

Fossil Remains of *Natrix tessellata* from the Late Cenozoic Deposits of the East European Plain

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Abstract. At present, only 10 localities with fossil remains of *Natrix tessellata* of Pliocene-Holocene age are known from the East European plain. They are exclusively represented by trunk vertebrae. Due the application of a single diagnostic character, the CL/NAW ratio (centrum length/width of interzygapophyseal constriction), the majority of East European *Natrix* fossils were determined as *Natrix* cf. *natrix*, and a smaller number as *Natrix* cf. *tessellata*. The oldest fossil records of *N. natrix* and *N. tessellata* originate from the Middle Pliocene. The data conclude that *N. tessellata* inhabited the East European plains continuously since the Late Pliocene until present, but that its range varied due to the frequent climatic and topographic changes.

Key words. *Natrix tessellata*, fossils, stratigraphic distribution, East European Plain, history.

Introduction

Fossil finds of the dice snake, *Natrix tessellata*, or its immediate predecessor are not numerous. HOLMAN (1998) and SZYNDLAR (1991) identified 14 Pliocene and Pleistocene localities in Central and Western Europe, which are in Hungary (Uppermost Pliocene MN 17: Villány-3, Nagyharsány-hegy, Villány-6; Lower Pleistocene: Beremend-4), Poland (Lower Pleistocene: Żabia Cave), Czech Republic (Lower Pleistocene: Stránzá Skála Hill), Romania (Lower Pleistocene: Betfia; Middle Pleistocene: Braşov), Greece (Middle Pleistocene: Tourkobounia; Upper Pleistocene: Gerani 1), Germany (Upper Pleistocene: Holocene: Euerwanger Bühl, Malerfels, Spitzbubenhöhle), and Croatia (Upper Pleistocene: Šandalja). Older *Natrix* fossils from the Late Miocene (MN 13) of Polgárdi, Hungary, were allocated to *N. tessellata* (SZUNYOGHY 1932). However, VENCZEL (1994) re-investigated the same remains and concluded that they represent an intermediate morphology between *N. longivertebrata* and *N. natrix*. They are determined now as *Natrix* cf. *N. longivertebrata* and the presence of *N. tessellata* and *N. natrix* at this locality has been concluded as erroneous.

Results and Discussion

Natrix Taxa and Diagnosis of Fossils

The delicate morphological elements of fossil remains of snakes are frequently destroyed and leave little physical evidence to work with. Since all fossil remains are represented by trunk vertebrae, we have only the presence and shape of the hypapophysis to allocate the bones to the correct subfamily within the Colubridae (see Figs. 1 and 2). Such hypapophyses are widespread within the snake families, and, for example, are also present in the Viperidae and Elapidae. The distinct vertebral structures of these groups and their diagnostic features have been

described elsewhere (HALLOCK et al. 1990, HOLMAN et al. 1990, HOLMAN 1991, 1998, SZYNDLAR 1984, 1991, IVANOV 1996). The vertebrae of the subfamily Natricinae differ from those of the Viperidae in having a sigmoid hypapophysis, posteriorly vaulted neural arches, shorter parapophyseal processes and much longer centra. Furthermore, they differ from those of the Elapidae in having lightly built vertebrae, exhibiting much longer centra and strong subcentral ridges.

Sensu SZYNDLAR (1984), trunk vertebrae of *Natrix tessellata* differ from those of *N. natrix* by having pointed distal hypapophyses and parapophyseal processes, whereas these structures in the latter species are characterized by obtuse tips (Fig. 3). But HOLMAN (1998) found some variation of these characters in *N. natrix*. Comparative material investigated by the senior author confirms these variations (see Figs. 1 and 2), and renders these characters less useful. Unfortunately, the fragile elements distinguishing *Natrix* species are rarely available as fossil remains, requiring an alternative method to diagnose and allocate bony structures to closely related snake taxa. Such a method was introduced by AUFFENBERG (1963), who applied complementary distinctive features based on measurements and numerical indexes. Especially the ratio CL/NAW (centrum length/width of interzygapophyseal constriction) yielded a valuable tool (Fig. 4). The ratio ranges in *N. tessellata* between 1.08 and 1.44, but exhibits significant higher values in *N. natrix*, 1.45–2.07 (SZYNDLAR 1984, and personal data). The majority of the East European fossil remains, classified as *Natrix* cf. *tessellata*, were determined by the CL/NAW ratio.

