

FOSSIL RECORD OF THE TRUE VIPERS

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ABSTRACT: The known fossil record of the Viperinae (true vipers) ranges in age from the earliest Miocene (ca. 23.8–22.8 Ma) until Recent, and specimens originate from Europe, Africa, and Asia. At least 171 localities have yielded fossils of viperines, and the majority have come from Europe and belong to the modern genus *Vipera* (*sensu lato*). Specimens from Africa and Asia are restricted to several localities, and those from Africa are of the genera *Bitis*, *Causus*, *Cerastes*, *Vipera*, and perhaps *Daboia*. The taxonomic allocation of Asiatic fossils, however, is unstable. With few exceptions, fossils of Crotalinae (pitvipers) have not been reported from the Old World. The oldest true vipers, known from isolated vertebrae and fangs, do not differ significantly from their extant relatives. Although paleontologists at this time cannot provide much useful information on the origin and earliest history of viperines, these events must have taken place prior to the Miocene and outside of Europe.

INTRODUCTION

In this paper we summarize the current knowledge of the fossil history of true vipers (Viperinae). A review of the fossil history of Old World vipers was provided by Szyndlar and Rage (1999), but that study was restricted almost exclusively to the oldest remains, particularly those from lower and middle Miocene deposits. In this study we include all fossil remains of true vipers and their localities, from their first appearance in the lowermost Miocene (ca. 23.8 Ma) until the latest Pliocene (ca. 2 / 1.64 Ma). The latest Pliocene is sometimes considered the lowermost Pleistocene because several decades ago the limit between the Pliocene and Pleistocene was placed about 2 / 1.8 Ma, whereas today this boundary is fixed at 1.64 Ma (Harland et al., 1990). Basic data on particular Neogene fossils and their localities are listed in Appendix I and II, and localities are mapped on Figures 1 and 2. We have gathered published and unpublished information on 171 fossil sites, of which 110 are Miocene and Pliocene localities. Hence, this work reviews the fossil record of nearly all Old World Viperidae, considering that with few exceptions (e.g. Hasegawa et al., 1973; Hasegawa, 1980; Ivanov, 1999) fossil pitvipers have not been reported from the Eastern Hemisphere.

Fifteen fossil species of the Viperinae (or presumed Viperinae) have been described. Unfortunately, the taxonomic status of most species and their phylogenetic relationships to extant vipers is unstable. The last published list of extinct Viperidae was compiled by Rage (in Golay et al., 1993), and herein we present an updated version (see Appendix III).

The present work includes mostly members of *Vipera* (*sensu lato*), because the majority of fossil finds

of Old World Viperidae have been referred to this genus. We employ the division of the genus *Vipera* (*sensu lato*) into four groups, based on osteological traits that have commonly been used in paleontological literature over the past two decades: (1) the *Vipera berus* complex (comprised of, among others, the extant species *berus*, *seoanei*, and *ursinii*); (2) the *Vipera aspis* complex (*ammodytes*, *aspis*, and *latastei*); (3) *Vipera* “Oriental vipers” (*deserti*, *lebetina*, *mauritanica*, *palaestinae*, *schweizeri*, *xanthina*); and (4) *Daboia* (with a single living species, *russelii*). The reasons for using this arrangement (following, in part, a concept introduced by Groombridge, 1980, and Obst, 1983) are explained below (Szyndlar and Rage, 1999).

OSTEOLOGY OF VIPERS: IMPLICATIONS FOR PALEONTOLOGY

Recent systematic studies of Old World vipers based on molecular data are in disagreement with the morphological findings of paleontologists, and it appears necessary to briefly state our views regarding problems arising from these molecular studies. The systematics and taxonomy of extant members of the Viperinae have recently undergone important changes. Within the genus *Vipera* (*sensu lato*), several complexes have been established and subsequently, entirely or in part, removed from that genus and placed in another. Opinions about relationships among particular members of the group have also been controversial.

During the past decade, most proposed systematic changes of the Viperinae have been based on biochemical rather than morphological analyses. Herrmann et al. (1992), for example, used immunological albumin comparisons and found the taxa *russelii* and *lebetina* (including former subspecies of the latter) phylogenetically distinct, and revalidated the generic names *Daboia* and *Macrovipera*, respectively. The remaining related species (*xanthina*, among others) were retained in the genus *Vipera*. Recent studies (partly by the same authors), however,

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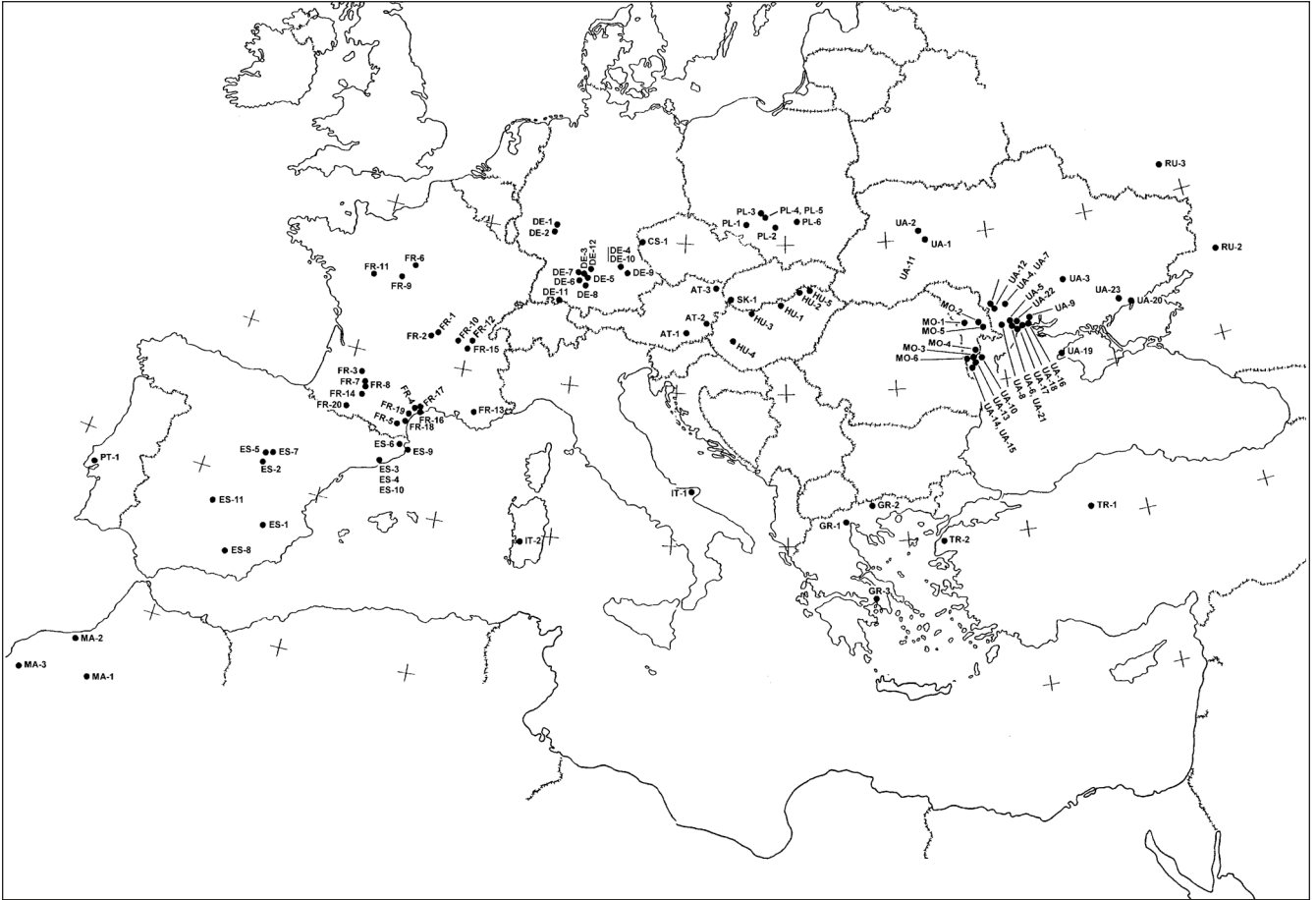


Fig. 1. Neogene localities of the Viperinae in the West Palearctic. See abbreviations in Appendix I.

based on mitochondrial DNA (Joger et al., 1999; Lenk et al., 2001), revealed that the taxa *palaestinae* and *mauritanica* (the latter previously considered a member of *Macrovipera*) should be placed in the genus *Daboia*, whereas *xanthina* was considered to be a member of the genus *Macrovipera*.

It is not our present aim to comment extensively on interpretations and conclusions presented in the aforementioned studies, as well as other papers, but we contend that the radical changes in taxonomy (and hence nomenclature) proposed in those studies based on discoveries restricted to a single (or several) characters are not advisable. Although mtDNA evidence, for example, apparently supported including *V. mauritanica* and *V. palaestinae* in the genus *Daboia*, and *V. xanthina* in *Macrovipera* (Joger et al., 1999; Lenk et al., 2001), earlier results generated from blood serum albumin characters produced different results (Herrmann et al., 1992). Our concern with molecular studies is in the methods of determining which molecules are better suited for sorting taxa and reconstructing phylogenies. Are blood serum albumins less important than mitochondrial DNA? To us, it would

appear that such choices regarding selection of molecular markers are more subjective than realized.

