata, the type-species of the genus, was based merely on three trunk vertebrae (Holman 1973). The most important diagnostic features of this small extinct snake, reported from several Miocene sites of North America, were the reduced hypapophysis and low neural spine (Holman 1979, 1982, and references therein). As seen from several illustrations published by Holman, vertebrae referred to *N. elongata* displayed high intraspecific variation in the shape of their hypapophyses, neural spines, and parapophyseal processes (Szyndlar 1987). Another North American member of this genus, *N. magna,* known exclusively from a single trunk vertebra, differed from the type-species by, among others, much larger absolute size (Holman 1982).

Occurrence of the genus *Neonatrix* was then reported from the French Middle Miocene by Rage & Holman (1984), who described two distinct species, *N. europaea* and *N. crassa*; both species were based exclusively on trunk vertebrae. Rage & Holman (1984) retained the original diagnosis of the genus *Neonatrix,* i. e., diagnosing it as a small natricine snake with a weakly developed hypapophysis and low neural spine. Nevertheless, hypapophyses of both French *Neonatrix* as well as neural spines of *N. europaea,* were apparently better devoloped than the homologous structures in the North American members of the genus; the neural spine of *N. crassa* remains unknown, but apart from that this species resembles by its overall vertrebral morphology the living genus *Natrix* (Rage & Holman 1984: figs. 4 and 5). The other fossil snake referred to the genus *Neonatrix* was *N. nova* from the Bohemian Miocene (Szyndlar 1987), a form distinctly larger than the French *Neonatrix*; similar vertebrae were later reported, as *Neonatrix* sp., from the Slovakian Miocene (Szyndlar 1991b); these snakes were characterized by low neural spines and moderately developed (but not strongly reduced) hypapophyses. It should be stressed that among living natricine snakes the hypapophysis is in most cases well developed throughout the column, but the neural spine is quite often relatively low (cf. figs. 112d.1–13 in Dowling & Duellman 1978).

AUGÉ & RAGE (in press), describing recently some natricine vertebrae from the French Miocene locality of Sansan, referred this material to the genus *Neonatrix,* despite the fact that the vertebrae were provided with very well devoloped neural spines. Consequently, the generic diagnosis of *Neonatrix* was considerably restricted by AUGÉ & RAGE who diagnosed it merely as «a small „natricine“ with a short hypapophysis».

The referal of so many fossil species to a single genus has resulted in the fact that the entire assemblage displays a very broad spectrum of intrageneric variation; it is therefore possible that the genus *Neonatrix,* in the present meaning of this name, is actually polymorphic. On account of that, we postulate to restrict the generic name *Neonatrix* exclusively to its North American members, i. e., *N. elongata* and *N. magna,* both characterized by the combination of strongly reduced hypapophyses and very low neural spines. Consequently, we consider the European species members of another genus (or, even more likely, more than one genus). Although the European natricines referred to *Neonatrix* distinctly differ from members of the other genera known from the Miocene of Europe, namely *Natrix* and *Palaeonatrix,* their proper generic allocation remains, however, uncertain; assignment of these fossils in a recent genus (or genera) occurring presently beyond Europe, is also not unlikely. Considering close zoogeographical links between Europe and Asia in the Lower/Middle Miocene, a possible generic distinction of the European fossils (including also *Palaeonatrix*) should be tested by comparing them with at least several natricine genera inhabiting presently Asia; so far, axial osterology of most of the latter forms has not been studied in detail.

Natricinae indet.

Material: 249 trunk vertebrae (BSP 1976 XXII 6844–7092), 212 trunk vertebrae (SMNS 57899/1–3).

Most likely, these vertebrae belonged overwhelmingly to the three natricine snakes described above, in particular to the genera *Natrix* and *«Neonatrix»;* poor preservation of these elements does not enable their exact generic allocation.

However, among the material listed above, a few vertebrae are completely preserved (among others BSP 1976 XXII 6844, 6845, 6847) but their taxonomic status is highly unclear. The vertebrae strongly differ from other fossil natricines known from Europe; they are characterized by extremely small dimensions (centrum length 2.2 to 2.5 mm), relatively well developed (but not very long) hypapophyses, and vestigial neural spines. It is not fully certain whether these vertebrae actually belonged to the Natricinae; their allocation among the Elapidae cannot be excluded.

Subfamily Colubrinae OPPEL, 1811

Genus *Coluber* LINNAEUS, 1758

Coluber caspioides n. sp.

Fig. 6

Holotype: One trunk vertebra, BSP 1976 XXII 7096 (Fig. 6 D-H).
Type locality: Petersbuch 2 near Eichstätt, Bayern, southern Germany.
Age: Lower Miocene (middle Orleanian; MN 4).
Derivatio nominis: *caspioides* = *caspius*-like, the name derived from the close similarities shared by the fossil snake and the living *Coluber caspius.*

Referred material: 557 trunk vertebrae (BSP 1976 XXII 7093–7095, 7097–7649), 117 trunk vertebrae (SMNS 57899/5–6).

Diagnosis. – Snake closely resembling the living *Coluber caspius*, differing from the latter in some minor features only: more depressed neural arch; more lightly built paradiapophyses with diapophyses less expanded laterally; prezygapophyses projected anterolaterally rather than laterally; zygosphene in posterior trunk vertebrae concave in dorsal view.

Description of the holotype

The almost completely preserved vertebra (except for the broken left prezygapophyseal process and slightly damaged anterodorsal corner of the neural spine) comes from the middle portion of the column.

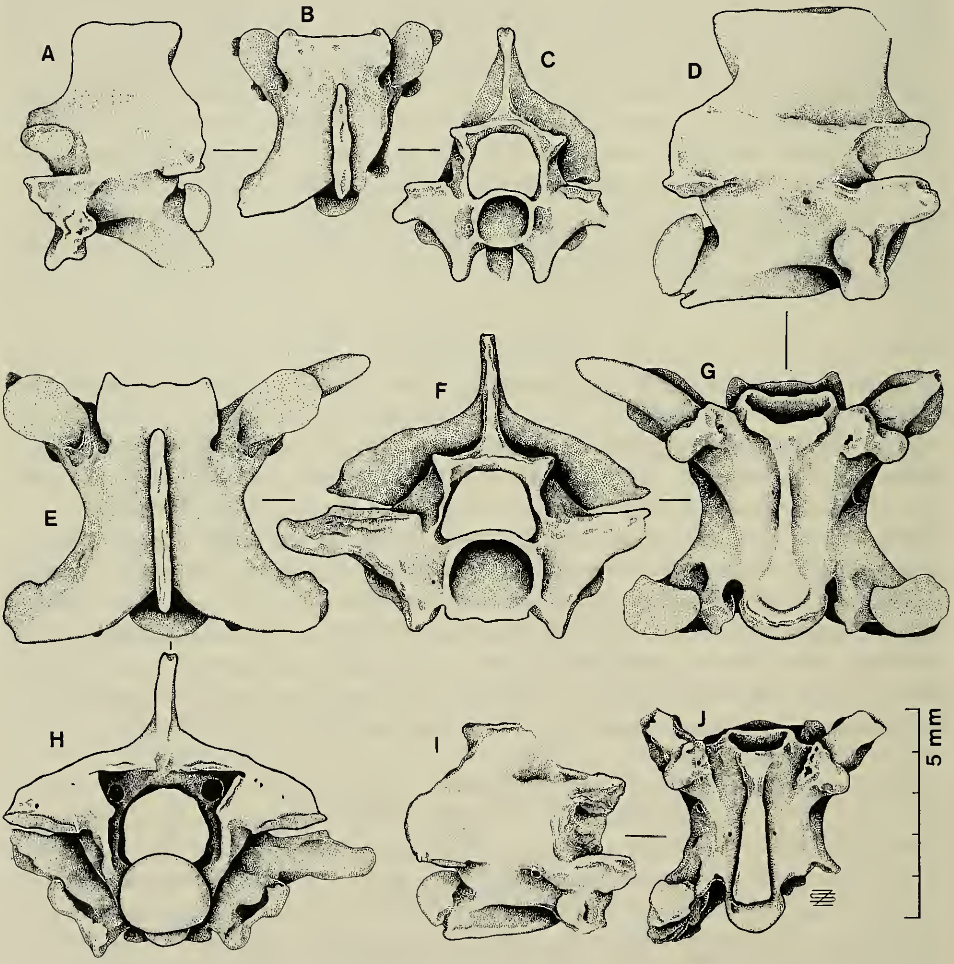


Fig. 6. *Coluber caspioides* n. sp. A–C: cervical vertebra (BSP 1976 XXII 7094); D–H: mid-trunk vertebra (holotype; BSP 1976 XXII 7096); I–J: posterior trunk vertebra (BSP 1976 XXII 7099). – A: left lateral view; B, E: dorsal views; C, F: anterior views; D, I: right lateral views; G, J: ventral views; H: posterior view.