There are two other *Natrix* species, with which fossil remains of *N. tessellata* could be easily confused, *N. maura* (HOLMAN 1998) and *N. megalcephala* (ORLOV & TUNIJEV 1987, 1992). However, the current range of the former species lies far to the west from the East European plain. For this reason, we regard *N. maura* as an unlikely candidate for the fossils studied, though theo-

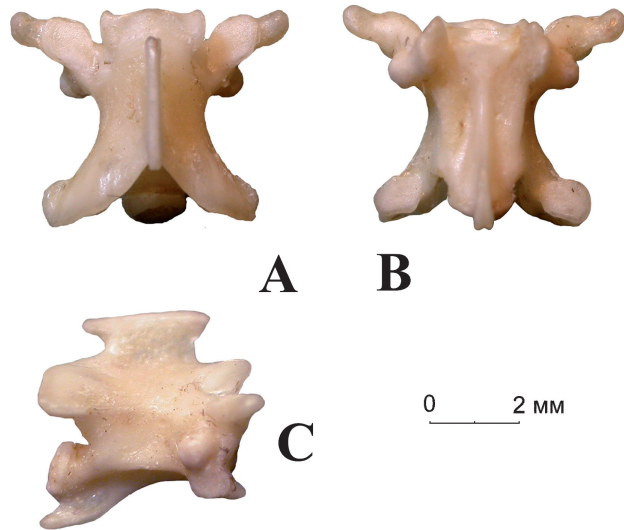


Fig. 1. Trunk vertebra of *Natrix natrix*: A – dorsal view, B – ventral view, C – lateral view.

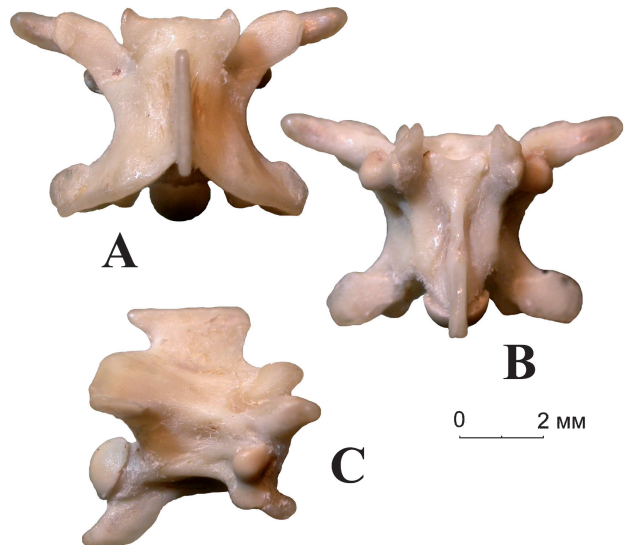


Fig. 2. Trunk vertebra of *Natrix tessellata*: A – dorsal view, B – ventral view, C – lateral view.

retically, any vertebrae could belong to *N. maura*, especially those from older sediments. Fossil remains of the second taxon, *N. megalcephala*, a species closely related to or being conspecific with *N. natrix*, were not available for this study. Moreover, this species is not unanimously regarded as valid (e.g. VELENSKÝ 1997, ORLOV & TUNJEV 1999, GUICKING et al. 2006).

Fossil Remains of *Natrix tessellata*

Within the East European plain, there are currently 10 localities known that revealed fossil remains of *Natrix tessellata* from the Pliocene through the Holocene (Fig. 5, RATNIKOV 2002a, b 2003). Table 1 shows the numbers

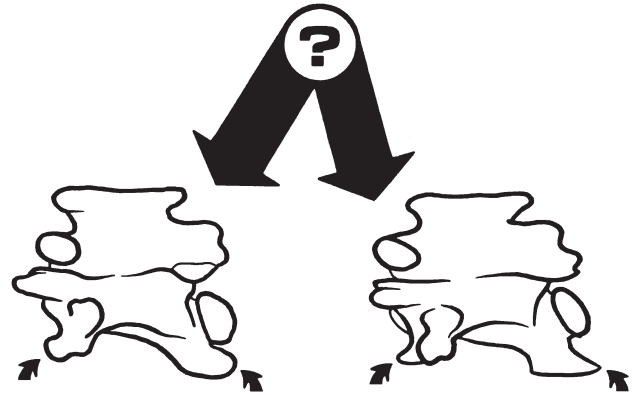


Fig. 3. Morphological differences between trunk vertebrae of *Natrix natrix* (left) and *N. tessellata* (right) (after Szyndlar 1984).