In paleontology, estimates of the taxonomic status of a given fossil and its relationship with extinct or extant species rely on comparisons of skeletons with those of extant relatives. Phylogenetic relationships hypothesized from skeletal characters are not always concordant with those based on molecular characters. On the basis of osteology, most members of extant Oriental vipers (*deserti*, *lebetina*, *mauritanica*, *palaestinae*, *schweizeri*, *xanthina*) closely resemble each other, a situation that also occurs within the *V. berus* and *V. aspis* complexes. For example, when we work with fossil remains of European Oriental vipers, it is normal practice to first compare all remains with skeletons of *lebetina* and *xanthina*, species that today inhabit areas in Asia Minor located near ancient migratory routes. With rare exceptions, ophidian fossil remains are fragmentary and usually consist of isolated vertebrae. Considering the close osteological similarities of these recent species, in most cases it is clear that fossil remains cannot answer the crucial question of which lineage is represented. For this reason, we



Fig. 2. Neogene localities of the Viperinae in the Old World, exclusive of the West Palearctic. See abbreviations in Appendix I.

feel that the use of the generic name *Macrovipera* (recently used in paleontological papers) is baseless, although one of us (JCR) was obliged to use this genus for practical reasons in Golay et al. (1993).

The osteology of recent Viperinae is poorly studied, and the lack of comparative materials has made identification of fossil remains difficult or impossible. There is great intraspecific variation in the skeletal elements of the Viperinae, which remains largely unknown due to the scarcity of viperine skeletons in museum collections, and only a few authors have discussed intraspecific variation in the skull bones (Zerova and Chikin, 1992; Chikin, 1997).

Another example of the aforementioned problems is the taxonomic status of *V. burgenlandica* of the Austrian Miocene. In the description of this extinct species, Bachmayer and Szyndlar (1987) considered it to be a close relative of the extant *V. xanthina*, based mostly on the similarity of the basiparasphenoid. Discovery of another basiparasphenoid, apparently belonging to *V. burgenlandica* but resembling that of *V. lebetina*, and not that of *V. xanthina*, suggests a broad spectrum of intraspecific variation in *V. burgenlandica*

(Szyndlar, 1991). Paradoxically, while our knowledge of fossil species has increased, their relationships with extant species become enigmatic.

A more interesting example of intraspecific variation that occurs in fossil snakes is found in *V. gedulyi* from the Hungarian Miocene, described by Bolkay in 1913. Although the description was based on a large number of cranial elements, only four bones (a maxilla, a fragmentary ectopterygoid, a basioccipital, and a basiparasphenoid) were illustrated (Bolkay, 1913, Plate 12: Figs. 9–12). This material was subsequently examined by von Szunyogy (1932), but remained inaccessible until 1991 when one of us (ZS) was allowed to examine Bolkay's collection (see Szyndlar, 1991: notes added in the proof). For a detailed description of the snake and numerous illustrations, see Venczel, 1994. Figure 3 shows four of 16 syntype basiparasphenoids of *V. gedulyi*, whereas Figure 4 presents nine of 16 syntype maxillae of the same snake. Differences among the bones are striking, and if it was the case that these particular bones originated from different paleontological localities, they could have been described as distinct species! This is easily

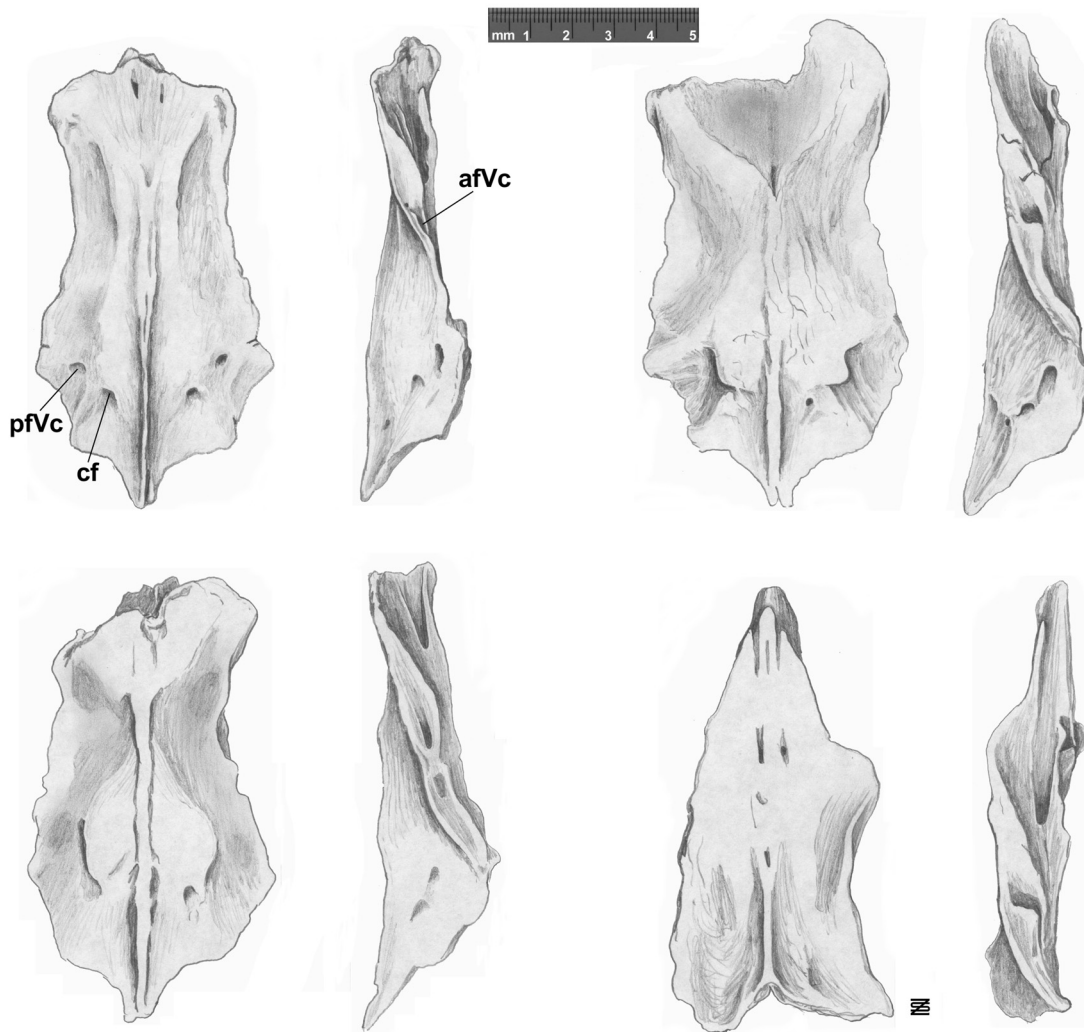


Fig. 3. *Vipera gedulyi* Bolkay, 1913 from the Miocene of Polgárdi. Four basiparasphenoids, in ventral and left lateral views (syntypes, part.; Museum of the Hungarian Geological Institute, Budapest, Ob-4467/Vt.74). Abbreviations: afVc, anterior foramen of Vidian canal; cf, cerebral foramen; pfVc, posterior foramen of Vidian canal. Note the intraspecific variation in the general shape of the bone as well as in the disposition of the foramina.

understood considering that ophidian paleontologists, unfortunately, usually have few (if any) comparative skeletons of related Recent snakes to examine.

Osteologically, disregarding variation at the species level, the subfamily Viperinae, and *Vipera* (*sensu lato*) in particular, form a highly homogeneous group with certain members displaying similar morphology in both skulls and vertebrae, unlike in other snakes. For example, in the Colubridae, it is usually difficult to properly identify isolated fossil vertebrae, but in most cases identification of cranial bones of European colubrids is not troublesome (von Szunyoghy, 1932; Rabeder, 1977). Despite these problems, the osteology of the Viperinae generally

permits identification. More importantly, this allows us to recognize assemblages that are morphologically homogeneous. On this account, we stress that most osteological characters within *Vipera* (*sensu lato*) do not support the systematic changes proposed on the basis of molecular data.

Vertebral features of different groups of *Vipera* (*sensu lato*) were discussed by Szyndlar and Rage (1999). In summary, particular complexes of *Vipera* are characterized by differences in vertebral morphology, but it is extremely difficult (if not impossible) to differentiate vertebrae belonging to members of the same complex. Similarly, the cranial morphology of most extant members of *Vipera* (*sensu lato*) is highly



Fig. 4. *Vipera gedulyi* Bolkay, 1913 from the Miocene of Polgárdi. Nine maxillae (6 right and 3 left), in antero-ventral views (syntypes, part.; Museum of the Hungarian Geological Institute, Budapest, Ob-4467/Vt.74). Abbreviations: ap, ascending process; fdc, foramen of dental canal. Note the intraspecific variation in the shape of the ascending process as well as in the presence vs absence of the foramen piercing the process.

homogeneous, and morphological differences can be only observed between particular complexes rather than within them. The only exception is *russelii*. Its osteology fully supports placement in the genus *Daboia*, as suggested by Szyndlar (1988), and as indicated by molecular characters (for information on the distinctiveness of the vertebrae of *russelii*, see Szyndlar and Rage, 1999). In cranial osteology, significant differences are evident between *russelii* and other members of the genus *Vipera* (*sensu lato*), such as extremely elongated skull bones in *russelii* (an apomorphic character) (Fig. 5).

In summary, osteological characters support a division of the genus *Vipera* (*sensu lato*) into three separate complexes. In the following section we consider most extinct European viperines as members of the genus *Vipera*. Exceptions are *D. maxima* from the Spanish Pliocene, thought to be a close relative of the living *D. russelii*, and several fossil species that we consider *nomina dubia* or *nomina nuda*.

THE OLDEST TRUE VIPERS

The oldest Viperidae have been reported from a few lowermost Miocene (MN 1) sites in western Europe. They are *Provipera boettgeri* from Hessler, Germany (Kinkelin, 1892), *V. antiqua* from Weisenau, Germany (Szyndlar and Böhme, 1993), and perhaps a *Vipera* from St-Gérard-le-Puy complex, France (Hoffstetter, 1955). The systematic status of *P. boettgeri*, based on isolated venomous fangs, is uncertain and was considered a *nomen dubium* by Rage (1984). Although it is impossible to determine whether isolated fangs represent a true viper or pitviper, they no doubt belonged to a member of the family Viperidae. The remains from the two latter aforementioned localities represent snakes of the *V. aspis* complex (Szyndlar and Rage, 1999).