In lateral view, the vertebra is somewhat higher than long. The neural arch is low. The neural spine is approximately as high as long and it occupies three fourth of the length of the neural arch, its anterior magin is almost straight, while the posterior one is slightly overhanging. The interzygapophyseal ridge is weakly marked. The lateral foramina are large. The paradiapophyses are relatively small and rectangular in shape, with the parapophysis somewhat longer than the diapophysis. The subcentral ridges are distinct behind the parapophyses, but disappearing before the base of the condyle.

In dorsal view, the indentation between the pre- and postzygapophyses is well marked, while the posterior notch of the neural arch is relatively shallow. The neural spine is relatively thin and uniform in width throughout its length. The zygosphenal roof is straight but slightly notched medially and delimited laterally by two moderately developed lobes. The prezygapophyseal articular facets are oval and elongate; the right prezygapophyseal process, rather slender and weakly pointed distally, is somewhat shorter than the articular facet. The axis of the prezygapophysis is directed anterolaterally.

In ventral view, the centrum is distinctly longer than wide and triangular in shape. The haemal keel is prominent although very thin, and widening before the condyle base. The subcentral grooves, occurring lateral to the keel, are very shallow. The subcentral foramina are tiny but distinct. The postzygapophyseal articular facets are somewhat rectangular in shape and elongate laterally.

In anterior view, the vertebral body (apart from the high neural spine) is relatively low. The right prezygapophyseal process is strongly built, obtuse distally and bearing a distinct foramen below the outer edge of the articular facet. The parapophyses are triangular in shape; the diapophyses are small and weakly projected laterally. The zygosphenal roof is straight. The neural canal is relatively broad, somewhat wider than the cotyle, the latter slightly flattened dorso-ventrally. The paracotylar foramina are small but distinct.

In posterior view, the neural arch is rather flattened; its postzygapophyseal portions are pierced with several distinct foramina. The zygantrum is wider than the slightly depressed condyle.

Basic measurements. – Centrum length 5.2 mm; centrum width 4.0 mm; length between the outer edges of prezygapophyseal articular facets 7.6 mm; length between the outer edges of postzygapophyseal articular facets 7.5 mm; length from the anterior edge of prezygapophyseal articular facet to the posterior edge of postzygapophyseal articular facet 6.3 mm.

Description of the remaining material

The cervical vertebrae (Fig. 6 A-C) differ from the middle trunk ones by having a prominent hypapophysis instead of a haemal keel and (as characteristic for most snakes) by relatively shorter centra, broader neural canals, vaulted neural arches, and short parapophyseal processes directed downwards.

The mid-trunk vertebrae very closely resemble the type vertebra, although sometimes (but rarely) they possess shorter prezygapophyseal processes. Two especially large (incomplete) vertebrae (BSP 1976 XXII 7103 and 7104), with the centrum length 6.8 and 6.9 mm, centrum width 5.9 and 5.1 mm, respectively, evidence that even in overgrown snakes the vertebral body was well elongate. Besides these two specimens, the centrum length of 40 largest vertebrae is 5.0 to 6.1 mm, the centrum width 3.3 to 4.5 mm; centrum length/width ratio 1.2–1.6, mean 1.4. Midtrunk vertebrae with the centrum length below approximately 3.3–3.5 mm are considered as belonging to subadult or juvenile snakes.

The posterior trunk vertebrae (Fig. 6 I-J) are more elongate, their neural spine is distinctly lower, while the prezygapophyseal processes oriented downwards; the important difference is the distinctly convex zygosphenal roof in dorsal view. The haemal keel of the posterior trunk vertebrae is strongly built and thick, in a few vertebrae even distinctly flattened ventrally; in two fused vertebrae (BSP 1976 XXII 7102) that belong to the posteriormost trunk part of the column the keel is relatively very high.

Cloacal vertebrae referable to this snake were not found in the available material. We were also unable to select caudal vertebrae referable to *Coluber caspioides,* because of their presumed similarity to those belonging to *Natrix* aff. *N. sansaniensis* and perhaps also to *Vipera platyspondyla.*

Discussion

Identification of fossil vertebrae of non-natricine Colubridae is usually the most difficult task in ophidian paleontology, but fortunately this is not the case of the above described snake, considering its very close similarity to the living species *Coluber caspius.* Vertebrae of many fossil colubrids found in Europe display homogenous morphology that makes their identification to the generic level uncertain or even impossible. In particular, in most larger species the vertebral centra are relatively short, becoming approximately as long as wide in particularly overgrown specimens. *C. caspius,* however, is an exception from this rule, having distinctly elongated centra, the feature retained even in relatively very large specimens and also well seen in *C. caspioides* from Petersbuch 2.

The relatively abundant material of *C. caspioides* enables detailed comparison with several recent specimens of *C. caspius,* also considering individual variation observed within both species. The comparison evidenced, as shown in the diagnosis, that the morphological differences between both species are minute and they are consequently considered as very closely related forms. The fossil age of the species from Petersbuch 2 counted on our decision to create a new fossil species rather than to identify it as a living species.

Coluber caspius, inhabiting presently south-eastern Europe and western Asia, was reported from at least 13 Neogene and Pleistocene localities of central and eastern Europe (cf. SZYNDLAR 1991a, for review; owing to the fact that until recently *caspius* was commonly considered a subspecies of *C. jugularis,* in most previous papers it was reported under the latter name). VON SZUNYOGHY (1932) postulated its presence in the uppermost Miocene of Hungary, but this record (based exclusively on compound bones, subsequently lost) is of doubtful value; other reports of *C. caspius* come from Upper Pliocene and younger sites.

There are at least three important conclusions that can be drawn from the close relationship observed between the above described fossil snake and the living *Coluber caspius*: 1) it evidences that members of the lineages leading to the snakes inhabiting presently Europe were present in the area already in the Lower Miocene; 2) moreover, it evidences very small morphological differences between Lower Miocene snakes and their living descendants or relatives; 3) such a very slow rate of evolution leading to the living species suggests indirectly that the radiation of the extant genera must have taken place long before the Neogene (although outside Europe).

These important conclusions, concordant with similar observations made previously by Szyndlar (1991c), are additionally confirmed by the presence in Petersbuch 2 of *Vipera antiqua*, the snake closely related with the living European species *V. ammodytes* (cf. below).

Family Elapidae
Subfamily Bungarinae

Genus *Naja* Laurenti, 1768

Naja romani (Hoffstetter, 1939)
Fig. 7

Material: 552 trunk vertebrae (BSP 1976 XXII 7650–7664, 7671–7750, 7751–8107), 77 trunk vertebrae (SMNS 57901/1), 2 cloacal vertebrae (BSP 1976 XXII 7665–7666), 6 caudal vertebrae (BSP 1976 XXII 7667, 8108–8112), one right dentary fragment (SMNS 57905), one venomous fang (SMNS 57906), one supraoccipital (BSP 1976 XXII 7668), one frontal (BSP 1976 XXII 7669), one fragmentary compound bone (BSP 1976 XXII 7670).

Description

This snake is represented by numerous vertebrae coming from all parts of the vertebral column. An overwhelming part of these heavily built vertebrae belonged to relatively large specimens.

In cervical vertebrae (Fig. 7 A-D), the hypapophysis is longer than in the mid-trunk vertebrae and it is directed ventrally rather than posteroventrally; the parapophyseal processes are directed anteroventrally; besides, differences between the cervical and mid-trunk vertebrae are weakly expressed.

The middle trunk vertebrae (Fig. 7 E-I) are relatively short, with rather weakly developed indentation between the pre- and postzygapophyses. The centrum length of 40 largest midtrunk vertebrae is 6.4–9.3 mm, centrum width 5.2–8.3 mm; the centrum length/width ratio 1.0–1.4, on average 1.2. The broad centra are triangular in ventral view, with a flat or slightly concave ventral surface. The subcentral ridges are well developed. In elapid snakes, similarly to natricines, the hypapophysis is present throughout the trunk portion of the column; the hypapophysis is thick, strongly inclined posteriorly, with the straight antero-ventral margin and with obtuse distal tip. The neural arch is rather depressed. The neural spine is thick, twice longer than high, with the anterior margin straight and overhanging posteriorly. The paradiapophyses are strongly built, with short but prominent parapophyseal processes looking anteriorly. The zygosphenal roof is provided with three distinct lobes. The pre- and postzygapophyseal articular facets are of variable shape, from orbicular to subsquare. The prezygapophyseal processes are thick and obtuse, usually half as long as the prezygapophyseal articular facets. The cotyle and condyle are orbicular or slightly flattened dorso-ventrally; they are distinctly broader than the neural canal. The subcentral, lateral, and paracotylar foramina are distinct, often very large.

