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On the Quaternary reptilian fauna of Bashkortostan (South Urals, Russia)

Zur Quartären Reptilienfauna von Baschkortostan (Südural, Rußland)

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KURZFASSUNG

Die Geschichte der quartären Reptilienfauna von Baschkortostan (Südural, Rußland) wird im Zusammenhang mit einem kurzen Überblick zur Entwicklung des Klimas, der Landschaften und der Vegetation dargestellt. Fünf Reptilienarten (*Lacerta agilis, Anguis fragilis*, *Lacerta vivipara*, *Natrix natrix*, *Vipera berus*) sind für das Spätquartär des Untersuchungsgebietes anhand von Fossilbelegen nachgewiesen. Die neuzeitliche Herpetofauna des Urals begann sich im späteren Pliozän herauszubilden. Die gegenwärtige Reptilfauna entwickelte sich im mittleren Holozän, mit der Rückkehr der Reptilien aus den eiszeitlichen Refugialräumen. Die Gebirgsketten des Urals sowie die Tätigkeit des Menschen hatten auf die Ausbildung der gegenwärtigen Kriechtierfauna der Region keinen bedeutenden Einfluß.

ABSTRACT

The history of the Quaternary reptilian fauna of Bashkortostan (South Urals, Russia) is described and the development of climate, landscapes and vegetation are briefly reviewed. Five late Quaternary fossil reptile species (*Lacerta agilis, Anguis fragilis*, *Lacerta vivipara*, *Natrix natrix*, *Vipera berus*) had been identified for the region. The modern herpetofauna of the Urals started to form approximately in the Late Pliocene. In the South Urals the complete present day herpetofauna had established in the Middle Holocene due to reptiles dispersion from glacial refugia. The Ural Mountains as well as anthropogenic factors had little influence on the evolutionary history of the recent reptile fauna in the region.

KEY WORDS

Reptilia, paleontology, evolutionary history, Quaternary, Pliocene, Pleistocene, Holocene, post-glacial dispersion, glacial refugia, Republic of Bashkortostan, South Urals, Russia

INTRODUCTION

Origin and evolutionary history of present-day faunas are among the most interesting and intricate topics in zoology. They were poorly studied and challenged as far as the North Eurasian temperate zone reptilian fauna is concerned, the evolutionary history of which, especially in the Pleistocene, was rather dramatic. This paper presents a synthesis of our knowledge of the Quaternary herpetofauna of Bashkortostan (South Urals, Russia) urged by the paucity and fragmentation of literature on that issue (i.e. GARANIN 1983; KHABIBULLIN 2001a, 2002).

The modern reptilian fauna in temperate North Eurasia (and therefore in Bashkortostan) is primarily a result of the Late Cenozoic post-glacial dispersion from glacial refugia in South Europe and South-West Asia (NIKOLSKY 1947; LENK et al. 1999). Therefore the evolutionary history of the modern herpetofauna of Bashkortostan is restricted to the history of post-glacial colonization.

MATERIALS AND METHODS

Published data is summarized from the fields of paleontology, paleogeography and biogeography and the stratigraphic scheme proposed for the former USSR by YAKCHIMOVICH (1965, 1992) was used. A general picture was created to analyze not