The oldest European vipers are also the oldest representatives of the family Viperidae. The oldest viperine fossil in the New World, slightly younger than European fossils, is a vertebral fragment resembling

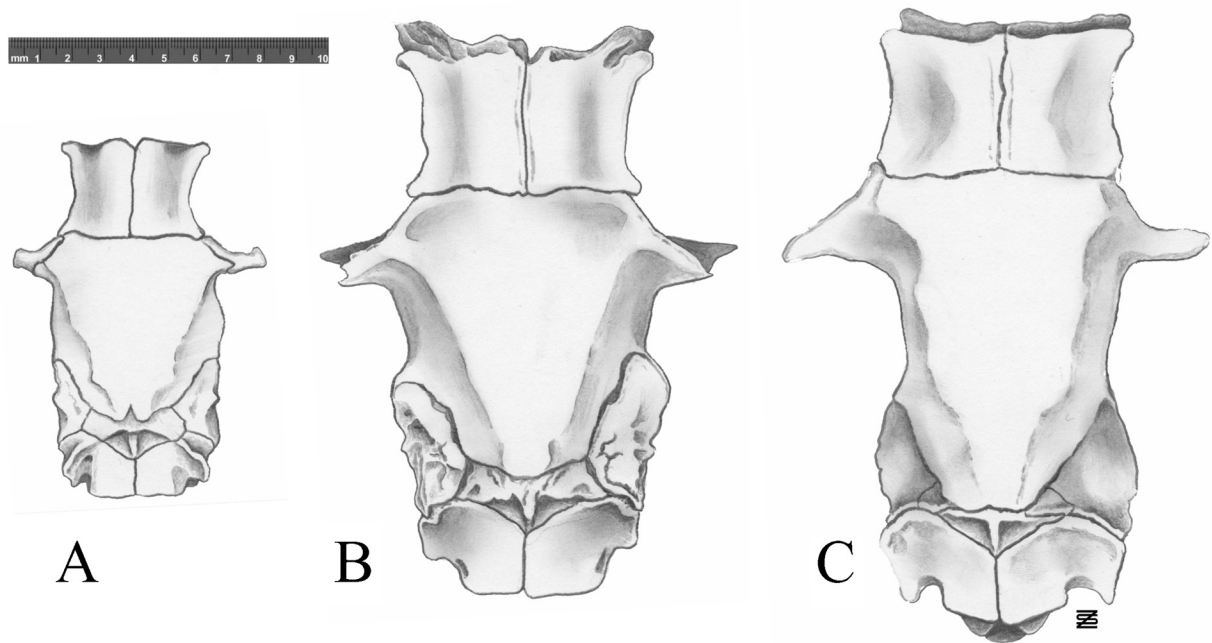


Fig. 5. Dorsal view of the braincase of three extant vipers: (A) *Vipera berus*; (B) *Vipera lebetina*; (C) *Daboia russelii*. All specimens from the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences (catalogue numbers 415, 481, and 362, respectively)

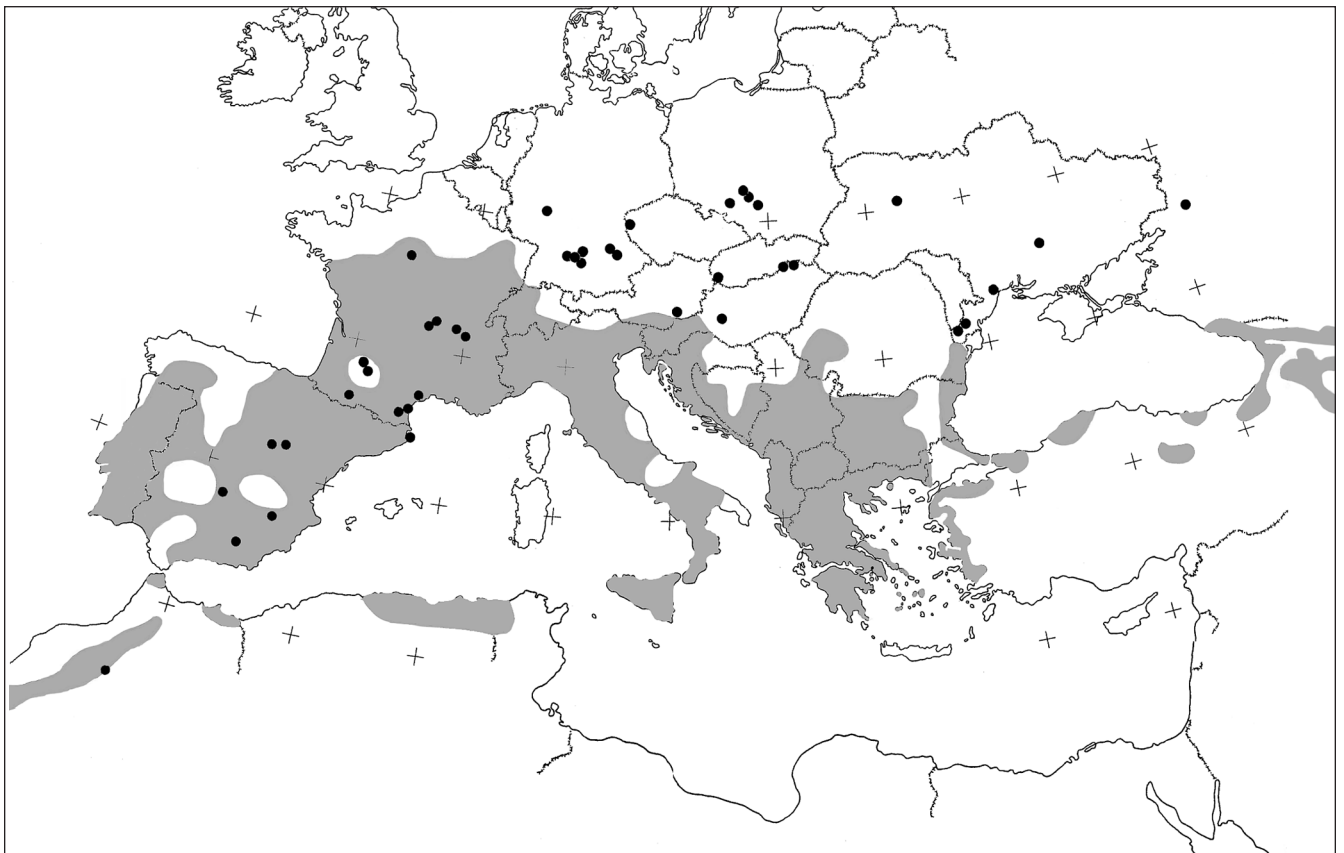


Fig. 6. Neogene and recent occurrence of *Vipera* (*aspis* complex) in the West Palearctic. The range of recent distribution (shaded area) after Gasc et al. (1997) (Europe), Joger (1997) (West Asia), Bons and Geniez (1996), and Schleich et al. (1996) (North Africa).

the pitviper *Sistrurus* from the lower Miocene (latest Arikareean) of Nebraska (Holman, 1981). Apart from three badly preserved remains, which are impossible to identify at the subfamily level, all other viperid fossils from North America have been referred to as pitvipers (Holman, 2000).

As with other snakes, fossil remains of the Viperidae are mostly isolated vertebrae. The oldest fossils of the Viperidae in Europe are vertebrae (localities of Weisenau and the St-Gérard-le-Puy complex) and fangs (Hessler and St-Gérard-le-Puy). Hoffstetter (1962) reported the presence of “un maxillaire et des crochets comparables à ceux des Vipères modernes” from the French Aquitanian (probably Saint-Gérard-le-Puy and/or other localities), but unfortunately the maxilla has not been found. The oldest maxillae available are those of *V. maghrebiana* from the middle Miocene (MN 7-8) of Beni Mellal in Morocco (Rage, 1976) and *Vipera* from the coeval La Grive in France. The latter locality has also yielded a number of basi-parasphenoids from members of the Oriental vipers and the *V. aspis* complex. The cranial bones from La Grive remain undescribed (see Szyndlar and Rage, 1999).

Cranial elements of the Viperidae are more fragile than homologous elements from most other snakes, and thus skull remains are rarely found. The most notable exception is the fossil remains of *V. gedulyi* from the Hungarian latest Miocene (MN 13), which consist of abundant and diverse cranial elements (Bolkay, 1913; Venczel, 1994; see Figs. 3–4). Skeletal elements of the Viperidae, including the oldest forms, do not differ substantially from the bones of recently living species. For example, the vertebrae of the oldest viper, *Vipera* cf. *V. antiqua* from the lowermost Miocene of Weisenau, are strikingly similar to those of the living *V. ammodytes* (Szyndlar and Böhme, 1993; Fig. 6). Therefore, although there is no direct supportive evidence, the genus *Vipera* must have evolved before the Miocene, and apparently outside of Europe. Important events in the history of the Viperinae are presented in Table 1.

HISTORY OF VIPERS IN EUROPE

Lower and Middle Miocene

Appearance of the “*aspis*-like” vipers was one of the most important novelties in the composition of the European snake fauna at the beginning of the Miocene (MN 1). From that point on, remains of the genus *Vipera* are abundant in European fossil sites.

At the lower / middle Miocene transition (i.e., around the biozone MN 4), dramatic changes occurred in the

composition of the European ophidian fauna. This phenomenon is correlated with the thermal maximum observed in European climate, and results from competition of autochthonous species with new waves of invaders from the East, composed principally of modern colubrids, elapids, and large members of the genus *Vipera* (i.e., Oriental vipers). Following the arrival of new snakes at the end of the lower Miocene, “archaic” components of the European snake fauna (mainly boas) became rare in fossil materials and disappeared before the end of the middle Miocene. Interestingly, an overwhelming majority of “modern” elements of the European snake fauna that inhabited Europe from the middle Miocene onward were closely related to recent species, although not necessarily in the European continent (Demarcq et al., 1983; Szyndlar and Böhme, 1993; Szyndlar and Schleich, 1993). Members of the genus *Vipera*, both Oriental vipers and *aspis*-like snakes, were important components of the modern ophidian fauna of the European Miocene.