Posterior trunk vertebrae (Fig. 7 J-L), characterized by a very low neural spine and deep subcentral grooves, are relatively small and distinctly elongate; however, the posteriormost trunk vertebrae possess strongly shortened vertebral body.

Several anterior cloacal vertebrae (Fig. 7 M-N) possess, as typical for snakes, lymphapophyses (distally broken) instead of paradiapophyses; as characteristic for elapids, they are provided with strong haemal keels and not with paired haemapo-

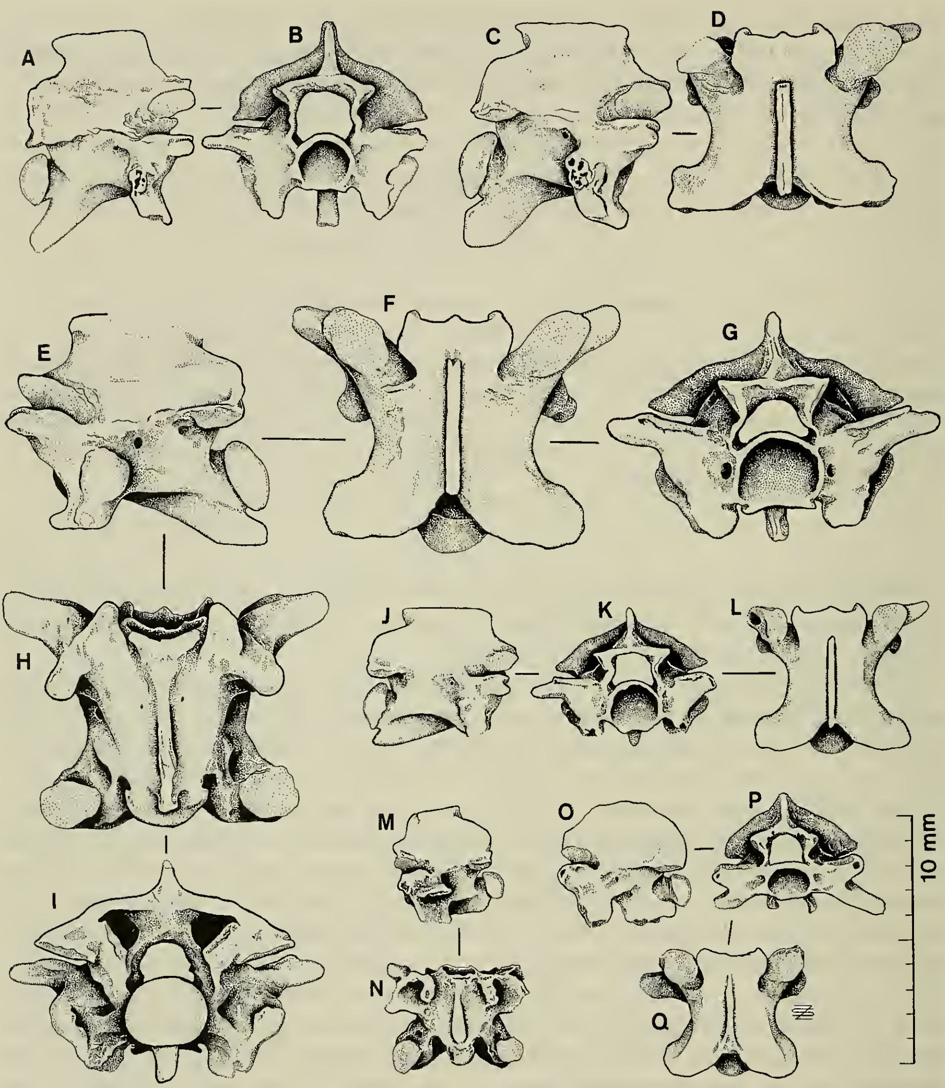


Fig. 7. *Naja romani.* A–B: anterior cervical vertebra (BSP 1976 XXII 7651); C–D: posterior cervical vertebra (BSP 1976 XXII 7652); E–I: mid-trunk vertebra (BSP 1976 XXII 7656); J–L: posterior trunk vertebra (BSP 1976 XXII 7663); M–N: anterior cloacal vertebra (BSP 1976 XXII 7666); O–Q: anterior caudal vertebra (BSP 1976 XXII 7667).– A, C, J: right lateral views; B, G, K, P: anterior views; D, F, L, Q: dorsal views; E, M, O: left lateral views; H, N: ventral views; I: posterior view.

physes; posterior cloacal vertebrae (bearing haemapophyses in elapids) have not been found in the available material. The cloacal as well as several anterior caudal vertebrae (Fig. 7 O-Q) referred to *Naja romani* are massively built unlike those belonging to other advanced snakes present in Petersbuch 2.

The few skull bones, usually fragmentary, closely resemble those of *Naja romani* described previously from other European localities (Hoffstetter 1939; Bach-

MAYER & SZYNDLAR 1985). The supraoccipital referred to *N. romani* is reported here for the first time; this bone, short and wide, provided with strongly developed and expanded laterally occipital crests, does not differ from supraoccipitals of most members of the genus *Naja*.

Discussion

Naja romani, originally described by HOFFSTETTER (1939) as a member of the fossil genus *Palaeonaja* from the Middle Miocene French locality La-Grive-Saint-Alban, belonged to commonest snakes in the European Miocene. Besides France, it was found in the Late Miocene of Austria (BACHMAYER & SZYNDLAR 1985; originally described as *N. austriaca*), the Ukraine (SZYNDLAR & ZEROVA 1990), and Hungary (the locality Rudabánya; SZYNDLAR, unpublished). As evidenced by examination of its cranial bones coming from several European localities, *N. romani* was closely related to the living Asiatic members of the genus but differed from the latter by some primitive features (SZYNDLAR & RAGE 1990). Axial osteology of this species was especially well documented from the type locality (HOFFSTETTER 1939: pl. 2); comparison of the vertebrae from La-Grive-Saint-Alban and Petersbuch 2, in both cases coming from all major parts of the column, reveals no substantial differences between them and therefore the cobra from Petersbuch 2 is clearly referable to *N. romani*. It is worthy to notice that by the morphology of its hypapophysis in the posterior trunk vertebrae (strongly reduced and directed posteriorly rather than postero-ventrally) *N. romani* considerably differs from its living Asiatic relatives.

Subfamily Elapinae BOIE, 1827

Genus *Micrurus* WAGLER, 1842

Micrurus gallicus RAGE & HOLMAN, 1984

Fig. 8

Material: 27 trunk vertebrae (BSP 1976 XXII 8113–8139).

Description

These rather small vertebrae display homogenous morphology; most of them represent the middle trunk portion of the column; those supposed to come from the posterior part of the column differ very little from the latter. The centrum length is 3.5–4.5 mm, centrum width 2.1–2.5 mm; the centrum length/width ratio 1.7–1.8. The highly characteristic feature of these vertebrae is that the outer margin (usually slightly curved) of the hypapophysis forms a very acute angle with the main axis of the vertebral body; the hypapophyseal tip is acute and it often projects distinctly beyond the condyle. Owing to the orientation of the hypapophysis in the posterior direction along with the presence of a very low and long neural spine, the vertebrae are strongly elongate in lateral aspect. The neural arch is moderately vaulted. The centrum is very long and flat in ventral view. The subcentral ridges are fairly well developed. The zygosphene is triangular or convex in dorsal view, provided laterally with two distinct lobes. The prezygapophyseal articular facets are rounded and slightly elongate; the prezygapophyseal processes are usually thin and acute, approximately as long as the articular facets, and slightly inclined downwards in anterior view. The postzygapophyseal articular facets are relatively very small, orbicular or

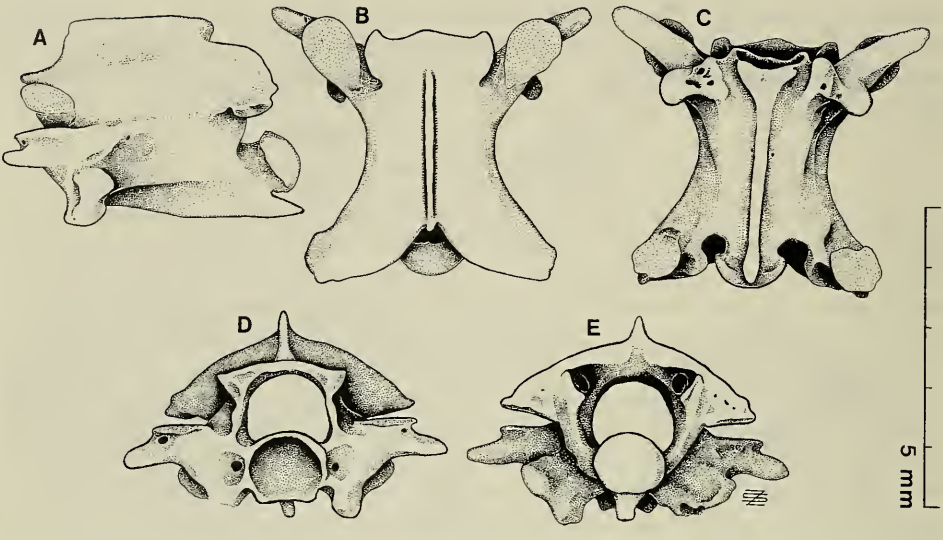


Fig. 8. *Micrurus gallicus*, mid-trunk vertebra (BSP 1976 XXII 8113). A: left lateral view; B: dorsal view; C: ventral view; D: anterior view; E: posterior view.

subsquare in shape. The paradiapophyses are small, with short parapophyseal processes directed anteriorly. The cotyle and condyle are orbicular and narrower than the neural canal. The lateral and subcentral foramina are well marked; the paracotylar foramina are often very large.

