The first European pit viper from the Miocene of Ukraine

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The first discoveries of European pit vipers (Crotalinae gen. et sp. indet. A and B) are reported from the Ukrainian Miocene (MN 9a) locality of Gritsev. Based on perfectly preserved maxillaries, two species closely related to pit vipers of the '*Agkistrodon*' complex are represented at the site. It is suggested that the European fossil representatives of the '*Agkistrodon*' complex are Asiatic immigrants. Pit vipers probably never expanded into the broader areas of Europe during their geological history.

Key words: Snakes, Crotalinae, migrations, Miocene, Ukraine.

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Introduction

Gritsev is located in the western part of Ukraine, in the Khmelnitsk area, Shepetovski district. The locality contains karstic fillings within a limestone quarry on the right bank of the Khomora river, less than 5 km west of the village of Gritsev. The stratigraphic age of the site corresponds to the Upper Miocene (lower – 'novomoskevski' – horizon of the Middle Sarmatian, MN 9a Mammal Neogene faunal zone). This locality corresponds to the Kalfinsky Formation ('Kalfinsky faunistic complex') and to the Gritsev layers ('Gritsev faunistic complex'). Fossil reptiles from Gritsev have already been investigated. Thus far, Agamidae, Gekkonidae, Lacertidae, Anguidae, Scincidae, ?Amphisbaenia, Boidae (subfamily Erycinae), Colubridae, Elapidae and Viperidae have been reported (Lungu *et al.* 1989; Szyndlar & Zerova 1990; Zerova 1987, 1989, 1992). Gritsev (Fig. 1) is one of the many Ukrainian localities which together form a continuous sequence of sediments from the Upper Miocene (MN 9a) to the Lower Pleistocene. Numerous faunal relicts occur in Gritsev and the fossil assemblage corresponds to the those of humid forests (Zerova 1993).

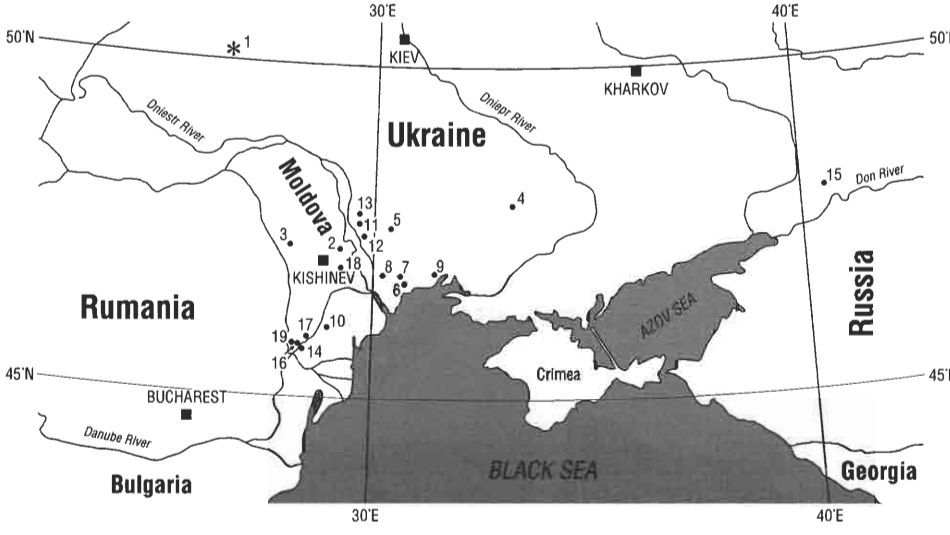

Fig. 1. Distribution of the Neogene snake localities with representatives of the family Viperidae (Viperinae + Crotalinae) in the territory of Ukraine, Moldova and Russia: 1, Gritsev (MN 9a); 2, Kalfa (MN 9b); 3, Buzhor (MN 9b); 4, Krivoy Rog (MN 11a); 5, Novoelizavetovka (MN 11b); 6, Cherevichnoie (MN 12a); 7, Novaya Emetovka (MN 12a); 8, Novoukrainka-1 (MN 13); 9, Andreievka (MN 13); 10, Orekhovka (MN 13); 11, Frunzovka-2 (MN 14); 12, Kuchurgan (MN 14); 13, Frunzovka-1 (MN 14); 14, Kotlovina (MN 15, MN 16); 15, Obukhovsky quarry (MN 15); 16, Etuliya (MN 15); 17, Musait (MN 15); 18, Novye Tanatary (MN 16); 19, Chishmikioy (MN 16). Based on Szyndlar (1991) and Zerova (1993).