Late Miocene and Pliocene

In the long period between the lower / middle Miocene transition and the end of the Pliocene, Oriental vipers and members of the *V. aspis* complex occurred sympatrically as part of the common European snake faunas, as indicated by the abundant fossil record from many localities, especially from areas close to the Mediterranean basin.

Most extinct species of the Viperidae described from Europe are Oriental vipers of Miocene age. Unfortunately, due to the scarcity of fossils and the osteological similarity of many vipers, it is not surprising that most extinct species are hardly distinguishable from one another and from extant relatives (Szyndlar and Rage, 1999). An important event in the middle Pliocene in Spain was the appearance of a giant viper (*V. maxima*) with vertebrae that resemble those of the living genus *Daboia* from southern Asia. The relationship between *V. maxima* and *D. russelii* is evident in their posterior trunk vertebrae; both have high neural spines and short hypapophyses, unlike the Oriental vipers (Szyndlar, 1988). The presence of a close relative of a viper in western Europe that today inhabits tropical Asia may seem astonishing. There is, however, evidence supporting a close affinity between Iberian and north African faunas in the Neogene. Moreover, there is evidence that many Neogene animals, including several snakes, may have inhabited vast areas along the southern coast of the

Table 1. Stratigraphic chart showing the timespan covered by the present study. The European Mammal Units (MN) and boundary dates between succeeding epochs are included (mostly after Mein, 1999, and Steininger, 1999). The right column indicates important events (primarily first appearances) in the history of the Viperinae.

EPOCH	MN	Europe	Asia	Africa
0.0 Ma				
QUATERNARY				
1.65 Ma				
PLIOCENE	17	<i>berus</i> -like <i>Vipera</i>		First <i>Cerastes</i> appears
	16	(western Europe)		(Tanzania and Morocco)
	15			
4.9 Ma				
LATE	14			
MIOCENE				
MIOCENE	13			
	12			
	11			
11.1 Ma	10	?First <i>berus</i> -like <i>Vipera</i>		
	9	(Ukraine)		
MIDDLE	7 + 8			First African <i>aspis</i> -like <i>Vipera</i>
MIOCENE				(Morocco)
	6			
17.0 Ma				
LOWER	5			
MIOCENE	4	First European "Oriental vipers"		Oldest African Viperidae:
		(central and western Europe)		<i>Bitis</i> and "Oriental viper" or <i>Daboia</i>
	3		Oldest Asiatic Viperidae (indet.)	(Namibia)
	2		(Thailand and ?Kazakhstan)	
23.8 Ma	1	Oldest Viperidae (<i>aspis</i> -like <i>Vipera</i>)		
		(Germany and France)		
OLIGOCENE				

Mediterranean Sea, from Iberia in the West to western Asia in the East (Szyndlar, 1985, 1987b, in press, b).

Fossil material from western and central Europe indicates that the smallest representatives of the genus *Vipera* (i.e., the *V. berus* complex) were absent in the area in the Miocene and Pliocene. The only known exceptions are remains resembling *V. ursinii* from the late Miocene (MN 12) of Tardosbánya in Hungary (M. Venczel, unpublished), and a single vertebra presumably of *V. berus* from the late Pliocene (MN 16) of Bad Deutsch Altenburg 20 (Szyndlar, 1991). Besides these records, members of the *V. berus* complex appeared in western and central Europe during the transition between the latest Pliocene and lowermost Pleistocene (MN 17).

In eastern Europe (the Ukraine), however, small vipers with strongly reduced neural spines on their trunk vertebrae (and thus referred to the *V. berus* complex) were common from at least the end of the Miocene. The taxonomic status of the oldest remains

found in the area (in Gritsev and other sites), originally reported as "*Vipera (Pelias)* sp." (Zerova, 1987, 1993) is uncertain, because of the poor state of preservation of available material (Szyndlar, 1991). The inability of these snakes to colonize the rest of Europe in the late Miocene and Pliocene may have resulted from the presence of *aspis*-like snakes in areas east of the Ukraine. The true vipers inhabiting the Ukraine in the late Miocene were accompanied by pitvipers, as evidenced by crotaline maxillae (with characteristic fossa in the pit organ) found in Gritsev (Ivanov, 1999). This fossil is the only evidence that confirms the existence of the Crotalinae in Europe.

Pleistocene

There are no significant differences between Pleistocene vipers and those living today. Pleistocene faunas most likely consisted of extant species that inhabited roughly the same areas as today. For this reason, we deal with the relatively modern record



Fig. 7. Neogene and recent occurrence of *Vipera* (Oriental viper complex) in the West Palearctic. The range of recent distribution (shaded area) is after Joger (1997) (West Asia), Bons and Geniez (1996), and Schleich et al., (1996) (North Africa).

superficially, and neither Pleistocene fossils nor their localities are listed in the appendices. Information on Pleistocene vipers, however, can be found in several published works. The most comprehensive review is that of Szyndlar (1991), which covers 10 countries in central and east Europe, and includes localities, fossil materials, their whereabouts and catalogue numbers, and numerous illustrations and maps. Unfortunately, two other extensive monographs (Bailon, 1991, Spain and France; Ivanov, 1997, central Europe) have remained largely unpublished. The most up-to-date review of European Pleistocene herpetofaunas is that by Holman (1998), which covers 41 fossil sites of *Vipera* in 10 countries. Unfortunately, Europe (*sensu* Holman, 1998) does not include Bulgaria, Romania, Russia, and other countries of the former Soviet Union. Detailed information about Pleistocene vipers from the countries omitted in Holman's book (ca. 20 localities) is found in the following sources: Ratnikov (1997a, 1998, Russia); Ratnikov (1997b, Moldova); Bolkay (1913, and Venczel 1989, 1990, 1992, Romania); Venczel (1997, 1998b, 2001, Hungary); and Szyndlar (1991, Bulgaria).

The most striking event in the history of European reptiles around the Pliocene / Pleistocene boundary was the considerable impoverishment of the fauna. This phenomenon resulted from the gradual cooling of the European climate that took place from middle Pliocene onward. Eventually, snakes with higher thermal requirements withdrew to refuges in southeastern Europe (erycines, scolecophidians) or disappeared entirely from the European continent (cobras).

The influence of climatic deterioration on the distribution of the genus *Vipera* is especially visible in the case of Oriental vipers. In the late Pliocene these snakes were still present along the Mediterranean coast (Bailon, 1989, 1991; Szyndlar, 1987b, 1991), and the only members of this group reported from Europe from the succeeding epoch come from the middle Pleistocene of Chios (Schneider, 1975) and Varbeshnitsa in Bulgaria (Szyndlar, 1991). The European range of the Oriental vipers in the Pleistocene, therefore, may have been restricted to the southeastern part of the continent, perhaps as relicts (like present-day scolecophidians and erycines in that area). The relictual distribution of Oriental vipers in the Aegean area can be observed today (*V. schweizeri*



Fig. 8. Neogene and recent occurrence of *Vipera* (*berus* complex) in the West Palaearctic. The range of recent distribution (shaded area) is after Gasc et al. (1997).

from Chios), and no doubt that this species had a much broader range in the past.

Unlike Oriental vipers, Pleistocene distribution of *berus*-like and *aspis*-like snakes did not differ considerably from that currently observed. The key event in the history of the European Viperidae at the Pliocene / Pleistocene boundary, however, was the invasion of members of the *V. berus* complex. Largely absent in western and central parts of the continent prior to the end of the Neogene, *berus*-like vipers rapidly colonized most of Europe. The available fossil record, as well as recent distributional patterns of the *V. aspis* and *V. berus* complexes, indicate that the invasion of the latter group must have been connected with withdrawal of the former to the south. Withdrawal of the *aspis*-like vipers may have been influenced by climatic deterioration and/or by competition with the *berus*-like vipers (see Szyndlar and Rage, 1999).

Contrary to the situation observed in the preceding epoch, Pleistocene *aspis*-like vipers occurred, without exception, in areas south of the Carpathians. In the Pleistocene, the areas north of the Carpathians were inhabited exclusively by *V. berus*, as evidenced by

abundant materials from several Polish localities (Szyndlar, 1984). All but one species presently inhabiting Europe have been found as fossils in numerous European Pleistocene sites: *V. ammodytes*, *V. aspis*, and *V. latastei* (*V. aspis* group) as well as *V. berus* and *V. ursinii* (*V. berus* group). Holman (1998) lists 29 localities of *berus*-like and seven localities of *aspis*-like vipers, and 12 localities yielding indeterminate *Vipera*.

A characteristic feature of the distribution of European vipers at the beginning of the Pleistocene is the sympatric occurrence of *berus*-like and *aspis*-like snakes. In most cases, this phenomenon is restricted to areas in central Europe where their ranges presumably overlap. For instance, *V. ammodytes* and *V. berus* were reported from Malá Dohoda (Ivanov, 1994), whereas *V. cf. ammodytes* and *V. cf. ursinii* were found in Stránská Skála (Ivanov, 1995), both sites in Czechia. Interestingly, withdrawal of snakes belonging to the *V. aspis* complex to the south did not conclude until recently. For example, *V. ammodytes* was present in Moravia at the beginning of the 20th century (Remeš, 1923).