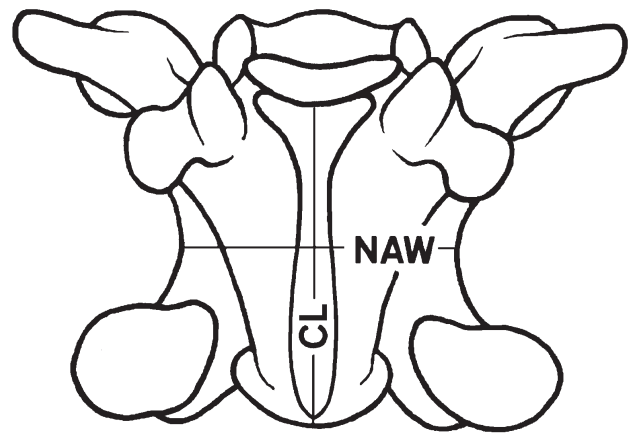


Fig. 4. Principal measurements of snake vertebrae applied (after AUFFENBERG 1963): CL – centrum length, NAW – width of interzygapophyseal constriction.

of fossils found at each locality in the East European plain. A previous record of *N. tessellata* from Zmeevka-2 (RATNIKOV 1989, 2002a) has subsequently been determined as incorrect.

Stratigraphic positions of localities are shown in Table 2. The oldest fossil records of *N. tessellata* in Eastern Europe are from the Pliocene sediments of Kotlovina (Ukraine). Unfortunately, the fauna sample at this site is mixed from three horizons, consisting of very little Lower Pliocene (MN 15b: approx. 4.0–3.5 million BP), about 70% from the Middle Pliocene (MN16: 3.5–2.6 million BP), and about 30% from the Upper Pliocene (MN17: 2.6–1.8 million BP) (A.S. TESAKOV pers. comm.). The most likely age of *N. tessellata* vertebrae is Middle Pliocene due to the large proportion of this horizon. Thus, if this hypothesis is correct, the oldest fossil of *N. tessellata* dates back to the Middle Pliocene. Vertebrae of *N. natrix* are found at the same locality, which roughly coincides with its oldest fossil remains from Central Europe from the Beremend-1 locality in Hungary (SZYNDLAR 1991).

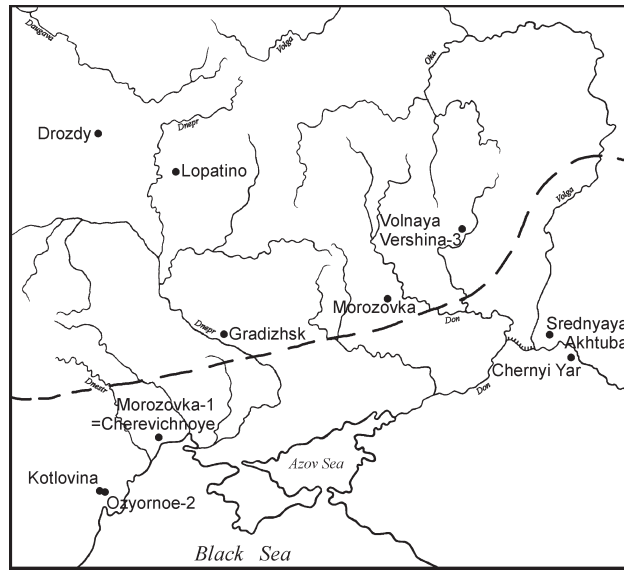


Fig. 5. Locations of fossil finds of *Natrix tessellata*. Broken line indicates the northern limits of its current range.