Discussion

Micrurus gallicus was described from the Middle Miocene of La Grive M in France (Rage & Holman 1984: fig. 6); it may have also occurred in the somewhat older locality of Vieux Collonges; the vertebrae from Petersbuch 2 do not differ from those coming from the type locality. Rage & Holman argued that *Micrurus*, with the present distribution restricted to the tropical America, belonged to the wave of North American invaders that reached Europe in the Lower and Middle Miocene via the Beringian land bridge. Although the vertebral morphology displayed by the fossil snake is well concordant with that of the living members of *Micrurus*, its possible relationships with some small south Asiatic elapids cannot be excluded (not compared with the type material: Augé & Rage, in press; cf. also below: Elapidae indet.).

Elapidae indet.

Material: 16 trunk vertebrae (SMNS 57901/2, 3).

These minute vertebrae, with the centrum length ranging between 1.7 and 2.2 mm, and the centrum width 1.1–1.4 mm, by many aspects resemble those of *Micrurus gallicus*, especially by the elongation of the vertebral body and shape of the hypapophysis. There are, however, some important differences, first of all a vestigial neural spine, but also very short prezygapophyseal processes and (in a vertebra interpreted as posterior trunk) a very shallow notch in the posterior margin of the neural arch.

Interestingly, in one cervical vertebra (relatively short and with the hypapophysis directed posteroventrally, as indicated by its remnant) referred to this snake, the neural spine is also extremely low, although not vestigial as in the more posterior vertebrae.

The systematic allocation of these peculiarly built vertebrae is unclear. Most likely, this snake was closest to the small «euproteroglyph» elapids (sensu McDowell 1987, i. e. subfamilies Calliopheinae, Maticorinae, and Elapinae) as indicated by their similarity to *Micrurus* and *Maticora*. But no ultimate conclusions can be drawn because we are not familiar with the axial osteology of most genera of these snakes and descriptions of them do not exist in literature; we cannot exclude a possibility that these vertebrae did not belong to elapid snakes.

Family Viperidae Oppel, 1811
Subfamily Viperinae Oppel, 1811

Genus *Vipera* Laurenti, 1768
('*Vipera aspis*' complex)

Vipera antiqua Szyndlar, 1987
Fig. 9

Material: 708 trunk vertebrae (BSP 1976 XXII 8143–8849), 86 trunk vertebrae (SMNS 57900/2).

Description

In vipers (similarly to natricines and elapids), owing to the presence of hypapophyses throughout the trunk portion of the column, there exists no sharp difference between the cervical and mid-trunk vertebrae. Proper allocation of isolated vertebrae must be necessarily arbitrary; in our case at least those vertebrae having the neural spine approximately as high as long can be certainly interepreted as cervical. Besides, they differ from those located more posteriorly in the column by having relatively longer hypapophyses and broad neural canals (Fig. 9 A-C).

The middle trunk vertebrae (Fig. 9 D-H) have moderately elongate and somewhat cylindrical centra, with weakly developed subcentral ridges and subcentral grooves. The hypapophysis is usually relatively long and thick, straight in lateral view and directed postero-ventrally. The neural arch is flattened. The neural spine is thin, twice to three times longer than high, with the anterior and posterior margins slightly overhanging. The paradiapophyses are narrow and elongate dorso-ventrally in lateral view, provided with relatively long and thin parapophyseal processes looking ventrally rather than anteroventrally. The zygosphenal roof is provided with three lobes, the central one relatively broad. The prezygapophyses are slightly tilted upwards. The pre- and postzygapophyseal articular facets are relatively small, usually rounded in shape and slightly elongate. The prezygapophyseal processes are thin and relatively very short. The cotyle and condyle are orbicular or slightly flattened dorso-ventrally. The neural canal is relatively wide and high. The subcentral, lateral, and paracotylar foramina are distinct, often very large.

The centrum length of 40 mid-trunk vertebrae, being the largest in the available material, ranges between 3.7 and 4.6 mm, the centrum width beteen 2.6 and 3.9 mm. The centrum length/centrum width ratio is 1.2 to 1.5, mean 1.3. A few fragmentary vertebrae present in the material are somewhat larger, but their referal to *V. antiqua*

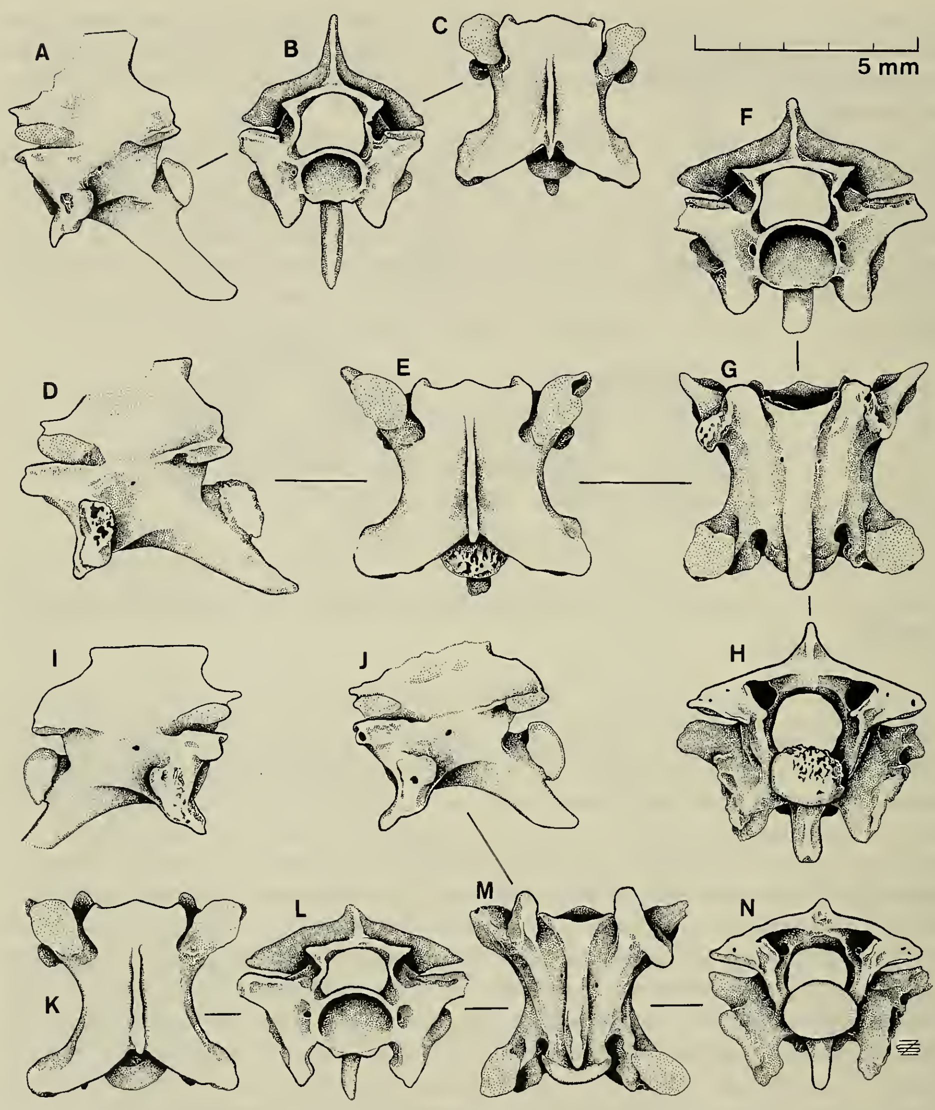


Fig. 9. *Vipera antiqua*. A–C: cervical vertebra (BSP 1976 XXII 8143); D–H: mid-trunk vertebra (BSP 1976 XXII 8148); I: posterior trunk vertebra (BSP 1976 XXII 8146); J bis N: posterior trunk vertebra (BSP 1976 XXII 8147). – A, D, J: left lateral views; B, F, L: anterior views; C, E, K: dorsal views; G, M: ventral views; H, N: posterior views; I: right lateral view.

cannot be demonstrated with full confidence. The centrum length of overwhelming majority of the trunk vertebrae exceeds 3.0 mm.