HISTORY OF TRUE VIPERS BEYOND EUROPE

The majority of formally described Old World viperid fossils originate from Europe, and only a few (based on vertebrae and/or maxillae), have been reported from Asia and Africa. Neogene vipers from Asia have never been described in detail or illustrated. The oldest Asiatic viperid fossils come from the lower Miocene of Thailand (Rage and Ginsburg, 1997) and Kazakhstan (Chkhikvadze, 1985), but unfortunately we cannot demonstrate whether these scarce materials (vertebrae) belonged to true vipers or pitvipers. For further comments on the Neogene fossils from Asia, see Szyndlar and Rage (1999). Middle Pleistocene remains of Oriental vipers were described from two eastern Mediterranean sites: Emirkaya-2 in Turkey (Kessler and Venczel, 1993; Venczel and Sen, 1994) and the archaeological site of Aetokremnos in Cyprus (*V. lebetina*; Bailon, 1999). These fossil sites are located in the areas where Oriental vipers (*V. xanthina* and *V. lebetina*, respectively) have survived until today.

The oldest African viperids come from the lower Miocene (equivalent to the European biozone MN 3 or MN 4) of Arrisdrift, Namibia, and are represented by vertebrae from two taxa. One taxon is *Bitis* sp., a typical African genus, but unfortunately, it is not possible to determine whether the other is a species of *Daboia* or of the Oriental complex of *Vipera* (Rage, in press). Today, Oriental vipers in Africa are restricted to the northernmost region of the continent, and *Daboia* is found in Asia.

A younger African viper, *V. maghrebiana*, comes from the middle Miocene of Beni Mellal in Morocco (Rage, 1976). This extinct species is represented by a maxilla and trunk vertebrae, and belongs to the *aspis* complex. All but one of the remaining African fossils have been found in several latest Pliocene or lowermost Pleistocene localities, including another extinct species, *B. olduvaiensis* from Olduvai in Tanzania (Rage, 1973), and vertebrae identified as *Bitis* and *Cerastes* from other Tanzanian and Moroccan sites (Meylan, 1987; Bailon, 2000; J.-C. Rage, unpublished). Additionally, a fragmentary vertebra probably belonging to *Causus* was reported from the late Pleistocene of Egypt (Szyndlar, 1993).

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APPENDIX I

Neogene (Miocene and Pliocene) localities of the Viperinae.

Fossil localities are arranged separately for each country, from the geologically oldest to the youngest. "MN" biozonation is employed exclusively for Europe and adjacent areas and follows Mein (1999). Fossil localities are shown on the maps (Figs. 1–2). Symbols introduced below for each locality (AT-1, etc.) are concordant with those employed in Appendix II and on maps.

EUROPE

Austria

- AT-1: lower Miocene (MN 4), Oberdorf;
- AT-2: late Miocene (MN 11), Kohfidisch;
- AT-3: late Pliocene (MN 16), Bad Deutsch Altenburg 20.

Czechia

- CS-1: lower Miocene (MN 4), Dolnice.

France

- FR-1: lowermost Miocene (MN 1 and / or 2), Saint-Gérard-le-Puy complex;
- FR-2: lower Miocene (MN 2), Marcoin;
- FR-3: lower Miocene (MN 2), Laugnac;
- FR-4: lower Miocene (MN 2), Bouzigues;
- FR-5: lower Miocene (MN 3), Serre de Verges;
- FR-6: lower Miocene (MN 4), Artenay;
- FR-7: lower Miocene (MN 4), Bezian;
- FR-8: lower Miocene (MN 4), Montréal-du-Gers;
- FR-9: lower Miocene (MN 4), Suèvres;
- FR-10: lower/middle Miocene (MN 4/5), Vieux Collonges;
- FR-11: middle Miocene (MN 5), Pontigné;
- FR-12: middle Miocene (MN 7-8), Isle d'Abeau;
- FR-13: middle Miocene (MN ?6), Baume Bonne;
- FR-14: middle Miocene (MN 6), Sansan;
- FR-15: middle Miocene (MN 7-8), La Grive;
- FR-16: middle Pliocene (MN 15), Sète;
- FR-17: late Pliocene (MN 16), Balaruc II;
- FR-18: ?late Pliocene, Mas Gégégals;
- FR-19: ?late Pliocene, Vallée de la Canterrane;
- FR-20: latest Pliocene (MN 17), Montoussé 5.

Germany

- DE-1: lowermost Miocene (MN 1), Hessler;
- DE-2: lowermost Miocene (MN 1), Weisenau;
- DE-3: lower Miocene (MN 3), Stubersheim 3;
- DE-4: lower Miocene (MN 4), Petersbuch 2;
- DE-5: lower Miocene (MN 4), Langenau;
- DE-6: middle Miocene (MN ?5), Schiessen;
- DE-7: middle Miocene (MN 5/6), Randecker Maar;
- DE-8: middle Miocene (MN 5/6), Edelbeuren-Mauerkopf;
- DE-9: middle Miocene (MN 6), Sandelzhausen;
- DE-10: middle Miocene (MN 6), Petersbuch 39;
- DE-11: middle Miocene (MN 7-8), Öhningen (= Oeningen);
- DE-12: middle Miocene (MN 7-8), Steinheim am Albuch.

Greece

GR-1: latest Miocene or lowermost Pliocene (MN 13 or 14), Karabournu;

GR-2: latest Miocene or lowermost Pliocene (MN 13 or 14), Maramena;

GR-3: late Pliocene (MN 16), Tourkobounia 1.

Hungary

HU-1: middle Miocene (MN 6 or 7-8), Mátraszőlős;

HU-2: late Miocene (MN 9), Rudabánya;

HU-3: late Miocene (MN 12), Tardosbánya;

HU-4: latest Miocene (MN 13), Polgárdi (2, 4, 5);

HU-5: lowermost Pliocene (MN 14), Osztramos 1.

Italy

IT-1: late Miocene (MN 13), Cava Passalacqua;

IT-2: lower Pliocene (MN 14), Mandriola (Sardinia).

Moldova

MO-1: late Miocene (MN 9b), Buzhor (= Bujor);

MO-2: late Miocene (MN 9b), Kalfa;

MO-3: middle Pliocene (MN ?15), Etuliya;

MO-4: middle Pliocene (MN ?15), Musait;

MO-5: late Pliocene (MN ?16), Novye Tanatary;

MO-6: late Pliocene (MN ?16), Chishmikiyoy.

Poland

PL-1: middle Miocene (MN 7-8), Opole;

PL-2: lower Pliocene (MN 14), Podlesice;

PL-3: middle Pliocene (MN 15), Weże 1;

PL-4: late Pliocene (MN 16), Rębielice Królewskie 1A;

PL-5: late Pliocene (MN 16), Rębielice Królewskie 2;

PL-6: latest Pliocene (MN 17), Kadzielnia.

Portugal

PT-1: lower Miocene (MN 4), Quinta das Pedreiras (Lisboa).

Russia

RU-1: middle Miocene (MN 5), Belomechetskaya (Precaucasus);

RU-2: middle Pliocene (MN 15), Obukhovsky (lower layer);

RU-3: late Pliocene, Korotoyak.

Slovakia

SK-1: middle Miocene (MN 6), Děvínska Nová Ves (= Neudorf a.d. March).

Spain

ES-1: lower Miocene (MN 4), Agramon;

ES-2: lower Miocene (MN 4b), Córcoles;

ES-3: middle/late Miocene, San Quirze de Galliners;

ES-4: middle/late Miocene, Hostalets de Pierola;

ES-5: latest Miocene (MN 13), Algora;

ES-6: lower Pliocene (MN ?14), Vilafant;

ES-7: middle Pliocene (MN 15), Layna;

ES-8: middle/late Pliocene (MN 15/16), Zújar;

ES-9: latest Pliocene (MN 17), Medas;

ES-10: latest Pliocene (MN 17), Cova Bonica;

ES-11: latest Pliocene (MN 17), Las Higuieruelas.

Ukraine

- UA-1: late Miocene (MN 9a), Gritsev;
- UA-2: late Miocene (MN 9a), Klimentovichi;
- UA-3: late Miocene (MN 11a), Krivoy Rog;
- UA-4: late Miocene (MN 11b), Novoelizabetovka (lower layer);
- UA-5: late Miocene (MN 12a), Novaya Emetovka-2;
- UA-6: late Miocene (MN 12a), Cherevichnoie (lower layer);
- UA-7: late Miocene (MN 12a), Novoelizabetovka-2;
- UA-8: latest Miocene (MN 13), Novoukrainka-1;
- UA-9: latest Miocene (MN 13), Andreevka;
- UA-10: latest Miocene (MN 13), Orekhovka;
- UA-11: lower Pliocene (MN 14), Frunzovka-2;
- UA-12: lower Pliocene (MN 14), Kuchurgan;
- UA-13: middle Pliocene (MN 15), Vinogradovka;
- UA-14: middle Pliocene (MN 15), Kotlovina (lower layer);
- UA-15: late Pliocene (MN 16), Kotlovina (middle/upper layer);
- UA-16: latest Pliocene (MN 17), Tiligul (= Morskoi);
- UA-17: latest Pliocene (MN 17), Zhevakhova Gora;
- UA-18: latest Pliocene (MN 17), Kryzhanovka (upper layer);
- UA-19: latest Pliocene (MN 17), Tarkhankut;
- UA-20: latest Pliocene (MN 17), Nogaisk;
- UA-21: latest Pliocene (MN 17), Cherevichnoie (upper layer);
- UA-22: latest Pliocene (MN 17), Bolshevik-2;
- UA-23: latest Pliocene (MN 17), Tikhonovka 1 & 2.

ASIA

Georgia

GEO-1: late Miocene, Rustavi.

Kazakhstan

KZ-1: lower Miocene, Zaisan;

KZ-2: middle Miocene, Zaisan.

Saudi Arabia

SA-1: lower Miocene, Al-Sarrar.

Thailand

TF-1: lower Miocene, Li Mae Long.

Turkey

TR-1: late Miocene (MN 9/10), Sinap 84;

TR-2: late Miocene (MN 10/11), Kuçuk.