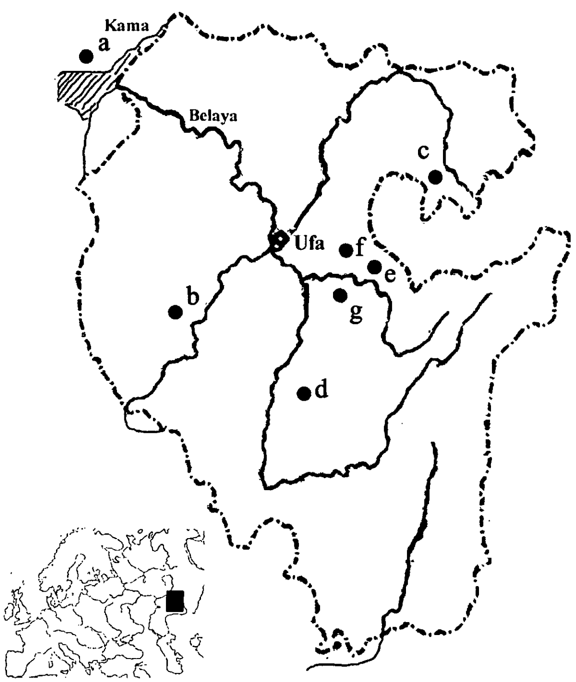

Fig. 1: Map of locations of late Cenozoic reptile remains in the territory of the Republic of Bashkortostan (RB) and adjacent regions. a – Krasny Bor; b – Akkulaevo; c – Kyzyrbak; d – Ziganskaya; e – Zapovednaya I, II; f – Lemeza I, II, IV; g - Nukatskaya. The administrative border of RB is represented by a dash-dotted line.

Abb. 1: Karte der Fundorte spätkänozoischer Reptilienreste auf dem Territorium der Republik Baschkortostan und angrenzender Gebiete. a – Krasny Bor; b – Akkulaevo; c – Kyzyrbak; d – Ziganskaya; e – Zapovednaya I, II; f – Lemeza I, II, IV; g - Nukatskaya. Die administrativen Grenzen der Republik Baschkortostan sind durch die strich-punktierte Linie bezeichnet.

only data from the precise area within the administrative borders of Bashkortostan, but also from adjacent territories.

Fossil reptile remnants from six excavation sites were analyzed (fig. 1). Quaternary reptilian fossil materials were found mainly in caves (eight out of ten sites). Only data on Late Cenozoic fossil materials is presented.

All interpretations below if not stated otherwise, primarily refer to Bashkortostan and the South Urals (within the administrative borders of Bashkortostan, Orenburg and Chelyabinsk regions). But as far as the evolutionary history of the modern reptilian fauna of Bashkortostan is concerned, it is tightly associated with that of the adjacent Ural region and the whole Eastern Europe, and most generalizations can be extrapolated to the temperate zone of North Eurasia.

Brief characteristics of Bashkortostan

Bashkortostan (Republic of Bashkortostan, RB) is one of 89 administrative units of the Russian Federation with over four million inhabitants and a total area of 143,000 square kilometers. Bashkortostan is situated in the South Urals at the "meeting point" of Europe and Asia between 51°31' - 56°25' N and 53°10' - 60°00' E. The watershed of the Uraltau mountain ridge divides Bashkortostan into the following natural regions: the western part of RB (Fore-Urals) belongs to the Volga river basin while the eastern part (Trans-Urals) belongs to the Ural and Ob river basins. In between these two parts are the Ural Mountain ridges that form the mountainous part of RB. The elevations of Bashkortostan range from 58.7 m to 1,640 m a.s.l., with the average altitude

Table 1: The recent reptile fauna of Bashkortostan (South Urals, Russia) according to KHABIBULLIN (2001a).
Tab. 1: Die rezente Reptilienfauna von Bashkortostan (Süd-Ural, Rußland) nach KHABIBULLIN (2001a).

Order Ordnung	Suborder Unterordnung	Family Familie	Species Art
Testudines	Cryptodira	Emydidae	*Emys orbicularis* (LINNAEUS, 1758)
Squamata	Sauria	Anguidae	*Anguis fragilis* LINNAEUS, 1758
		Lacertidae	*Lacerta agilis* LINNAEUS, 1758
			Zootoca vivipara (JACQUIN, 1787)
	Serpentes	Colubridae	*Coronella austriaca* LAURENTI, 1768
			Elaphe dione (PALLAS, 1773)
			Natrix natrix LINNAEUS, 1758
			Natrix tessellata (LAURENTI, 1768)
		Viperidae	*Vipera berus* (LINNAEUS, 1758)
			Vipera ursinii (BONAPARTE, 1835)

being 326 m a.s.l. (KHISMATOV & AKHMETOV 1984). Climate in RB is continental with substantial differences between seasons and regions (mountainous parts, Fore- and Trans-Urals). RB is one of the most continental regions in Europe: for example, the annual range of temperatures is up to 87 °C (from minimal -50°C in January to maximal +37°C in July). The Ural Mountains greatly influence climate, landscape, vegetation and other environmental parameters and cause great differences between mountainous regions and their western and eastern slopes. Humid air masses from the Atlantic Ocean cannot cross the Ural Mountains and thus, precipitate over the western slopes. Thus, the climate of eastern slopes and the Trans-Ural region is much more arid and continental with very hot summers and rather cold winters, however with very little snow coverage. Cold air masses from the Arctic Ocean and dry air masses from Kazakhstan also influence the climate conditions of the region.