Fossil vipers from Gritsev were studied for the first time by Zerova (1987). She reported on the genus *Vipera* sp. belonging to the 'Oriental vipers' group (*sensu* Groombridge 1986). Zerova (1992) later described the extinct species *Vipera ukrainica* Zerova, 1992 on the basis of both cranial bones and vertebrae, which probably belongs to the '*xanthina*' complex (*sensu* Groombridge 1986). The vipers of the 'European vipers' group of the '*berus*' complex are represented by the species *Vipera* cf. *berus* ('*Pelias* cf. *berus*' *sensu* Zerova 1987).

Recently, the representatives of the Viperidae from Gritsev were reinvestigated by Ivanov (1997a, 1997b, 1997c). Several morphotypes of the genus *Vipera* were distinguished, based only on the cranial bones. The present discovery of the subfamily Crotalinae is unique as it represents the first doubtless finding of the representatives of this subfamily in Europe.

The fossil material is deposited in the Department of Palaeozoology, Institute of Zoology, Kiev (IZAN).

Systematic part

Family Viperidae Oppel, 1811
Subfamily Crotalinae Oppel, 1811
Crotalinae gen. et sp. indet. A

Crotalinae gen. et sp. indet.; Ivanov 1997a: p. 156, pl. 19A.

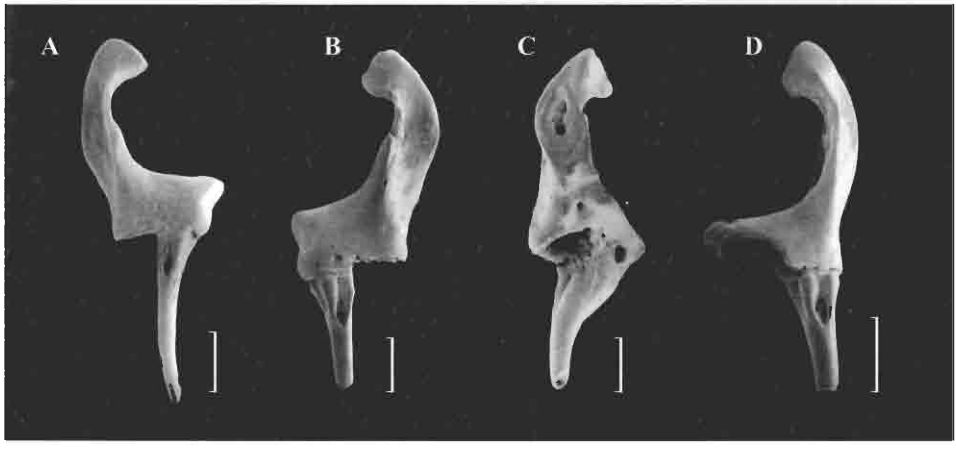

Fig. 2. Crotalinae gen. et sp. indet. A and B from the Upper Miocene (MN 9a) of Gritsev (Ukraine). **A–C**. Crotalinae gen. et sp. indet. A. Left maxillary (IZAN 3748) (**A**), right maxillary (IZAN 3739) (**B**, **C**). **D**. Crotalinae gen. et sp. indet. B. Right maxillary (IZAN 3751) (**D**). **A**, **B**, **D** in anterior aspect, **C** in postero-lateral aspect (scale bars 1 mm).

Material. — 3 (1 left + 2 right) maxillaries (IZAN 3739, IZAN 3747, IZAN 3748).

Maxillary (Figs 2A–C, 3A–C). — Viewed anteriorly, the body of the bone is low, the process for maxillary-prefrontal articulation is strikingly long and located entirely on the medial border of the bone. A distinct ridge (here named r1) extends from the base of the process to the nearby labial curvature (IZAN 3748, IZAN 3739). Another ridge (here named r2) occurs on the antero-medial border of the process (IZAN 3748, IZAN 3739). The process for maxillary-prefrontal articulation is markedly bent labially, and a very short, distinct outgrowth is present on its distal end. On its labial surface, the bone projects as a short process which is directed medially. In posterior view, the fangs are fused with the narrow portion of the bone. A distinguishable fossa for maxillary--ectopterygoid articulation is lacking. Only a transverse crest bordering this fossa on its dorsal side is developed. This crest, located near the bases of the fangs, continues up to the labially directed process. A distinct oval orifice can be seen from the postero--lingual aspect. Two foramina may be observed in this orifice (Fig. 3C). One foramen (here named o1) is directed dorsally, another foramen (here named o2) is directed ventrally. The dorsal foramen (o1) pierces the process for the maxillary-prefrontal articulation, the opposite orifice of this foramen can be seen in lingual aspect. This oval and sometimes very large (IZAN 3739) orifice is located not far from the tip of the process for maxillary-prefrontal articulation.