AFRICA

Morocco

MA-1: middle Miocene (MN 7-8), Beni Mellal;

MA-2: latest Pliocene, Ahl al Oughlam;

MA-3: Pliocene/Pleistocene boundary, Irhoud Ocre.

Namibia

NA-1: lower Miocene, Arrisdrift.

Tanzania

TZ-1: Pliocene, Laetoli;

TZ-2: latest Pliocene/Pleistocene, Olduvai.

APPENDIX II

Neogene (Miocene and Pliocene) remains of the Viperinae.

The fossils listed below are arranged separately for each taxonomic group, from the geologically oldest to the youngest. The following information is given for particular fossil remains: abbreviation showing the geological age and geographical location of the fossil site (see Appendix I); original systematic allocation of the remains (literal spelling), accompanied by appropriate references; recent systematic allocation (if different) followed with references. For detailed information on fossil species, see Appendix III.

Bitis

NA-1: *Bitis* sp.-Rage (in press).

MA-2: *Bitis* sp.-Bailon (2000:553).

TZ-1: *Bitis arietans* or *Bitis olduvaiensis*-Meylan (1987:81).

TZ-2: *Bitis olduvaiensis* Rage, 1973 (p. 5, Fig. 1, pl. 1:5–15); see Appendix III.

Cerastes

MA-3: *Cerastes* sp.-J.-C. Rage (unpublished).

Daboia (sensu stricto)

ES-6: *Vipera maxima* Szyndlar, 1988 (p. 698, Figs 6-7); *Daboia maxima*-Szyndlar and Rage (1999:15); see Appendix III.

Daboia or Vipera

NA-1: ? *Daboia* sp. or ? *Vipera* sp. (Oriental viper)-Rage (in press).

Vipera aspis complex**lower Miocene**

DE-1: *Vipera* cf. *V. antiqua*-Szyndlar and Böhme (1993: Appendix, Fig. 6).

FR-1: “Vipères”-Hoffstetter (1955: 659); *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1, Fig. 7:1–6).

FR-2: *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1, Fig. 7:10).

FR-3: *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1).

FR-4: *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1).

FR-5: *Vipera* (*V. aspis* complex)-J.-C. Rage (unpublished).

DE-3: *Vipera* sp.-Szyndlar and Böhme (1993: Appendix).

AT-1: *Vipera* sp.-Szyndlar (1998:36, Fig. 4 e–f).

CS-1: *Vipera antiqua* -Szyndlar (1987a:68, Fig. 11); see Appendix III.

FR-6: *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1).

FR-7: *Vipera* (*V. aspis* complex or Oriental viper)-J.-C. Rage (unpublished).

DE-4: *Vipera antiqua*-Szyndlar and Schleich (1993:31, Fig. 9).

DE-5: *Vipera* sp.-Szyndlar and Böhme (1993: Appendix).

ES-1: *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1, Fig. 7:10).

FR-10: *Vipera* (*Vipera aspis* complex)-Szyndlar and Rage (1999: Table 1).

middle Miocene

DE-7: *Vipera* sp.-Szyndlar and Böhme (1993: Appendix).

DE-9: *Vipera* sp.-Szyndlar and Böhme (1993: Appendix).

SK-1: *Vipera* sp. (*aspis* group)-Szyndlar (1991:250).

FR-15: *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1, Fig. 7:11–17).

DE-12: *Vipera* sp.-Szyndlar and Böhme (1993: Appendix); *Vipera* (*V. aspis* complex)-Szyndlar and Rage (1999: Table 1, Fig. 7:18–22).

PL-1: Viperidae subfam., gen. et sp. indet.-Szyndlar (in Mlynarski et al. 1982:117, Fig. 11).

MA-1: *Vipera maghrebiana* Rage, 1976 (p. 64, Figs 7–8, pl. 14); see Appendix III.

late Miocene

HU-2: *Vipera* sp. (*aspis* group)-Szyndlar (in press a).

UA-2: “medium-sized vipers”-Zerova (1993:274).

UA-3: *Vipera* (*Vipera*) sp.-Zerova (1993:276).

UA-6: *Vipera* (*Vipera*) *meotica* Zerova, 1992 (in Szyndlar and Zerova: p. 94, Figs. 19–24); see Appendix III.

HU-4: *Vipera* cf. *aspis*-von Szunyoghy (1932:52); *Vipera* cf. ?*ammodytes* (= *V. Gedulyi*, part.) -von Szunyoghy (1932:53); *Vipera* sp. 2-Venczel (1994:26, Fig. 13 f–g).

ES-5: Viperidae indet.-Szyndlar (1985:462, Fig. 10).

UA-10: *Vipera* (*Vipera*) cf. *V. meotica* sp.-Zerova (1993:277).

lower and middle Pliocene

HU-5: *Vipera* cf. *ammodytes*-Venczel (2001).

PL-2: Viperidae indet. (form “B”)-Szyndlar (1984:51, Fig. 18:3–4).

PL-3: Viperidae gen. non det.-Mlynarski (1961:13); *Vipera ammodytes*-Szyndlar (1984:82, Fig. 31).

RU-2: *Vipera* (*Vipera*) sp.-Zerova (1993:277).

ES-7: “a small member of the genus *Vipera*”-Szyndlar (1988:688).

UA-14: *Vipera* (*Vipera*) sp. -Zerova (1993:277).

ES-8: *Vipera* sp. (groupe *aspis*) -Bailon (1991:31).

late and latest Pliocene

PL-4: Viperidae indet.-Mlynarski (1964:343); *Vipera ammodytes*-Szyndlar (1984:82).

PL-5: *Vipera ammodytes*-Szyndlar (1984:82, Fig. 32).

FR-18: *Vipera* sp. (groupe *aspis*)-Bailon (1991:31).

FR-20: *Vipera* sp. (groupe *aspis*)-Bailon (1991:31).

ES-9: *Vipera* sp. (groupe *aspis*)-Bailon (1991:31).

ES-11: *Vipera* sp. (*aspis* complex)-Szyndlar (in press b).

Vipera “Oriental vipers”

lower Miocene

CS-1: *Vipera platyspondyla* Szyndlar, 1987a (p. 67, Fig. 10); see Appendix III.

FR-6: *Vipera* (Oriental vipers)-Szyndlar and Rage (1999: Table 2, Fig. 8:4–8).

FR-8: *Vipera* (Oriental viper)-J.-C. Rage (unpublished).

FR-9: *Vipera* (Oriental viper)-J.-C. Rage (unpublished).

DE-4: *Vipera platyspondyla*-Szyndlar and Schleich (1993:35, Fig. 10).

DE-5: *Vipera* sp.-Szyndlar and Böhme (1993: Appendix); *Vipera* (Oriental vipers)-Szyndlar and Rage (1999: Table 2, Fig. 8:1–3).

PT-1: Viperidae-Antunes and Rage (1974:56, Fig. 4); *Vipera* sp. (Oriental vipers complex)-Szyndlar (2000:313).

FR-10: *Vipera* (Oriental vipers) or *Daboia*-Szyndlar and Rage (1999:14, Fig. 9).

middle Miocene

FR-12: *Vipera* (Oriental viper)-J.-C. Rage (unpublished).

DE-6: *Vipera* (Oriental viper)-Z. Szyndlar (unpublished).

RU-1: *Vipera* (*Daboia*) sp.-Zerova (1992:246).

DE-8: *Vipera* (Oriental viper)-Z. Szyndlar (unpublished).

FR-13: *Vipera* (Oriental viper)-S. Bailon (unpublished).

FR-14: *Vipera aegertica* Augé et Rage, 2000 (p. 303, Figs 29–30); see Appendix III.

DE-10: *Vipera* (Oriental viper)-Z. Szyndlar (unpublished).

FR-15: *Vipera* (Oriental vipers) -Szyndlar and Rage (1999: Table 2, Fig. 8:15–20).

DE-12: *Vipera* sp.-Szyndlar and Böhme (1993: Appendix); *Vipera* (Oriental vipers)-Szyndlar and Rage (1999: Table 2, Fig. 8:9–14).

late Miocene

HU-2: *Vipera* sp. (Oriental viper)-Szyndlar (in press a).

- HU-3: *Macrovipera*-M. Venczel (unpublished).
 MO-2: *Vipera sarmatica* Chkhikvadze et Lungu, 1987 (in Zerova et al. 1987:92, Fig. 2, pl. 5: a–e); see Appendix III.
 UA-1: *Vipera (Daboia) ukrainica* Zerova, 1992 (p. 236, 1–10); see Appendix III.
 TR-1: “fragments of a large viper”-J.-C. Rage (unpublished).
 AT-2: *Vipera* sp. (= *Daboia* sp.-Bachmayer and Szyndlar (1985:96, Fig. 6); *Vipera burgenlandica* Bachmayer and Szyndlar, 1987 (p. 33, Figs 5–6, pl. 1:5-6); see Appendix III.
 UA-4: *Vipera* sp. (*aspis* group)-Szyndlar (1991:250); *Vipera (Macrovipera)* sp.-Zerova (1993:276).
 GEO-1: *Vipera* sp.-Zerova et al. (1987: 97, pl. 6:e); *Vipera (Daboia)* sp.-Zerova (1992: 246); “(...) actually may have belonged to the Boidae rather than to the Viperidae”-Szyndlar and Rage (1999:18).
 HU-4: *Vipera Gedulyi* Bolkay, 1913 (p. 201, Fig. 4, pl. 12:9–12); *Vipera gedulyi*-Venczel (1994:19, Figs 9–12, 13a–d); see Appendix III.
 HU-4: *Vipera* sp. 1-Venczel (1994:26, Fig 13e).
 IT-1: *Vipera* sp. (Oriental vipers group-M. Delfino and Z. Szyndlar (unpublished).
 GR-2: *Vipera* sp.-Szyndlar (1995:42, Fig. 1j).