Posterior trunk vertebrae (Fig. 9 I-N) are characterized by distinctly longer centra, lower neural spines, shorter hypapophyses, deep subcentral grooves, and distinctly longer parapophyseal processes.

Discussion

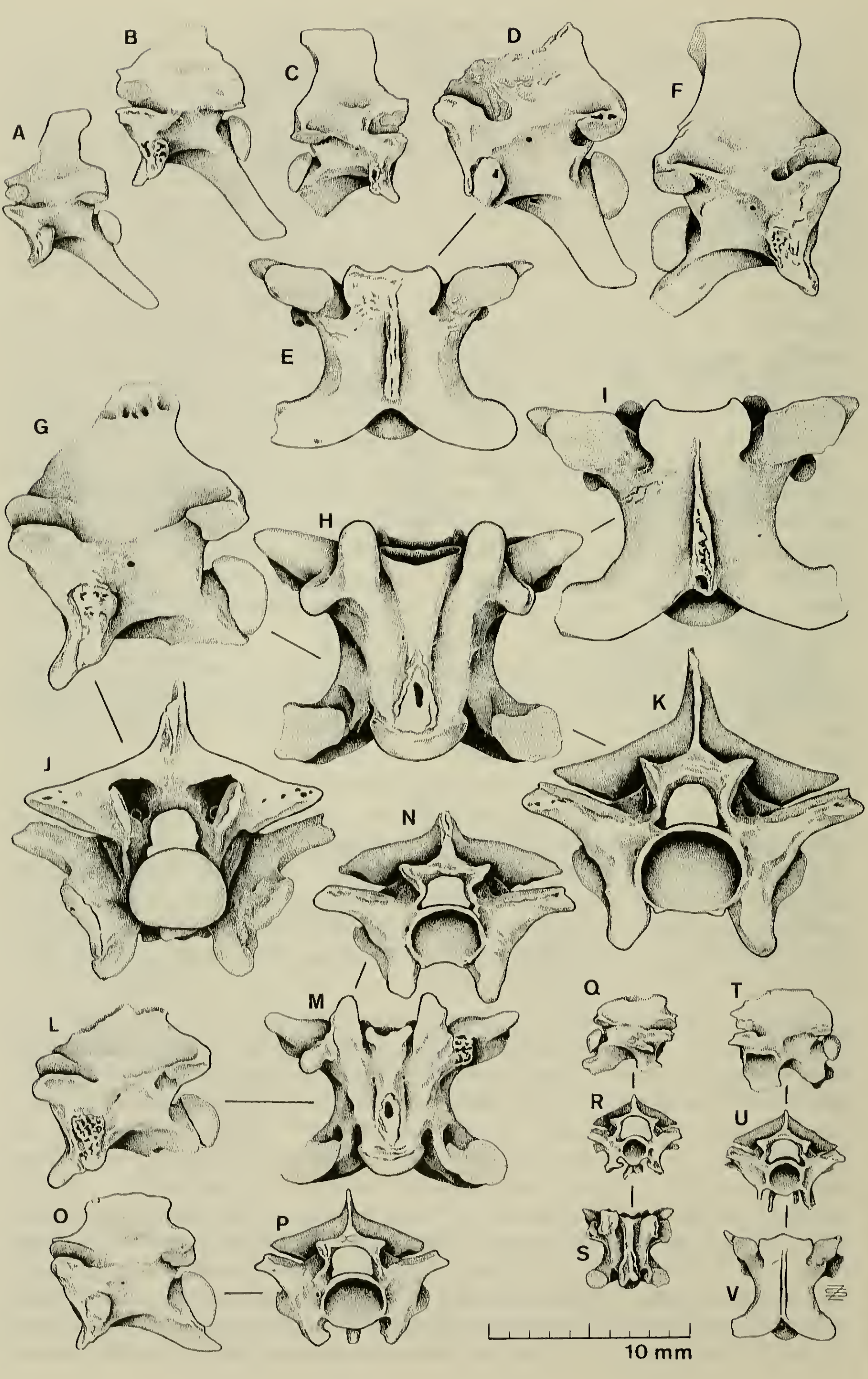
The oldest worldwide fossil records of the family Viperidae come from the lowermost Miocene (early Agenian; MN 1) of France and Gemany. The first fossil viper described from this period was *Provipera boettgeri* KINKELIN (1892) from Hessler in Germany (see also SCHLEICH 1988). Generic and specific distinction of *Provipera*, based merely on an isolated venomous fang (figured by KINKELIN 1896), was questioned by COPE (1892) and subsequently considered a nomen dubium by RAGE (1984a). Although allocation of *Provipera* in the family Viperidae was correct, however, even subfamilial identification is impossible on the basis of isolated fangs.

HOFFSTETTER (1955) reported the presence of viperid vertebrae and fangs from the Aquitanian (= Agenian) of the Limagne area in France; he observed that the fossil elements were very similar to those of the living subfamily Viperinae. In his later paper, HOFFSTETTER (1962) noticed that the Viperidae appeared suddenly in the Aquitanian of Europe; he confirmed his previous observations about similarity between the fossils (now maxillae and fangs) and the «Vipères modernes». RAGE (1984a) repeated the above information as follows: «The Viperidae are first reported in the fossil record in the Lower Miocene of Europe (Agenian = Aquitanian; HOFFSTETTER 1962)». Unfortunately, neither HOFFSTETTER nor RAGE described these fossils in detail. According to unpublished data kindly provided by J. C. RAGE (in litt.), the oldest French fossils known from the Limagne area come from localities of the Saint-Gérand-le-Puy complex (MN 1 and 2) and from Marcoin (MN 2); the remains belong to small viperid snakes.

The oldest unquestionable record of the genus *Vipera* comes from the German locality of Weisenau; recent examination of these remains (seven trunk vertebrae belonging to the SMNS collection) reveals that the snake from Weisenau is comparable with the extinct species *V. antiqua*.

Vipera antiqua was originally described from the Bohemian locality of Dolnice (SZYNDLAR 1987). Its description was based on six vertebrae only, but these bones were relatively well preserved and represented all major parts of the trunk portion of the column. There are no substantial differences between the snake from Dolnice and that from Petersbuch 2 and therefore the identification of the latter as *V. antiqua* seems well grounded. Noteworthy that the abundant material of *V. antiqua* from Petersbuch 2 does not display any considerable intraspecific variation, in contrary to *V. platyspondyla*, the other viper occurring in the same locality (cf. below).

Vipera antiqua was a relatively small snake, considered by SZYNDLAR (1987) a member of the '*V. aspis*' complex (sensu GROOMBRIDGE 1986), consisting of the three living European species: *V. aspis*, *V. latastei*, and *V. ammodytes*. These species display rather homogenous vertebral morphology, there are, however, some peculiarities that enable differentiating between *V. aspis* and *V. latastei* on one hand and *V. ammodytes* on the other: in the former group the hypapophysis becomes distinctly curved in posterior trunk vertebrae, whereas in *V. ammodytes* it remains distinctly straight until the end of the trunk portion of the column (the pattern observed in *V. aspis* and *V. latastei* is concordant with that of smallest European vipers, i. e., *V. berus* and other species). Abundant material from Petersbuch 2, containing a large number of posterior trunk vertebrae, indicates that *V. antiqua* closely resembled the living *V. ammodytes*, the latter inhabiting presently southeastern Europe. The siginificance of this observation was discussed earlier in this paper (cf.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C. caspioides: Discussion). Of a special importance is the fact that the viper from the lowermost Miocene of Weisenau perhaps also belonged to the same lineage.

('Oriental vipers')

Vipera platyspondyla Szyndlar, 1987

Fig. 10

Material: 794 trunk vertebrae (BSP 1976 XXII 8850–8860, 8867–9649), 61 trunk vertebrae (SMNS 57900/1), 6 cloacal vertebrae (BSP 1976 XXII 8861–8866), above 11 venomous fangs (SMNS 57904).

Description

Vipera platyspondyla was the largest snake in the assemblage from Petersbuch 2. The centrum length of 40 largest mid-trunk vertebrae ranges between 7.2 and 10.8 mm, the centrum width between 5.3 and 9.1 mm. The centrum length/centrum width ratio is 1.05 to 1.45, mean 1.2. Most vertebrae belonged to large specimens; the centrum length of smallest mid-trunk vertebrae is rarely lower than 4.5 mm.