The mosaic of landscapes in the South Urals is very diverse. The region is characterized primarily by its transitional character from low grasslands to mountain forests. But a variety of habitats including swamps (both lowland and mountain), grassland, woodland thicket and colonizing scrub is also represented.

The Ural Mountains are of Paleozoic origin. Until the Late Oligocene, the South Ural Mountains were relatively low with average heights around 300-400 m a.s.l. Their modern appearance and the present day heights were obtained only in the Cenozoic Era after Neogene (Miocene) tectonic activity (YAKCHIMOVICH 1992).

Modern reptilian fauna of Bashkortostan

The modern reptilian fauna of Bashkortostan consists of 10 widespread species including one turtle, three lizard and six snake species (KHABIBULLIN 2001a) (table 1); species endemic to RB are not known.

RESULTS

A summary of paleontological data

Late Cenozoic reptile remnants from ten excavation sites were analyzed (fig. 1). Quaternary reptilian fossil materials were found mainly in caves (eight out of ten sites).

The main source of bone concentrations were owl fecal pellets which were "practically teemed with lizard scutes, frog bones and tiny unidentified fossil particles" (SUKHOV 1972a: 137). Remnants of five reptile species were identified; all five are widespread common recent species. Due to lack of quantitative analyses in the relevant publications a species list is all that could be compiled (table 2).

Fossil records of *Emys orbicularis* have not been described from the territory of RB so far (KHABIBULLIN 2001b) although

Table 2: Fossil reptile remains of the late Cenozoic from the area of the Republic of Bashkortostan (South Urals, Russia)

Tab. 2: Fossile Reptilienreste des späten Känozoikums aus dem Gebiet der Republik Baschkortostan (Südural, Rußland). Cave - Höhle.

Epoch Epoche	Locality Fundort	Fossil reptiles found Fossilfunde von Reptilien	Literature Schriften
Holocene	Zapovednaya (cave)	*A. fragilis*, *Z. vivipara*, *V. berus*	SATAEV & MAKAROVA (1997)
	Zapovednaya II (cave)	*A.fragilis*, *Z.vivipara*, *N.natrix*, *V.berus*, Unidentified snakes	YAKOVLEVA (2002)
	Ziganskaya (cave)	Unidentified lizards, snakes / unbestimmte Eidechsen, Schlangen	SUKHOV (1978)
	Lemeza (I) (cave)	*A. fragilis*, *N. natrix*, *V. berus*	YAKOVLEVA (2002)
	Lemeza (II) (cave)	*N. natrix*, *V .berus*	YAKOVLEVA (2002)
	Lemeza IV (cave)	*A. fragilis*, *N. natrix*, *V. berus*	YAKOVLEVA (2002)
	Nukatskaya (cave)	*A. fragilis*, *Z. vivipara*, *N. natrix*, *V. berus*	YAKOVLEV et al. (2000)
Pleistocene	Krasny Bor	*A. fragilis*, *L. agilis*, *N. natrix*, *V. berus*(?)	SUKHOV (1972b); CHKHIKVADZE & SUKHOV (1977)
	Kyzyrbak (cave)	Unidentified lizards, snakes / unbestimmte Eidechsen, Schlangen	SUKHOV (1978)
Eopleistocene	Akkulaevo	*Lacerta* sp.	SUKHOV 1972a

they are abundant in numerous excavations of Western and Central Europe, Ukraine, Caucasus, and Central European Russia (ROZHDESTVENSKY & TATARINOV 1964), i.e. within the limits of the turtle's present day geographical range.

In the South Urals *Anguis fragilis* is known from Late Pleistocene (near Krasny Bor: SUKHOV 1972b [age re-determined by A. G. YAKOVLEV 1996]), Holocene (Zapovednaya cave: SATAYEV & MAKAROVA 1997; Nukatskaya cave: YAKOVLEV et al. 2000; Zapovednaya II, Lemeza II caves: YAKOVLEVA 2002) and Late Holocene (Lemeza I, IV caves: YAKOVLEVA 2002) excavations. Fossil remnants of *A. fragilis* are abundant in Quaternary excavations in the European part of the former Soviet Union (ROZHDESTVENSKY & TATARINOV 1964).