Pliocene

- ES-6: *Vipera* sp.-Szyndlar (1987b: Fig. 2).
 UA-11: *Vipera* sp. (Oriental vipers)-Szyndlar (1991:247).
 UA-12: *Vipera kuchurganica* Zerova, 1987 (in Zerova et al. 1987:95, Fig. 3, pl. 6: a–d); see Appendix III.
 FR-17: cf. *Vipera*-Bailon (1989:23, Fig. 7c–f); *Vipera* sp. (groupe *xanthina*)-Bailon (1991:31).
 GR-3: *Vipera* sp. (Oriental vipers)-Szyndlar (1991:247, Fig. 13).
 FR-19: *Vipera* sp. (groupe *lebetina*)-Bailon (1991:31, Fig. 86).
 ES-10: *Vipera* sp. (groupe *xanthina*)-Bailon (1991:31, Fig. 87).
 MA-2: *Macrovipera* sp.-Bailon (2000:551, Fig. 8).
 MA-3: *Vipera* (? Oriental viper)-J.-C. Rage (unpublished).

***Vipera berus* complex**

late Miocene

- UA-1: *Pelias* cf. *berus*-Zerova (1987:130); *Vipera* sp. (*berus* group)-Szyndlar (1991:251).
 HU-3: *Vipera (ursinii-like viper)*-M. Venczel (unpublished).
 UA-4: *Vipera (Pelias)* sp.-Zerova (1993:276).
 UA-5: *Vipera (Pelias)* sp.-Zerova (1993:276).
 UA-8: *Vipera (Pelias)* sp.-Zerova (1993:276).
 UA-9: *Vipera (Pelias)* sp.-Zerova (1993:276).

lower and middle Pliocene

- HU-5: *Vipera* cf. *berus*-Venczel (2001).
 UA-11: *Vipera (Pelias)* sp.-Zerova (1993:277).
 RU-2: *Vipera (Pelias)* sp.-Zerova (1993:277).
 UA-13: *Vipera (Pelias)* sp.-Zerova (1993:277).
 UA-14: “*Vipera (Pelias)* sp. comparable in size with small steppe-viper *Vipera (Pelias) ursini*”-Zerova (1993: 277).

late and latest Pliocene

- AT-3: *Vipera* sp. (*berus* group)-Szyndlar (1991:251).
 GR-3: *Vipera* sp. (*berus* group)-Szyndlar (1991:251).
 UA-15: “*Vipera (Pelias)* sp. compatible in size and morphology with that of *V. (P.) berus*”-Zerova (1993:277).
 FR-20: *Vipera* sp. (groupe *berus*)-Bailon (1991:31).
 PL-6: Viperidae indet.-Mlynarski (1961:16); *Vipera berus*-Szyndlar (1984: Table XX).
 ES-11: *Vipera* sp. (*berus* complex)-Szyndlar (in press b).
 UA-16: “trunk vertebrae of *Vipera (Pelias)* sp. similar to *V. (P.) berus* and/or *V. (P.) ursini*”-Zerova (1993:277).
 UA-17: *Vipera (Pelias)* sp.-Zerova (1993:277).
 UA-18: *Vipera (Pelias)* sp.-Zerova (1993:278).

- UA-19: “trunk vertebrae of *Vipera (Pelias)* sp. close to *V. (P.) berus* and/or *V. (P.) ursini*”-Zerova (1993:278).
 UA-20: *Vipera (Pelias)* sp.-Zerova (1993:278).
 UA-21: *Vipera (Pelias)* sp.-Zerova (1993:278).
 UA-22: *Vipera (Pelias)* sp.-Zerova (1993:278).
 UA-23: *Vipera (Pelias)* cf. *V. ursini*-Zerova (1993:278).

Vipera (status unknown or uncertain)

lower and middle Miocene

- ES-2: ?Viperidae-Szyndlar (1985:463).
 FR-11: *Vipera* sp.-J.-C. Rage (unpublished).
 SK-1: *Vipera* sp. (status uncertain)-Szyndlar (1991:251).
 HU-1: Viperidae indet.-M. Venczel (unpublished).
 ES-3: *Vipera* sp.-Crusafont Pairó and de Villalta (1952:215).
 ES-4: *Vipera* sp.-Crusafont Pairó and de Villalta (1952:217).

late Miocene

- MO-1: Viperidae-Chkhikvadze and Lungu (1973:84).
 TR-2: “vipers”-J.-C. Rage (unpublished).

Pliocene

- IT-2: Viperidae (cf. *Vipera*)-Pecorini et al. (1974:313).
 FR-16: *Vipera* sp.-Bailon (1991:31).
 MO-3: *Vipera*-Redkozubov (1987:71)
 MO-4: *Vipera*-Redkozubov (1987:71)
 MO-5: *Vipera*-Redkozubov (1987:71)
 MO-6: *Vipera*-Redkozubov (1987:71)
 RU-3: Viperidae-Ratnikov (1996:79).

Remaining Viperidae

- KZ-1: “*Pelias* (a small species)” and “much larger viper of the size of *Vipera xanthina*”-Chkhikvadze (1985:234).
 KZ-2: *Pelias* sp.-Chkhikvadze (1985:234).
 Remark: The above finds “may also be presumably attributed to the subfamily Crotalinae” (Chkhikvadze in Zerova, 1992:246).
 SA-1: Viperidae indet.-Rage (1982:117).
 TF-1: [unidentified] Viperidae-Rage and Ginsburg (1997:168).

Non-Viperidae: Erroneous reports

Piveteau (1927:94, pl. 9:5–6) reported a complete specimen in matrix coming from a lower Pliocene Spanish locality as belonging to *Bitis*. According to Hoffstetter (in Marx and Rabb 1965:182): “this fossil snake is a member of the family Colubridae, having a ‘maxillaire supérieur de type Colubridé’.”

Szyndlar and Böhme (1993: Appendix), followed by Szyndlar and Rage (1999: Table 1), reported remains of *Vipera* sp. (*V. aspis* complex) from the middle Miocene (MN 5/6) of Oggenhausen in Germany; actually, the material from Oggenhausen does not contain any viperid remains.

Szyndlar and Rage (1997:204) announced presumed presence of *Vipera berus*-like snakes in the lower Miocene of France and Germany. This supposition, however, was based on two badly damaged vertebrae that actually are from non-vipers (Szyndlar and Rage, 1999:16).

APPENDIX III

Extinct Species of Viperinae.

The following list, describing members of the Viperinae and presumed Viperinae, is an extended supplement to the list of fossil venomous snakes included by Rage in Golay et al. (1993). Synonyms accompanying particular species include name changes and new taxonomic combinations. All papers containing original illustrations of fossil remains are included.

Bitis olduvaiensis Rage, 1973

Bitis olduvaiensis Rage, 1973 (p. 5, Fig. 1, pl. 1:5–15)

Bitis olduvaiensis† -Rage in Golay et al. (1993:263)

Type locality: Olduvai (Rift Valley), Tanzania; latest Pliocene / Pleistocene.

Type: A maxilla (National Museum Dar es Salaam, Tanzania, uncatalogued). Referred material: Another maxilla and several vertebrae.

Range: Possibly also present (vertebrae and a fang reported as “*Bitis arietans* or *Bitis olduvaiensis*”) in the Pliocene of Laetoli (Tanzania) (Meylan, 1987:81).

“*Coluber*” *kargii* von Meyer, 1845

Coluber Kargii von Meyer, 1845 (p. 41, pl. 6:2)

Echidna Kargii-de Rochebrune (1880:292)

Vipera kargii-Kuhn (1971:22)

“*Coluber*” *kargii*-Szyndlar (1992:692)

Vipera kargii† -Rage in Golay et al. (1993:285)

Type locality: Öhningen (= Oeningen), Germany; middle Miocene (MN 7-8).

Type: An imprint of a nearly complete skeleton and its counterpart (Paläontologisches Institut und Museum der Universität Zürich, A/III 163 and A/III).

Range: Known only from the type locality.

Remarks: The fossil was first reported (as a “Natter”) by Karg (1805:30, pl. 2:2); Karg’s description was the first report of any ophidian fossil worldwide. Szyndlar (1992) redescribed the snake, considering it a *nomen dubium*; the fossil may have represented a juvenile of an Oriental viper.

Daboia maxima (Szyndlar, 1988)

Vipera maxima Szyndlar, 1988 (p. 698, Figs 6–7)

Daboia? maxima† -Rage in Golay et al. (1993:267)

Daboia maxima-Szyndlar and Rage (1999:15)

Type locality: Layna, Spain; middle Pliocene (MN 15).

Type: A trunk vertebra (Museo Nacional de Ciencias Naturales, Madrid, 10032). Referred material: 19 vertebrae.

Range: Known only from the type locality.

Remarks: The largest known viperine species. Considered a close relative of the living *Daboia russelii*, based on the peculiar morphology of the posterior trunk portion of the vertebral column (Szyndlar, 1988).

Laophis crotaloides Owen, 1857

Laophis crotaloïdes Owen, 1857 (p. 199, pl. 4:2–3)

Laophis crotaloides† -Rage in Golay et al. (1993:273)

Type locality: Karabournu, Greece; latest Miocene or lowermost Pliocene (MN 13 or 14).

Type: 13 vertebrae (lost).

Range: Known only from the type locality.

Remarks: Its taxonomic status remains uncertain. Rage (1984:58) considered *Laophis crotaloides* a *nomen dubium*.

See Szyndlar (1991:224) for discussion on the morphology of *Laophis* and its possible taxonomic allocation.

Provipera boettgeri Kinkelin, 1892*Provipera Boettgeri* Kinkelin, 1892 (p. 94)*Provipera boettgeri*-Kinkelin (1896:40, Fig. on p. 39)*Provipera boettgeri*† -Rage in Golay et al. (1993:276)

Type locality: Hessler, Germany; lowermost Miocene (MN 1).

Type: An isolated fang (Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt am Main, 4186)

Range: Known only from the type locality.