Crotalinae gen. et sp. indet. B

Crotalinae gen. et sp. indet.; Ivanov 1997a: p. 156, pl. 19B.

Material. — 2 (1 left + 1 right) maxillaries (IZAN 3741, IZAN 3751).

Maxillary (Figs 2D, 3D). — It differs from the maxillary described above as follows: 1, the process for the maxillary-prefrontal articulation is much more slender, especially at its base; 2, the r1 ridge extends from the base of the process for maxillary-prefrontal

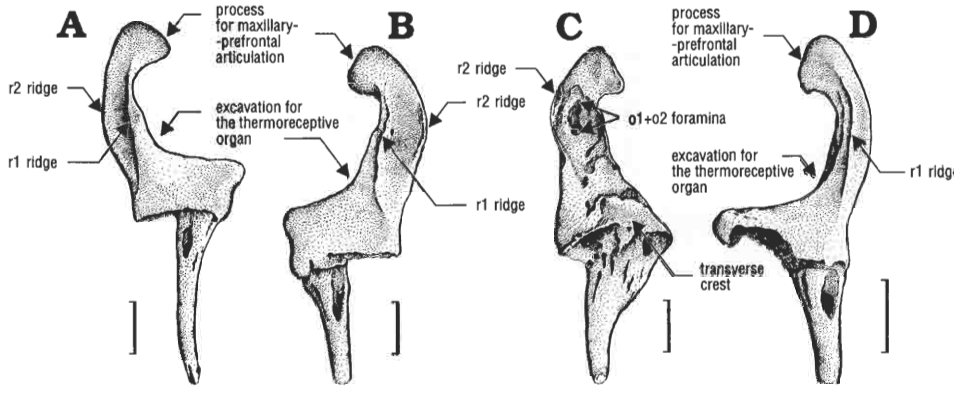

Fig. 3. The important morphological structures in maxillaries of Crotalinae gen. et sp. indet. A (**A**, **B**, **C**) and B (**D**). **A**, **B**, **D** in anterior aspect, **C** in postero-lateral aspect (scale bars 1 mm).

articulation to the vicinity of its distal end; 3, the r2 ridge is underdeveloped; 4, the oval orifice (with o1 and o2 foramina) on the postero-lingual side of the process for the maxillary-prefrontal articulation is smaller.

Discussion

The maxillary is postero-laterally excavated for the thermoreceptive organ, the most characteristic feature distinguishing crotaline snakes from true vipers. As a consequence, the process for maxillary-prefrontal articulation is located on the lingual margin of the bone. This is characteristic for all recent and fossil representatives of the Crotalinae (e.g., Brattstrom 1954, 1964; Meylan 1982). The shape of the r1 ridge is an important taxomonic character for distinguishing genera and species. In anterior view, it is smooth, and the facial pit remains open. This is characteristic for some snakes of the '*Agkistrodon*' complex (*sensu* Gloyd & Conant 1990). In comparison with the extant representatives, the described morphotypes closely resemble *Agkistrodon bilineatus* Günther, 1863, *Deinagkistrodon acutus* (Günther, 1888), and *Agkistrodon contortrix* (Linnaeus, 1758).

Most likely, two different extinct species belonging to the '*Agkistrodon*' complex occur in Gritsev. This is especially supported by the shape of the process for maxillary--prefrontal articulation of both morphotypes. In recent juveniles and subadults, some structures (including ridges, such as r1 and r2) are rudimentary, but both types of maxillaries have the r1 ridge strongly developed, suggesting that they represent adults. Therefore, the ontogenic variation may be excluded.