Various hypotheses of the current distribution of *Natrix* species have been proposed. Recently GUICKING et al. (2006) suggested that the three extant species (*N. maura*, *N. natrix* and *N. tessellata*) had already appeared in the Miocene. They concluded that *N. maura* is basal and diverged from their ancestor first between 18–27 mya, whereas *N. natrix* and *N. tessellata* are sister species that evolved million of years later, between 13–22 mya. Their results are based on a molecular clock constructed from two data sets. The first one relates to amino acid distances of diverging snake groups, whereas the second one applied the nucleotide sequences divergence of four protein-coding mitochondrial genes. The molecular clock was then calibrated with two geological events, the Messinian salinity crisis and the first collision of the African and Arabian plates with the Eurasia (GUICKING et al. 2006).

Table 1. List of localities and respective number of specimens studied (*n*).

Locality	<i>N</i>
Gradizhsk	1
Drozdy	1
Kotlovina	5
Lopatino	1
Morozovka	1
Morozovka-1 = Cherevichnoye	1
Ozyornoe-2	2
Srednyaya Akhtuba	25
Chernyi Yar	7
Volnaya Vershina-3	1

Table 2. Stratigraphic distribution of localities of *Natrix tessellata* fossils. The begin of the period of stratigraphic boundaries is given on the base of Stratigraphic Code (2006).

Division Superdivision Section	Begin of Division (Mya BP)	Level	Horizons, Superhorizons	Localities	
Holocene	0.01			Drozdy Lopatino Srednyaya Akhtuba	
Neopleistocene	0.8	Upper (Late)	Valdai		
			Mikulin	Morozovka	
		Middle	Srednerussky	Chernyi Yar	
			Lichvinian	Ozyornoye - 2	
		Lower (Early)	Oksky		
			Muchkupian	Volnaya Vershina-3	
			Don		
			Iliinsky	Gradizhsk	
				Pokrovian	
				Petropavlovsk	
Eopleistocene	1.8	Upper (Late)		Morozovka-1 = Cherevichnoye	
		Lower (Early)			
Pliocene	5.3		MN 17		
			MN 16	Kotlovina	
			MN 15		

However, there are no reliable fossil remains from the Miocene to corroborate this evolutionary scenario. In contrast, the fossil data of recent *Natrix* taxa are much younger. The earliest *N. maura* (reported as *N. cf. maura*) are not older than the lower Pliocene and originate from France (MN 15; BAILON 1991) and Spain (MN

16: BLAIN 2005). In this context, it is certainly interesting to notice, that there are up to 14 million years difference between the proposed origin of the *N. tessellata* lineage approximately 16–17 mya (GUICKING et al. 2006, GUICKING & JOGER 2011) and its oldest fossil data from the Middle Pliocene, approximately 3 mya (see above). Taking into account that intraspecific radiation in *N. tessellata* was suggested to have begun 5–6 mya at the Miocene-Pliocene boundary (GUICKING & JOGER 2009, 2011), it would leave that species with approximately 10 million years of stasis, a long period without any additional divergence nor evolutionary change. On the other hand, it reveals the limits of molecular clock applications and *N. tessellata* might be much younger than suggested by GUICKING et al. (2006).

The Pleistocene history of fauna is closely connected to large climatic fluctuations (cold glacial and warm interglacial periods) associated with the expansion and retraction of continental ice sheets, which in turn substantially affected the geographic composition of flora and fauna (see refs. in BLONDEL & VIGNE 1993, MEBERT 2010). Thus, geographic conditions during the Pleistocene constantly varied, and so did the distribution of species inhabiting temperate zones. However, natural zones and their inhabitants did not simply shift southward following the movements of ice sheets. Findings of so-called mixed faunas in the temperate zones in Pleistocene sites of Eastern Europe and America, including “northern” and “southern” species that are ecologically incompatible today, (e.g. AGADZHANYAN 1972, HOLMAN 1976, 1980, 1986, BLONDEL & VIGNE 1993, MARKOVA 1994, REKOVETS 1995, MEBERT 2010) suggest other, more complex version of events.

During continental glaciations there was a displacement of the tundra zone southwards and steppe zone northwards, as forest areas shrank and developed into a mosaic pattern (BARYSHNIKOV & MARKOVA 2002, MARKOVA 2000, 2004a, b, MARKOVA et al. 2002a, b, 2003, 2006, REKOVETS & NADACHOWSKI 2007). Large forests became ever less, being gradually reduced to small wooded fragments in river valleys. As a result, an extensive periglacial ‘hyperzone’ was formed, consisting of mixed landscapes with periglacial tundra-steppes, periglacial tundra-forest-steppes, and periglacial forest-steppes. There are no such analog landscapes today. The ranges of many animals moved in concert with the geographic changes of vegetation zones: tundra species penetrated far to the south, cold-resistant steppe species spread to the north, and forest species remained in the residual woodlands. Thus, refugia for forest species existed within the limits of periglacial hyperzone, inhabited mainly by steppe and tundra species.