Remarks: Kinkelin (1892) erected a new genus and species but at the same time stated that it is impossible to identify the fossil to the subfamilial level (“Ob der Zahn einer *Viperine* oder *Crotaline* angehört, ist nicht festzustellen”). The identification, based on a single venomous fang only, was strongly criticized by Cope (1892:224). Nevertheless, in a later paper, Kinkelin (1896) considered the fossil a member of the Crotalinae. Rage (1984:58) considered this species a *nomen dubium*.

Vipera aegertica Augé et Rage, 2000*Vipera aegertica* Augé et Rage, 2000 (p. 303, Figs 29–30)

Type locality: Sansan, France; middle Miocene (MN 6).

Type: A trunk vertebra (Institut de paléontologie du Muséum national d’Histoire naturelle, Paris, Sa 23714).

Referred material: 20 vertebrae.

Range: Known only from the type locality.

Remarks: Considered (with some doubts) an Oriental viper (Augé and Rage, 2000).

Vipera antiqua Szyndlar, 1987*Vipera antiqua* Szyndlar, 1987a (p. 68, Fig. 11)*Vipera antiqua*-Szyndlar and Böhme (1993: Fig. 6)*Vipera antiqua*† -Rage in Golay et al. (1993:279)

Type locality: Dolnice, Czechia; lower Miocene (MN 4).

Type: A trunk vertebra (Department of Paleontology of Charles University, Prague, 4538). Referred material: Five vertebrae.

Range: Reported also (only vertebrae) from two German lower Miocene localities, Petersbuch 2 (MN 4)

(Szyndlar and Schleich, 1993:31, Fig. 9) and Weisenau (MN 1) (Szyndlar and Böhme, 1993: Appendix, Fig. 6).

The latter (originally reported as “*Vipera* cf. *V. antiqua*”) is the oldest known member of the genus *Vipera*.Remarks: Originally considered a member of the *aspis* complex (Szyndlar, 1987a).***Vipera burgenlandica*** Bachmayer et Szyndlar, 1987*Vipera* sp. (= *Daboia* sp.)-Bachmayer and Szyndlar (1985:96, Fig. 6)*Vipera burgenlandica* Bachmayer et Szyndlar (1987:33, Figs 5–6, pl. 1:5–6)*Vipera burgenlandica*-Szyndlar (1991:246, Fig. 11)*Macrovipera? burgenlandica*† -Rage in Golay et al. (1993:273)

Type locality: Kohfidisch, Austria; late Miocene (MN 11).

Type: A basiparasphenoid (Naturhistorisches Museum, Geologisch-Paläont. Abteilung, Wien, 1986/3). Referred material: Another basiparasphenoid, a maxilla, a compound bone, a dentary, a basioccipital, 71 vertebrae.

Range: Known only from the type locality.

Remarks: Considered an Oriental viper (Bachmayer and Szyndlar, 1987).

Vipera gedulyi Bolokay, 1913*Vipera Gedulyi* Bolokay, 1913 (p. 201, Fig. 4, pl. 12:9–12)*Vipera Gedulyi*-von Szunyoghy (1932:50, Fig. 116)*Macrovipera? gedulyi*† -Rage in Golay et al. (1993:274)*Vipera gedulyi*-Venczel (1994:19, Figs 9–12, 13a–d)*Macrovipera gedulyi*-Venczel (1998a:19, Fig. 12)

Type locality: Polgárdi 2, Hungary; latest Miocene (MN 13).

Type (syntypes): 15 basiparasphenoids, 2 frontals, 6 prefrontals, 2 parietals, a prootic, an exoccipital, 8 basioccipitals, 19 maxillae, 206 isolated fangs, 25 compound bones, 30 ectopterygoids (Museum of the Hungarian Geological Institute, Budapest, Ob-4467/Vt.74). Referred material (Polgárdi complex): A basiparasphenoid, a frontal, a prefrontal, a prootic, 2 exoccipitals, a basioccipital, a maxilla, 6 compound bones, an ectopterygoid, 2 pterygoids, a palatine, 3 dentaries, 1430 vertebrae.

Range: Reported from several localities belonging to the Polgárdi complex (2, 4 “lower”, 4 “upper”, and 5), all of latest Miocene age (Venczel, 1994, 1998a).

Remarks: Kormos (1911:63 and 187) reported the presence of *Bitis* from Polgárdi, but it was never confirmed (nor mentioned) by later students of the herpetofauna of Polgárdi. The Kormos’ report may have been based on remains belonging to *Vipera gedulyi*. Bolkay (1913) and subsequent authors considered *V. gedulyi* a close relative of the extant *V. ammodytes*. Szyndlar (1988:702) observed that *V. gedulyi* is clearly referable to the Oriental vipers. The remains of *V. gedulyi* represent the most abundant and complete fossil material of the Viperinae, although the original description by Bolkay illustrates only four cranial bones. See Venczel (1994, 1998a) for detailed redescription of the species.

Vipera kuchurganica Zerova, 1987

Vipera kuchurganica Zerova, 1987 (in Zerova et al. 1987:95, Fig. 3, pl. 6:a–d)

Vipera kuchurganica Szyndlar (1991:247, Fig. 12)

Macrovipera? kuchurganica -Rage in Golay et al. (1993:274)

Vipera (Macrovipera) kuchurganica Zerova (1993:277)

Type locality: Kuchurgan, the Ukraine; lowermost Pliocene (MN 14).

Type: A trunk vertebra (Institute of Zoology of the Ukrainian Academy of Sciences, Kiev, 37-2536). Referred material: 2 vertebrae.

Range: Known only from the type locality.

Remarks: Originally considered a close relative of the extant *Vipera lebetina* (Zerova in Zerova et al., 1987).

Vipera maghrebiana Rage, 1976

Vipera maghrebiana Rage, 1976 (p. 64, Figs 7–8, pl.14)

Vipera maghrebiana† -Rage in Golay et al. (1993:286)

Type locality: Beni Mellal, Morocco; middle Miocene (MN 7–8).

Type: A maxilla (Institut de paléontologie du Muséum national d’Histoire naturelle, Paris, BML 905). Referred material: 7 vertebrae.

Range: Known only from the type locality.

Remarks: Rage (1976:65) noted “Par son maxillaire *V. maghrebiana* rappelle surtout *V. lebetina*...” Szyndlar (1988:704), based on the vertebral morphology, observed, “...this snake closely resembles smaller members of the genus *Vipera* (European vipers).”

Vipera meotica Zerova, 1992

Vipera (Vipera) meotica Zerova, 1992 (in Szyndlar and Zerova: p. 94, Figs. 19–24)

Vipera meotica† -Rage in Golay et al. (1993:287)

Type locality: Cherevichnoie (lower layer), the Ukraine; late Miocene (MN 12a).

Type: A basiparasphenoid (Institute of Zoology of the Ukrainian Academy of Sciences, Kiev, 45-5023).

Referred material: 18 vertebrae.

Range: Known only from the type locality.

Remarks: Considered a member of the subgenus *Vipera* of the genus *Vipera* (i.e., a member of the *aspis* complex) (Zerova, in Szyndlar and Zerova, 1992).

Vipera platyspondyla Szyndlar, 1987

Vipera platyspondyla Szyndlar, 1987a (p. 67, Fig. 10)

Vipera platyspondyla† -Rage in Golay et al. (1993:288)

Type locality: Dolnice, Czechia; lower Miocene (MN 4).

Type: A trunk vertebra (Department of Paleontology of Charles University, Prague, 940). Referred material: Seven vertebrae.

Range: Reported also (vertebrae and fangs) from the lower Miocene (MN 4) of Petersbuch 2 in Germany (Szyndlar and Schleich, 1993:35, Fig. 10).

Remarks: Originally considered an “Oriental viper” (Szyndlar, 1987a).

Vipera sansaniensis Lartet, 1851

Vipera? *Sansaniensis* Lartet, 1851 (p. 41)

Type locality: Sansan, France; middle Miocene (MN 6).

Type: fangs (lost).

Range: Known only from the type locality.

Remarks: Lartet (1851:41) described the species with some doubts (“avec réserve”). Rage (1984:60) considered *Vipera sansaniensis* a *nomen nudum*.

Vipera sarmatica Chkhikvadze et Lungu, 1987

Vipera sarmatica Chkhikvadze et Lungu, 1987 (in Zerova et al. 1987:92, Fig. 2, pl. 5:a–e)

Vipera sarmatica Chkhikvadze et Lungu, 1989 (in Lungu et al. 1989:64, Fig. 3)

Macrovipera? *sarmatica*† -Rage in Golay et al. (1993:276)

Vipera (Macrovipera) sarmatica) Zerova (1993:276)

Type locality: Kalfa, Moldova; late Miocene (MN 9b).

Type: A trunk vertebra (Tiraspol State Pedagogical Institute, 18/72-1). Referred material: 24 vertebrae.

Range: Known only from the type locality.

Remarks: *Vipera sarmatica* was described as a new species [sic] in two different papers (Zerova et al. 1987; Lungu et al. 1989). The snake belongs to the group of Oriental vipers (Szyndlar, 1991:246).

Vipera ukrainica Zerova, 1992

Vipera (Daboia) ukrainica Zerova, 1992 (p. 236, 1–10)

Vipera ukrainica† -Rage in Golay et al. (1993:289)

Vipera (Macrovipera) ukrainica)-Zerova (1993:276)

Type locality: Gritsev, the Ukraine; late Miocene (MN 9a).

Type: A maxilla (Institute of Zoology of the Ukrainian Academy of Sciences, Kiev, 22-1786). Referred material: 8 maxillae, an ectopterygoid, 3 basioccipitals, 8 compound bones, 5 dentaries, >100 vertebrae.

Range: Known only from the type locality.

Remarks: Considered a member of the subgenus *Daboia* of the genus *Vipera* (i.e., an Oriental viper) (Zerova, 1992).

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