Conclusion

The discovery of Late Miocene (MN 9a) representatives of crotaline snakes in Gritsev is the first unquestionable evidence of the subfamily Crotalinae in Europe (Fig. 4). The extinct genus *Laophis*, discovered in the lowermost Pliocene of Karabournu in the

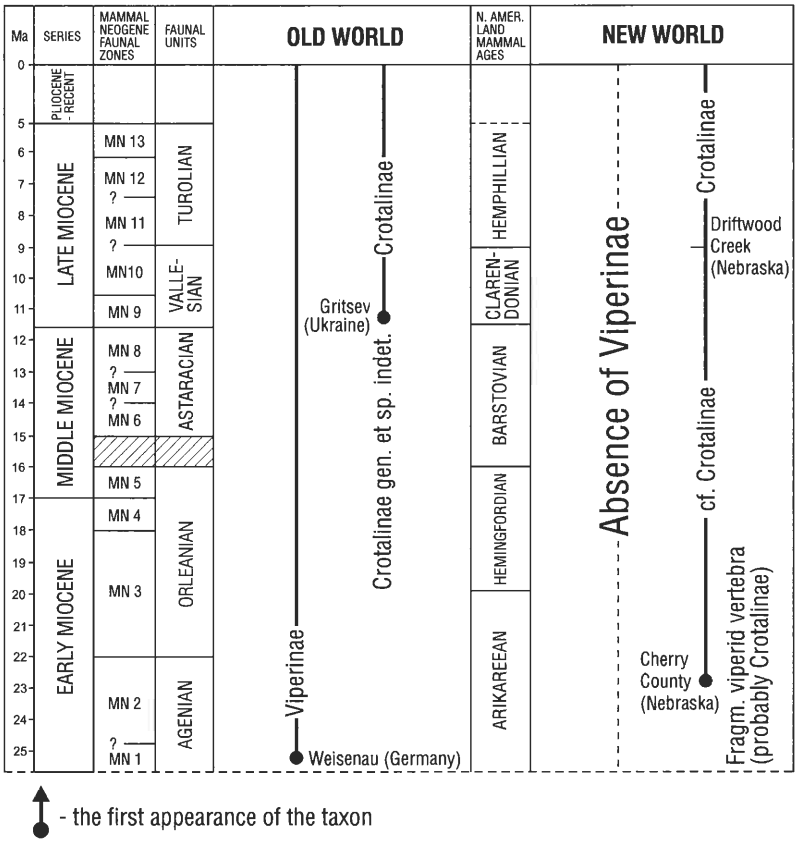

Fig. 4. The fossil evidence of the subfamilies Viperinae and Crotalinae in the territory of the Old World and the New World. Stratigraphic correlations based on Steininger *et al.* (1990) and Kelly (1998), remaining data after Brattstrom (1954), Holman (1979, 1981), Conant (1986), and Szyndlar & Böhme (1993).

Thessalonica area (Greece), is considered by Rage (1984) as a *nomen dubium*. Szyndlar (1991) assumes that *Laophis* might have been a *Bitis*-like snake rather than a pit viper, thus, the problem of the validity of this genus is unresolved.

The oldest known pit viper (Holman 1981) comes from the Lower Miocene (Arikareean) of Nebraska, North America (Fig. 4). A somewhat younger discovery (Holman 1977, 1979) comes from the lower Middle Miocene of Texas, but the only specimen, an isolated vertebra, has not been unquestionably determined even at the subfamily level ('cf. Crotalinae indet.').

Based on the zoogeographical and evolutionary studies of the genus *Agkistrodon* (*sensu stricto*) in the New World (Conant 1986; Gloyd & Conant 1990), the genus *Agkistrodon* (*s.s.*) might have diversified into two lineages probably even in the Oligocene. The first lineage reached the North America probably at the beginning of Miocene, though the oldest fossil data of the genus (Brattstrom 1954; Conant 1986) came from the Late Miocene (Clarendonian/Hemphillian) of Nebraska (Fig. 4). Conant (1986) assumed that an immigration of these earliest representatives of the genus *Agkistrodon* (*s.s.*) in the New World was followed by a gradual splitting of the