Below, we consider that the vertebrae with neural spines higher than long belonged to the cervical portion of the column, while those with the spines as high as long or lower represented the mid-trunk vertebrae. In recent «Oriental vipers» (except for *Vipera russelli*), the neural spine becomes approximately as high as long usually around the 50th vertebra, while it is twice longer than high around the 100th vertebra.

The cervical vertebrae (Fig. 10 A-F) are very short and high in lateral view, owing to the presence of a very long hypapophysis and a high neural spine; in more anterior cervical vertebrae the latter structure is twice higher than long (Fig. 10 A); in more posterior cervical vertebrae the spine is lower but still distinctly higher than long (Fig. 10 F). The zygosphene of the cervical vertebrae is generally trilobate (Fig. 10 E), but the shape and degree of developement of the zygosphenal lobes vary in particular specimens.

The middle trunk vertebrae (Fig. 10 G-K) are provided with moderately elongate centra, with the subcentral ridges well developed immediately behind the parapophyses. The hypapophysis (broken off in most vertebrae) is thick, long, straight in lateral view, and directed postero-ventrally. The neural arch is strongly flattened. The neural spine (broken off in most vertebrae) is thick at the base, usually straight anteriorly and slightly overhanging posteriorly; it is approximately as high as long in the anteriormost mid-trunk vertebrae and its height diminishes in more posterior vertebrae. The paradiapophyses are slender, strongly elongate dorso-ventrally, provided with long and obtuse distally parapophyseal processes, the latter directed ven-

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Fig. 10. *Vipera platyspondyla.* A: anterior cervical vertebra (BSP 1976 XXII 8850); B: anterior cervical vertebra (BSP 1976 XXII 8851); C: anterior cervical vertebra (BSP 1976 XXII 8852); D–E: posterior cervical vertebra (BSP 1976 XXII 8853); F: posterior cervical vertebra (BSP 1976 XXII 8854); G–K: mid-trunk vertebra (BSP 1976 XXII 8855); L–N: posterior trunk vertebra (BSP 1976 XXII 8856); O–P: posterior trunk vertebra (BSP 1976 XXII 8860); Q–S: anterior cloacal vertebra (BSP 1976 XXII 8866); T–V: posterior cloacal vertebra (BSP 1976 XXII 8862). – A, B, D, G, L, O, T: left lateral views; C, Q: right lateral views; E, I, V: dorsal views; H, M, S: ventral views; J: posterior view; K, P, R, U: anterior views.

trally rather than antero-ventrally. The zygosphene, especially in largest vertebrae, is usually straight or concave, rarely with well developed central lobe. The prezygapophyses are distinctly tilted upwards, but rather rarely to such a degree as in the vertebra shown on Fig. 10 K. The pre- and postzygapophyseal articular facets have usually the shape of rectangles, strongly elongate laterally; in rare cases, they are elliptical. The prezygapophyseal processes are very short, thick at the base and usually obtuse distally. The cotyle and condyle are orbicular or slightly flattened dorsoventrally; they are much broader than the neural canal, the latter relatively narrow even in smaller vertebrae. The subcentral, lateral, and paracotylar foramina are distinct.

Posterior trunk vertebrae (Fig. 10 L-M) are more flattened and they are provided with lower neural spines as well as shorter and directed more posteriorly hypapophyses; the paradiapophyses and parapophyseal processes are often more strongly built; the zygosphene is usually convex. In the vertebrae immediately preceding the cloacal region (Fig. 10 O-P), the neural spine is three times or more longer than high.

Several anterior cloacal vertebrae (Fig. 10 Q-S) possess, as characteristic for vipers, a long and forked distally hypapophysis instead of haemapophyses; typical paired haemapophyses appear in the posterior cloacal vertebrae (Fig. T-V). These cloacal vertebreae were assigned to *Vipera platyspondyla* and not to *V. antiqua* considering their relatively very large dimensions. For the same reason a few isolated viperid fangs present in the material are also assigned to *V. platyspondyla.*

Discussion

The informal name 'Oriental vipers' has been employed in paleontological papers for largest members of the genus *Vipera* (Szyndlar 1987, 1988, 1991b). All living species of the 'Oriental vipers', inhabiting recently Middle East, southern Asia, northwestern Africa and southeasternmost skirts of Europe, were separated off *Vipera* s. l. by Obst (1983), who revalidated for them the genus *Daboia.* The name *Daboia,* but as a subgenus of the genus *Vipera,* was also used in paleontology for inclusion of all presumed fossil members of the 'Oriental vipers' (Zerova in Szyndlar & Zerova 1992). It is little probable, however, that the entire group is monophyletic. Groombridge (1986) divided the ,Oriental vipers' into three complexes, namely '*lebetina*', '*xanthina*', and '*russelli*'. This subdivision was generally accepted by other students of viperine systematics (e. g. Nilson & Andrén 1986) except for the '*russelli*' complex, the latter consisting of *V. russelli* and *V. palaestinae* according to Groombridge. Osteologically, *V. russelli* differs greatly from the remaining members of the 'Oriental vipers' and it most deserves the status of a distinct genus (Szyndlar 1988; Szyndlar in Szyndlar & Zerova 1992). Recent studies, based on biochemical methods, confirmed the distinct status of this snake and consequently the generic name *Daboia* was restricted to its type species, *Vipera russelli* (Herrmann et al. 1992). At the same time, Herrmann et al. revalidated the generic name *Macrovipera* for the '*lebetina*' complex, while the systematic status of the '*xanthina*' complex and of *Vipera palaestinae* remains still unresolved. An especially strong demand for fragmentation of *Vipera* s. l. resulted from cladistic analysis, based principally on morphological characters, by Ashe & Marx (1988), who found the genus highly polyphyletic. Nevertheless, the consistency index computed for the most parsimonious cladogram of the viperine snakes (Ashe & Marx 1988: figs. 1 and 2) is scarcely 28.47% and thus the cladistic hypothesis presented by these authors seems weakly grounded. This brief summary of the current achievements in the viperine systematics shows that the status of the genus *Vipera* s. l. is still an open question; considering additionaly the convergent morphology of vertebrae of most of these snakes, we prefer to continue the use of the informal name 'Oriental vipers', at least with reference to paleontological record.

Although most descriptions of fossil 'Oriental vipers' were published during several last years, remains of these snakes were known much earlier from Europe; for example, HOFFSTETTER (1955) mentioned that «grosses Vipères» were abundant in the Miocene of France, Germany, Hungary, and other European countries and that they were replaced by smaller species in the Quaternary. Also SAINT GIRONS (1980), who postulated the occurrence of «un groupe de grandes Vipères plutôt méridionales, ancêtres des actuelles Lébétines» in the European Miocene and Pliocene, based his report on an unpublished fossil record; the viperid remains from the Spanish Upper Pliocene locality Îles Medas, mentioned by SAINT GIRONS, were recently described in detail (but not published) by BAILON (1991) as »*Vipera* sp. (groupe *lebetina*)». SAINT GIRONS further postulated that, in the course of the Pliocene, the range of the hypothetical ancestors of the living *Vipera lebetina* was restricted to the Mediterranean area. Although the SAINT GIRONS' observations were generally confirmed by later described fossil remains, the question whether the 'Oriental vipers' inhabiting Europe in the Neogene represented exclusively the *V. lebetina* complex remains unresolved until today. NILSON & ANDRÉN (1986) supported the SAINT GIRONS' hypothesis, suggesting that the disappearance of *V. lebetina* within its western (i. e., European) range in the Quaternary enabled the other 'Oriental viper', namely *V. xanthina*, to expand to the west; unfortunately, there is no direct evidence in favour of this supposition.

The first fossil species of the 'Oriental vipers' (reported as such) were described in 1987 from several Neogene sites of Central and Eastern Europe (BACHMAYER & SZYNDLAR 1987; SZYNDLAR 1987; ZEROVA et al. 1987). At the same time it was evidenced that *Vipera gedulyi* from the Hungarian Miocene, described as early as 1913 by BOLKAY, was also a member of the 'Oriental vipers' (SZYNDLAR 1988); previously, it was consistently considered in the literature as a close relative of the living *V. ammodytes*.

Up to now, as many as seven fossil species of the 'Oriental vipers' are known from the Neogene of Europe (cf. ZEROVA 1992, for the up-to-date review). Unfortunately, the specific distinction of a part of these species, based exclusively on vertebrae, was not properly demonstrated. Of them, only *Vipera maxima* from the Spanish Pliocene (SZYNDLAR 1988), seems closely related to the living *V. russelli* from southern Asia (the only living member of *Daboia* sensu HERRMANN et al. 1992). The relationship between both snakes is well evidenced by the morphology of their posterior trunk vertebrae, provided with as high as long neural spines along with relatively short hypapophyses. This condition does not occur in the remaining (both extant and extinct) 'Oriental vipers', having very low neural spines and relatively long hypapophyses.