In RB unidentified fossil *Lacerta* sp. remnants were found (SUKHOV 1972a) in the Akkulaevo excavation site (Eopleistocene). In the former USSR, fossils of the lizard genus *Lacerta* are known from the Pliocene of the Ukraine (ROZHDESTVENSKY & TATARINOV 1964), the Miocene of the Caucasus, the Eopleistocene of the Perm region (SUKHOV 1975), the Low Pleistocene of the Nizhny Novgorod region (RATNIKOV 1998) and the Pleistocene of the Belgorod region (RATNIKOV 1988). In the Pliocene, lacertid lizards had a wide distribution in the region north to the Black Sea (CHKHIKVADZE et al. 1983; ZEROVA & CHKHIKVADZE 1984).

In the South Urals, fossil *Lacerta agilis* were found in Krasny Bor (Late Pleistocene). Fossils of *Zootoca vivipara* were found in the Holocene sediments of the Zapovednaya cave (SATAYEV & MAKAROVA 1997), Nukatskaya cave (YAKOVLEV et al. 2000) and Lemeza IV cave (YAKOVLEVA 2002). *Lacerta agilis* evolved in the Early Pliocene (KALYABINA et al. 2001) within the Caucasus region (YABLOKOV 1976). Earlier information on fossil *Lacerta* found in Kazakhstan remained unconfirmed (CHKHIKVADZE et al. 1983). Possible explanations could be (KHABIBULLIN 2002): the recent *L. agilis* and *Z. vivipara*, currently distributed widely across Northern Kazakhstan, did not colonize Kazakhstan before the post glacial period; or both these species were not abundant and just not represented in examined fossil materials.

From RB, fossil bones of *Natrix natrix* are known from the Late Pleistocene (Krasny Bor excavation: SUKHOV 1972b; CHKHIKVADZE & SUKHOV 1977) and from the Middle (Nukatskaya cave: YAKOVLEV et al. 2000; Zapovednaya II and Lemeza II caves: YAKOVLEVA 2002) and Late (Lemeza I and Lemeza IV caves: YAKOVLEVA 2002) Holocene.

Fossil Colubridae are known from Quaternary excavations of Moldavia, Ukraine and European Russia (ZEROVA & CHKHIK-

VADZE 1984). Fossils of Eopleistocene *Elaphe dione* are known from Poland (KHOZATSKY 1982), from the Pleistocene of the Crimea (ZEROVA & CHKHIKVADZE 1984), and from the Low Pleistocene of the Nizhny Novgorod region (RATNIKOV 1998), far to the north of the present geographic range of the species. Fossil *Natrix tessellata* is known from the Pleistocene of the Crimea (ZEROVA & CHKHIKVADZE 1984), and the Pleistocene of the Belgorod region (RATNIKOV 1998), fossil records of *N. natrix* from Middle Pleistocene sediments of Georgia (BARYSHNIKOV & NESOV 1999), Ukraine (ZEROVA & CHKHIKVADZE 1984), and the Low Pleistocene of the Nizhny Novgorod region (RATNIKOV 1998).

Fossil *V. berus* is known from the Anthropogene of the Ukraine (ZEROVA & CHKHIKVADZE 1984), from the Middle Holocene (Zapovednaya cave: SATAYEV & MAKAROVA 1997; Nukatskaya cave: YAKOVLEV et al. 2000; Zapovednaya II, Lemeza II caves: YAKOVLEVA 2002) and Late Holocene (Lemeza I, IV caves: YAKOVLEVA 2002) of South Urals.. Fossil Upper Pleistocene remnants supposedly belonging to *V. berus* were found in Krasny Bor (SUKHOV 1972b; CHKHIKVADZE & SUKHOV 1977).

Fossil Viperidae (no species indicated) are known from the Low Pleistocene of the Nizhny Novgorod region (RATNIKOV 1998). *Vipera ursinii* is geochronologically older than *V. berus* (GARANIN 1983), which had possibly evolved only during the Ice Age in Central Europe in Romania (NIKOLSKY 1947; CARLSSON 2003; CARLSSON et al. 2004).