In accordance with the mixed vegetation zones, the on-site composition of mammal fossils from glacial periods shows a mixture of tundra and steppe species, occasionally added with forest forms (e.g. AGADZHANYAN 1972, MARKOVA 1994, REKOVETS 1995). This is in contrast with East European species of amphibians and reptiles, where no typical tundra forms exist, and no com-

parable mixed herpetofaunas have been observed. Only the degree of herpetofaunistic diversity distinguishes different climatic periods. The herpetofaunas from glacials usually are depauperate, whereas those from interglacials show an increased diversity including thermophilic southern forms. In the particular case of *N. tessellata* we suggest that its range extended rather than was reduced during the early phase of glacials, as a consequence of the replacement of wooded areas by steppes (RATNIKOV 2009). The associated decrease of shading vegetation during the early glacial promoted the expansion of *N. tessellata* north into the newly opened aquatic areas, facilitating solar radiation to reach the ground and substantially warming its preferred microhabitat, rocky shores, a habitat niche with which it is still associated today (GRUSCHWITZ et al. 1999).

East-European Plio-Pleistocene findings of *N. tessellata* are distributed across seven stratigraphic horizons (Tab. 2). They stem from warm interglacials, except the one from Chernyi Yar, which was formed during a glacial period, when the front of glaciers were at distances not less than 700 km (SHIK et al. 2006). The general climate during the formation of the Chernyi Yar site was very dry but warm. Its surrounding landscape was an open steppe or semidesert with disjunct meadows, whereas forest existed only in river valleys. The diversity of herpetofauna at this site was with approximately 15 species very high (RATNIKOV 2001, 2002a). But the fossil findings of a *Lemmus* sp., a small mammal, at the same site, representing the most southern site of a lemming on the Russian plain (KIRILLOVA & SVITICH 1994), indicates the contemporaneous existence of tundra elements, and thus, the mixed nature of the Chernyi Yar fauna. Three additional localities were formed during the Holocene. Overall, it appears likely that *N. tessellata* occupied the East European plain constantly since the Late Pliocene, but its range changed continuously according to environmental fluctuations.

Figure 5 shows the sites Kotlovina (Middle Pliocene), Morozovka-1 = Cherevichnoye (Eopleistocene), Ozyornoe-2 (Lichvin horizon of the Middle Neopleistocene) and Chernyi Yar (Middle Russia superhorizon of Middle Neopleistocene) which lie within the limits of the present range of *N. tessellata*. However, the fossils from the sites Gradizhsk (Iliinka horizon of the Lower Neopleistocene), Volnaya Vershina-3 (Muchkap horizon of the Lower Neopleistocene) and Morozovka (Mikulino horizon of Upper Neopleistocene) show significant deviations from the present range of *N. tessellata*. Moreover, two of the three Holocene localities of *N. tessellata*, Lopatino (Pre-Boreal Interstadial approximately 11.6–10.7 thousands BP) and Drozdy (Boreal stage, approx. 10.7–9.3 thousands BP), are located far north of the current range limit of this species. They explicitly confirm that the range of *N. tessellata* changed significantly in connection with variations of environmental conditions, even during the relatively short interglacial, the Holocene, that we experience today (MARKOVA et

al. 2003, MONIN 1980, MONIN & SHISHKOV 1979, STUIVER et al. 1998). The extralimital fossil records and the existence of several isolated populations of *N. tessellata* north of its present range between Germany and Russia (e.g. GRUSCHWITZ et al. 1999, KOTENKO et al. 2011, LITVINOV et al. 2011) are farther facts, that corroborate the existence of a larger range of *N. tessellata* in earlier periods of the Holocene. This range extension probably coincides with the climatic optimum of the Atlantikum (= HTM, Holocene Thermal Maximum), a period with slightly higher temperatures approximately 5700 to 9300 BP (see Atlantikum, Wikipedia 2011).

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