Apart from *Vipera maxima*, the other fossil species of the 'Oriental vipers' from the European Neogene belong either to the '*lebetina*' complex or to the '*xanthina*' complex. Of them, two fossil species, *V. gedulyi* and *V. burgenlandica*, both with fairly well recognized cranial osteology, seem well referable to the former group. *V. gedulyi* from the Hungarian Miocene is no doubt closely related to the living

V. lebetina, as evidenced by recent re-examination of its abundant skull bones (Szyndlar 1991b: Note added in the proof). In its original description (Bachmayer & Szyndlar 1987), the taxonomic status of *V. burgenlandica* from the Austrian Miocene was unclear, because the material then available suggested relationships with both the '*lebetina*' (vertebrae) and the '*xanthina*' complex (a single basiparasphenoid); however, discovery of new cranial remains, in particular another basiparasphenoid, enabled to recognize the intraspecific variation within the fossil species and, in consequence, to reject its possible relationships (as previously suspected) with *V. xanthina* (Szyndlar 1991b).

The problem becomes much more complicated with regard to the extinct species based exclusively on vetebrae, considering close similarity in vertebral morphology between the '*lebetina*' and '*xanthina*' complexes. Trunk vertebrae of *V. xanthina* differ from those of the '*lebetina*' complex by having elliptical-shaped (and not rectangular) prezygapophyseal articular facets, more upwardly tilted prezygapophyses (Szyndlar 1987), and the straight (and not overhanging) anterior edge of the neural spine (Zerova 1992). It should be noted, however, that these observations are based on limited comparative material of the living *V. xanthina,* skeletons of which are not available in most museum collections. On the other hand, the above listed characteristics of *V. xanthina* occur sometimes (although rarely) in members of the ‚*lebetina*‘ complex (Szyndlar, unpublished observations). It is quite possible that a more detailed examination of the axial osteology of recent 'Oriental vipers', in particular of *V. xanthina,* could help to resolve the problems of proper identification of fossil materials. Although *V. ukrainica,* newly described from the Ukrainian Miocene (Zerova 1992), was assigned to the '*xanthina*' complex, this decision was based almost exclusively on the cranial morphology. While the occurrence of *V. xanthina*-like snakes in the Ukrainian Miocene seems easily understandable also on the geographical ground, their possible presence in the Pliocene of Spain and southern France, as recently reported by Bailon (1991), would have been certainly surprising; the latter report, however, is based exclusively on vertebrae.

In its original description of *Vipera platyspondyla* from the Bohemian locality Dolnice, Szyndlar (1987) stated that this snake seemed closest to the living *V. xanthina*; nevertheless, considering scantiness of the fossil material from Dolnice (eight fragmentary vertebrae), Szyndlar noticed that the close relations between both snakes could not be demonstrated with confidence. The viperid remains from Petersbuch 2 described above, containing among others trunk vertebrae identical with the type material from Dolnice, are referred to *V. platyspondyla.* Nevertheless, the abundant material from Petersbuch 2 evidences clearly that this fossil snake was characterized by a broad spectrum of intraspecific variation and that the diagnostic features of *V. platyspondyla* (among others strongly upwardly tilted prezygapophyses, elliptical-shaped prezygapophyseal articular facets, three sharp lobes of the zygosphene) did not belong to prevailing conditions characteristic of this species. Most mid-trunk vertebrae found in Petersbuch 2 were characterized by moderately upwardly tilted prezygapophyses and rectangular-shaped prezygapophyseal articular facets, therefore the features characteristic of the '*lebetina*' complex. Although the vertebrae from Petersbuch 2 were mostly provided with neural spines not overhanging anteriorly (as characteristic for *V. xanthina*), on the other hand the number of vertebrae with entirely (or almost entirely) preserved neural spines was very scarce. In conclusion, the taxonomic status of this oldest 'Oriental viper' remains presently unresolved.

Serpentes indet.

Material: 147 trunk vertebrae (BSP 1976 XXII 9650–9796), 60 trunk vertebrae (SMNS 57902/1), 103 caudal vertebrae (BSP 1976 XXII 9797–9899), 205 caudal vertebrae (SMNS 57902/2), fragments of 3 dentaries, 2 pterygoids, and one maxilla (SMNS 57907).

The entire material belongs most likely to the advanced snakes (i. e., Colubridae, Elapidae, and Viperidae); there is no evidence that the vertebrae could belong to other forms than those described above. The trunk vertebrae were not identified to the familial level on account of their strong damage. Contrary to the latter, many caudal vertebrae are relatively well preserved. Of them, the largest vertebrae (especially those anterior caudal) display four somewhat different morphological patterns (especially in the shape of neural spines, zygosphenes, and prezygapophyseal processes) and therefore they could be theoretically referable to the four snakes reaching largest dimensions, namely *Natrix* aff. *N. sansaniensis*, *Coluber caspioides*, *Naja romani*, and *Vipera platyspondyla*. Vertebrae of *Naja romani*, usually easy for identification owing to their heavy built, were partly selected off the material. However, it appeared very hazardous to correlate the particular caudal vertebrae with those from the trunk portion of the column. In particular, it should be taken into consideration that the morphology of caudal vertebrae observed in recent members of the genera *Natrix*, *Coluber*, and *Vipera* is not necessarily reminiscent of that observed in their posterior trunk vertebrae.

Familial allocation of the few cranial elements, owing to their fragmentary nature, cannot be demonstrated.

3. Changes in the ophidian faunas of Germany in the Lower and Middle Miocene

A recent summary of the up-to-date knowledge on fossil snakes from the German territory (Szyndlar & Böhme, in press b) shows that the best recognized ophidian faunas come from the period between the Oligocene and Middle Miocene. Remains of pre-Oligocene snakes have not been adequately described, while Upper Miocene and Lower Pliocene snakes have never been reported from Germany.

The snake assemblage from Petersbuch 2 belongs to the most abundant and diverse ophidian faunas ever reported from Europe. This assemblage shows perfectly that the end of the Lower Miocene (middle Orleanian; MN 4) was one of the most important turning points in the history of the German ophidian faunas. The following brief review of ophidian fossil record available from the German Miocene indicates that a number of Lower Miocene snakes became extinct around the Lower/Middle Miocene transition and was replaced by new waves of modern snakes coming probably from the East.

Most Miocene snakes, described from several German sites mainly in the 19th century (von Meyer 1844, 1845; Fraas 1870; Kinkelin 1892; Schlosser 1916), were considered nomina dubia (Rage 1984a; Szyndlar 1992; Szyndlar & Böhme, in press b); of them, only *Coluber suevica* (originally described as a member of the elapid genus *Naja* by Fraas 1870) from Steinheim a. A. is with certainty a valid species. Thus, the following review is necessarily based on the fossil collections not described yet, coming from eleven Lower and Middle Miocene sites, located mainly in southern Gemany (cf. Introduction for the list of these localities).

In the Agenian and lower Orleanian (MN 1–3), the snake fauna of Germany was composed partly (perhaps mainly) of Oligocene survivors. Among them, the extinct aniliid *Eoanilius*, found in the Lower Miocene of Ulm-Westtangente and Stubersheim 3, was the only ophidian genus that occurred with certainty in Europe yet in the Eocene; remains of *Eoanilius* coming from Petersbuch 2 are the youngest fossil record of this genus. The other Oligocene snake, *Bransateryx vireti* or a closely related form, unexpectedly survived in Germany until the end of the Middle Miocene (upper Astaracian, MN 7+8), as evidenced by the material from Steinheim a. A. (= *Coluber steinheimensis* FRAAS, 1870, part; = cf. *Bransateryx*, RAGE 1984a; SMNS 51152). The other member of the genus, *B. septentrionalis*, is known exclusively from the uppermost Lower Miocene (middle Orleanian; MN 4). The boine *Bavarioboa* may have also occurred in the Oligocene, but it is not ultimately proved. Non-erycine boids did not survive in Europe beyond the Middle Miocene; remains of *Bavarioboa* from Rothenstein 13 belong to the youngest records of non-erycine Boidae in Europe.

Of special interest is the finding of a fragmentary vertebra comparable with those of the living *Eryx* in Stubersheim 3 (SMNS 57709/2). It would be the oldest record of this genus, but the generic allocation cannot be evidenced with confidence on the basis of a single incomplete vertebra. In Europe, *Eryx* was especially common in the Upper Miocene and Pliocene (SZYNDLAR 1991a, 1991b), i. e., the period from which no fossil snakes have been reported from Germany.