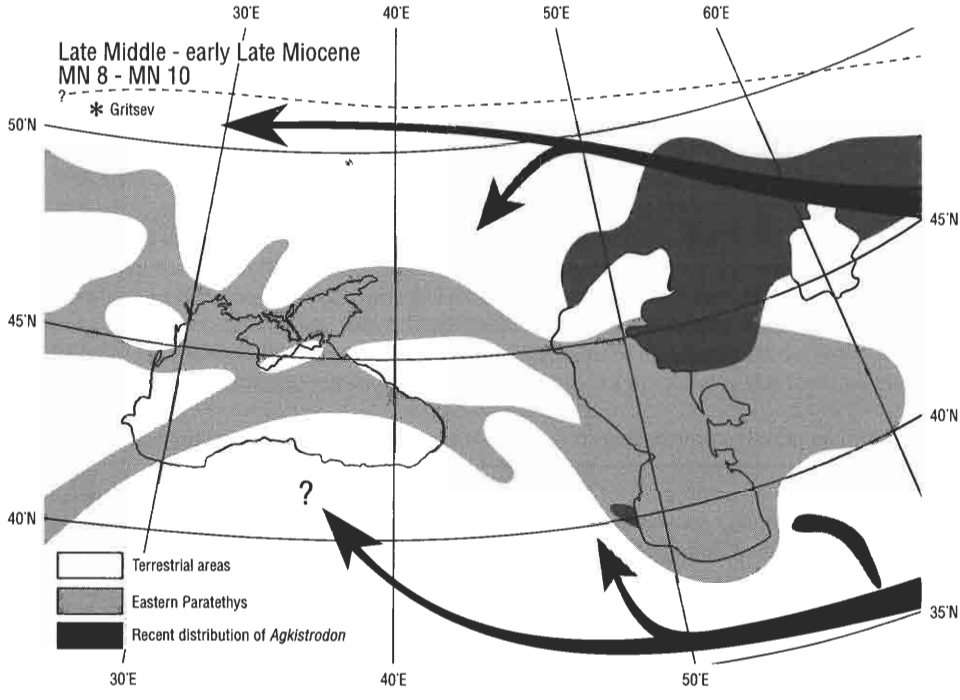

Fig. 5. Presumed migrations of Crotalinae, probably the representatives of the '*Agkistrodon*' (*sensu lato*) complex, from Asia into Eastern Europe (the areas around the Eastern Paratethys) till the beginning of the Late Miocene (MN 9a). The south way migration is not documented by the fossil evidence. The dotted line – presupposed northernmost distribution of Crotalinae during the Late Miocene. The palaeogeographic reconstruction after Jones & Simmons (1996); data regarding the recent longitudinal/latitudinal distribution of east European crotaline snakes, *Agkistrodon halys* (Pallas, 1775), after Bannikov *et al.* (1977).

lineage. This diversification resulted in the contemporary American taxa. The second lineage of the genus *Agkistrodon* (*s.s.*) might have migrated to the west already during the Oligocene and might have reached today's Eastern Europe at the beginning of the Late Miocene. This may be substantiated by the fact that the representatives of Crotalinae from Gritsev (MN 9a), are closely related to contemporary pit vipers of the genus *Agkistrodon* (*s.s.*). The discovery at Gritsev supports a Miocene occurrence of the European pit vipers in the areas north of the Eastern Paratethys but the issue of whether the pit vipers penetrated southwards of Paratethys remains open because of the lack of palaeontological data in the south-eastern part of Europe (Fig. 5).

Available data on the snake fauna from the oldest European Miocene localities support the view that pit vipers never penetrated into the Central and West Europe. However, cranial elements of the oldest European Viperinae are very scarce. An isolated venomous fang from Hessler in Germany (MN 1) is indistinct even at the subfamily level. The remains from the Limagne area (MN 1 and MN 2) in France belong to small viperid snakes (Szyndlar & Schleich 1993). Moreover, vertebrae of both Viperinae and Crotalinae may be quite similar to each other (Rage 1984). Szyndlar (1991) adds that the representatives of small viperine snakes can hardly be distinguishable (if at all) from some Asiatic members of Crotalinae, for instance the genus *Agkistrodon* (*s.s.*).

Because forms which are closely related to the snakes of the '*Agkistrodon*' complex have been discovered at Gritsev, it seems very probable that some vertebrae from Gritsev belonged unquestionably to the representatives of Crotalinae.

Acknowledgements

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Pierwszy europejski grzechotnik z miocenu Ukrainy

MARTIN IVANOV

Streszczenie

W pobliżu wioski Gricew na Ukrainie (obwód chmielnicki) odkryto liczne skamieniałości późnomioceńskich jaszczurek i węży, datowane na poziom biostratygraficzny MN9 (ok. 11 mln lat temu). W niniejszej pracy opisano dobrze zachowane kości szczękowe dwóch gatunków węży, pozwalające je zaliczyć do podrodziny Crotalinae, Oppel 1811. Oba gatunki grzechotnikowatych, pozostawione w taksonomii otwartej (Crotalinae gen. et sp. indet. A i B), wykazują duże podobieństwa do zespołu gatunków określanego jako „kompleks *Agkistrodon*". Zapewne ukraińskie grzechotniki są imigrantami z Azji; rodzina ta prawdopodobnie nigdy nie zasiedliła na dłużej znaczniejszych obszarów Europy.