A review of Late Cenozoic landscapes, climate and vegetation

The landscapes of modern appearance in the South Urals started development by the end of the Miocene (YAKCHIMOVICH 1992). At the same time (Late Miocene) the present-day two-rivered orography net established: waterflows from western and southern mountain slopes were part of the Paleo-Volga and Paleo-Ural river basins whose waters flowed into the Caspian Sea, while the waters from the eastern slopes were part of the Paleo-Ob river basin whose waters flowed into the Arctic Ocean. One of the most important biological structures to evolve in the Miocene was grass.

In the Pliocene, continentality and aridity increased greatly in the southeastern part of the Russian (East-European) plain. Coniferous mountain forests with patches of open grass and water/marsh vegetation dominated. The Lower Pliocene sediments were very rich in grass and bush pollen (NEMKOVA 1981), which indicates the presence of open grasslands. The basis of modern vegetation zones in the Fore-Urals was established by the Early Pliocene.

As a result of increased water levels, the Caspian Sea ingressed twice into the South Urals region in Late Eopleistocene (YAKCHIMOVICH 1970). The first, or Early Akchagyl ingression was chronologically shorter but caused deeper submergence of the land than the second. Simultaneously, the boreal waters from the Arctic Ocean expanded to the South Urals along the western slopes of the Ural Mountains. Thus, in Early Eopleistocene, the Ural region was cut off from the Russian Plain for a short period. The maximal sea ingression into the South Urals occurred in the Middle Akchagyl. Along the valleys of the ancient river systems waters invaded the South Fore-Urals: one arm from the north-west along the Paleo-Belaya river basin, the other from the south along the Paleo-Sakmara and its tributary river valleys. These two arms were demarcated by the hills of the Obschiy Syrt (YAKCHIMOVICH 1965). Thus, the South Ural was cut off from the Russian Plain in the Northwest, Southwest and South. However, the land connection was soon reestablished.

During the Pleistocene when much of the world's temperate zones were alternately covered by glaciers during cool periods and ice-free during the warmer interglacial periods, climate fluctuations had a striking impact on the floras and faunas. MONIN & SHISHKOV (1979) found that there were four consecutive glaciations in East Europe (fig. 2). According to these authors the Dniper glaciation, maximal for the Russian Plain, was not so for the Ural: in this region the first Ice period, Oka - about 18,000 years ago, had the biggest southward expansion when the Oka ice sheet had spread as far as 55° N to the south, i.e., all northern part of

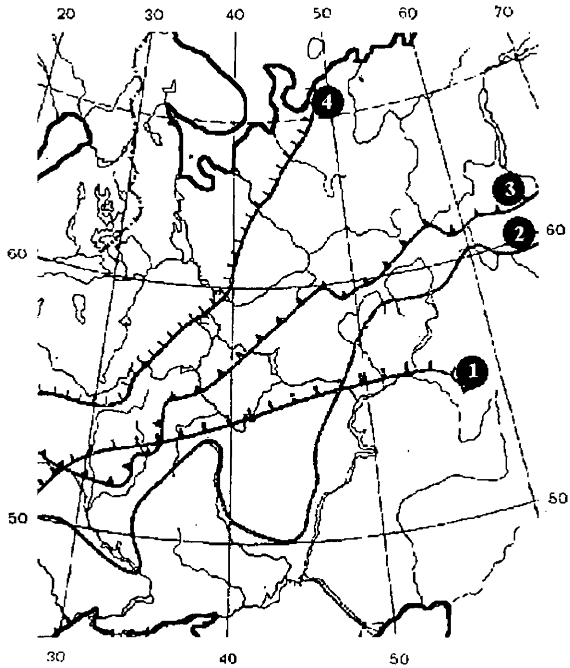

Fig. 2: Scheme of the southern limits of peistocene glaciations in the area of the Russian plain (according to MONIN & SHISHKOV 1979). 1 – Oka; 2 – Dniper; 3 – Moscow; 4 – Valday.

Abb. 2: Schematische Darstellung der Südgrenzen pleistozäner Vereisungen auf dem Gebiet der Russischen Tiefebene (nach MONIN & SHISHKOV 1979). 1 – Oka; 2 – Dnjepr; 3 – Moskau; 4 – Valdai.

the Republic of Bashkortostan was covered by ice.