Non-natricine Colubridae were represented in the German Lower Miocene by tiny snakes of unknown generic allocation, found in Weisenau (SMNS 59119) and Stubersheim 3 (SMNS 57709/4); that from Weisenau is comparable with *Coluber cadurci* (the generic assignment of this species to *Coluber* is uncertain), reported from the French Oligocene and perhaps also Lower Miocene (RAGE 1974, 1984a). The characteristic features of these and other Oligocene and Lower Miocene non-natricine Colubridae known from Germany and France are very small absolute size and the elongated vertebral form. It might be possible that the Lower Miocene colubrids were Oligocene survivors.

The most important novelty in the composition of the snake faunas in the beginning of the Miocene was the appearance of vipers in Europe. It is of special importance that the oldest known *Vipera*, coming from Weisenau (*Vipera* cf. *V. antiqua*, SMNS 59115, 59116), does not differ significantly from the living European species *V. ammodytes*. This record indicates clearly that the genus *Vipera* must have evolved long before the Miocene, but apparently outside the European territory. Since the beginning of the Miocene, remains of the genus *Vipera* are common in European fossil sites. In the Lower Miocene of Germany, fragmentary vertebrae of small *Vipera* (perhaps belonging to two different species) were also found in Stubersheim 3 (SMNS 57709/3).

Although the fossil record from most of the Lower Miocene (MN 1–3) is rather limited, it seems that the German snake fauna was subject to rather slow changes in this period. More drastic changes in the composition of the German ophidian faunas took place at the turn of the Lower Miocene (i. e., around the zone MN 4; middle Orleanian), the phenomenon resulting from competition of new waves of eastern invaders, composed principally of modern colubrids, large vipers, and elapid snakes. Arrival of these new snakes, well evidenced by the fossil record from Petersbuch 2, was probably connected with the thermal maximum observed in the European climate around the Lower/Middle Miocene transition (SCHLEICH 1985, 1986). Another characteristic event observed in those times was a faunal exchange between Eurasia and North America that brought to Europe several North American snake genera

(Rage & Holman 1984); as discussed in the previous chapter, it does not seem ultimately evidenced yet whether all these snakes were indeed of American origin. The Middle Miocene (upper Orleanian to upper Astaracian; MN 5–8) snake fauna of Germany differed little from that established at the end of the Early Miocene; although snake remains coming from a number of Middle Miocene localities are not very abundant, they contained most snakes (at least at the generic level) that appeared in Germany at the end of the Lower Miocene. A few snakes not recorded from the Lower Miocene of Germany and found in Middle Miocene sites belonged exclusively to non-natricine Colubridae.

The elapid snakes reported from Petersbuch 2 belonged to the oldest representatives of this family in Europe and elsewhere. Whereas the exact taxonomic position of *Micrurus gallicus* (supposed an immigrant from North America by Rage & Holman 1984) and the unnamed tiny elapid from Petersbuch 2 is unclear, the relationships of the fossil cobra *Naja romani* with the living Asiatic members of the genus are quite well recognized (Szyndlar & Rage 1990). Since its appearance at the end of the Lower Miocene, *Naja* belonged to the most common snakes in the European Neogene. In Germany, fragmentary vertebrae referable to this genus were also found in the Middle Miocene localities of Sandelzhausen (BSP 1959 II) and Rothenstein 13 (SMNS). Specific allocation cannot be, however, evidenced on the basis of the existing material; most likely, as in the case of other cobras inhabiting Europe except for the Iberian Peninsula, these snakes were related to the living Asiatic *Naja*.

Large members of the genus *Vipera*, the 'Oriental vipers', may have appeared in Europe as early as the lower Orleanian (MN 3). This supposition is based on a single vertebra reported from the Portuguese site of Lisboa by Antunes & Rage (1974: fig. 4) as Viperidae indet.; relatively large dimensions and morphology of the illustrated vertebra indicate that it may have belonged to the 'Oriental vipers'. The first certain record of these snakes comes from the middle Orleanian (MN 4) of Central Europe; the 'Oriental vipers' were represented by the fossil species *V. platyspondyla* from Dolnice and Petersbuch 2 as well as by an unnamed species found in Langenau (SMNS 53915); the latter is represented by several fragmentary vertebrae, morphologically resembling those of *V. platyspondyla*. Similarly to cobras, the 'Oriental vipers' belonged to commonest European snakes until the Pliocene. In the Middle Miocene of Germany, vertebrae of the 'Oriental vipers' were found in Sandelzhausen (BSP) and Steinheim a. A. (SMNS 53264/1–2). In Petersbuch 2, *V. platyspondyla* occurred sympatrically with a much smaller species, *V. antiqua*; similarly in Steinheim a. A., the 'Oriental viper' was accompanied by a small *Vipera* (= *Coluber steinheimensis* Fraas, 1870, part; = cf. *Vipera*, Rage 1984a; SMNS 51153), similar to the living *V. ammodytes*. It is quite possible that the small vipers from Weisenau (*Vipera* cf. *V. antiqua*), Petersbuch 2 (*V. antiqua*) and that from Steinheim a. A. belonged to a single lineage leading to the living *V. ammodytes*. The Miocene viperid fauna of Germany contained also representatives of another group of *Vipera*, namely the '*V. berus*' complex (sensu Groombridge 1986), consisting of smallest members of the genus, with the present centre of distribution located in Europe. Occurrence of these vipers is evidenced by fragmentary trunk vertebrae coming from Langenau (SMNS 53888/2) and Randecker Maar (SMNS 53960/2), characterized by very small dimensions, distinctly elongated centra, strongly reduced neural spines, and posteriorly curved hypapophyses; these are the oldest fossil records of the '*V. berus*' complex.

Apart from the invasion of elapids and 'Oriental vipers', another characteristic event at the end of the Lower Miocene was the appearance of a complex natricine fauna, as evidenced by the material from Petersbuch 2. Although natricine snakes occurred in Europe since the Oligocene (Rage 1988a), it seems that they were relatively rare until the end of the Lower Miocene; the oldest find from Germany consists of a few fragmentary vertebrae of an unidentified small natricine from Stubersheim 3 (SMNS 57709/6). Sudden appearance of several different forms of natricine snakes in Petersbuch 2 suggests that they represent mostly a new wave of immigrants rather than survivors inhabiting previously Europe. This complex natricine fauna occurred in Europe still in the Middle Miocene, as evidenced by abundant remains coming from the French locality of Sansan (Augé & Rage, in press). Apart from Petersbuch 2, vertebrae clearly referable to the fossil genus *Palaeonatrix* (cf. *P. lehmani*) were found in Langenau (SMNS 55807/1), while those comparable with *Natrix* in Oggenhausen (SMNS 57652/4); natricine vertebrae of unclear generic allocation were also found in Randecker Maar (SMNS 53960/1) and Sandelzhausen (SMNS 53995/1). Most of this abundant natricine fauna probably did not survive in Europe beyond the Middle Miocene; as evidenced by fossil record from a number of sites located outside Germany, natricine snakes inhabiting Europe from the Upper Miocene onwards were represented exclusively by the living genus *Natrix* (Rage in Demarcq et al. 1983; Szyndlar 1991b).

As mentioned above, before the end of the Lower Miocene the non-natricine Colubridae were represented exclusively by tiny snakes that may have reached Europe yet in the Oligocene. Large members of this group that appeared in Europe in the middle Orleanian were represented by *Coluber caspioides* in Petersbuch 2 and *C. dolnicensis* in the Bohemian site Dolnice (Szyndlar 1987). In the Middle Miocene large colubrids became common in Europe; in Germany they were represented by an unnamed snake from Sandelzhausen (perhaps *Coluber*; BSP 1959 II) and *Coluber suevica* from Steinheim a. A. (= *Naja suevica* Fraas, 1870; = ?*Coluber suevica*, Rage 1984a; SMNS 51026, 53240, 53257/1–2). Smaller colubrids were also present in the Middle Miocene of Germany, but apparently they were not related to the species known from the Lower Miocene. A single vertebra found in Randecker Maar (SMNS 53960/3) is comparable with those of the extinct *Texasophis meini* described from the French Middle Miocene (Rage & Holman 1984), while several perfectly preserved vertebrae from Oggenhausen (SMNS 57652/2) may belong to the living genus *Elaphe*.

A long gap in the fossil record does not enable to reconstruct changes in the German ophidian faunas that took place after the Middle Miocene. Data available from countries located both west and east from Germany indicate that from the Upper Miocene onwards a prevailing part of Europe was inhabited exclusively by members of modern ophidian genera; most likely, the snake fauna inhabiting then Germany was composed of similar elements. This supposition is supported by the fact that changes observed in the German ophidian assemblages from the Upper Pliocene onwards did not differ from those occurring in adjacent areas of Central Europe (Szyndlar & Böhme, in press b).

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