The south Ural Mountains and foothills were not glaciated even at the time of maximal (Dniper? Oka?) glaciation; when there were small ice caps only on the highest mountain peaks during the Middle and Late Pleistocene (YAKCHIMOVICH 1965).

Very typical for the Pleistocene were widespread birch forests with patches of coniferous and broad-leaved woods; to the south, the area was dominated by open grass vegetation with patches of gallery forest along the streams. Vegetation in the South Urals and adjacent territories was very scarce with fungi dominating, as is typical for periglacial steppes (YAKCHIMOVICH 1965).

Pleistocene biota were extremely similar to modern ones – many genera and even species of Pleistocene reptilians existed in that period.

During the following epoch, the Holocene, the climate in the South Urals was slightly warmer than during the Pleistocene. In the Boreal, the coniferous forests, especially pine forests, became dominant. Global warming and decline of continentality in the Early Holocene favored forests development, although in the Fore-Urals for the most of the Holocene as well as for interglacials, the notable role of broad-leaved woods as compared with the Russian Plain has been reported (NEMKOVA 1981; 1992). During the climate optimum of the Atlantic (with the climate conditions slightly warmer than in modern times), in medium height Ural mountains the broad-leaved forests became more abundant. For the Sub-boreal of the south, lime forests and increased portions of birch and broad-leaved forests have been reported. In the Sub-Atlantic, the vegetation patterns resembled those of today; the firpine woods with lime, oak and elm patches and the mainly woodless spaces emerged at the very end of the Sub-Atlantic. In the Holocene there was a general vegetation succession from cold to warm steppe-forests.

So, during the Cenozoic Era in the South Urals, a double flora succession took place: in the Oligocene the ancient Poltava evergreen flora was replaced by the Turgai broad-leaved forests, the latter transformed to the modern type flora (YAKCHIMOVICH 1992). The entirely modern flora in the South Urals has been formed by Apsheron (i.e. in Pre-Ice Age!) though the hypothesis of its Late Akchagyl origin was not fully rejected (NEMKOVA 1981; YAKCHIMOVICH 1992).

DISCUSSION

All recent families of the reptilian fauna of the former Soviet Union had already evolved by the end of the Paleogene (BAKRADZE & CHKHIKVADZE 1988). The substantial Middle Cenozoic cooling caused shrinkage of the geographic ranges of the thermo- and hygrophilous reptiles. It is believed that, during the Late Eocene – Early Oligocene the most significant changes occurred in the reptilian fauna of Kazakhstan, Caucasus and Europe (CHKHIKVADZE et al. 1983).

Unlike modern herpetofaunas of Central Asia and Kazakhstan, which most likely started to form no later than in the Middle Oligocene – Early Miocene (CHKHIKVADZE et al. 1983), the modern herpetofauna of the Urals must have begun formation in the Late Pliocene (KHABIBULLIN 2002). All genera and most recent reptile species which today represent the North Eurasian herpetofauna, had already evolved by the Early Pliocene.

Despite the fact that Lacertidae are the only fossil reptiles known from the Pliocene of Bashkortostan (KHABIBULLIN 2001b), fossil materials of other widespread and numerous present-day families (Anguidae, Colubridae and Viperidae) can be expected to be found. Until now there are no records of Pliocene-Holocene reptilian fossils which differ from recent taxa and also no records on other fossil reptiles that inhabited the territory of Bashkortostan in the past. The paucity of paleontological materials on the South Urals Quaternary reptiles does not allow for more comprehensive conclusions.

The gradual cooling in the Pliocene – Eopleistocene and particularly the Pleistocene Ice Age (with the Oka Ice Age as a probable exception) had a striking impact on the reptilian fauna of the Urals, as well as on that of the whole Palearctic. Even though the ice sheets did not cover the territory of the South Urals, the periglacial cold zone and ice-related events spread over the whole Ural Mountain region (VELICHKO 1975). By the end of the Valday glaciation the southernmost edge of permafrost extended southward as far as 46° N. Moreover, the regions of formerly only seasonal Siberian-like congelation now reached the Caucasus and the North of the Caspian Sea (GERASIMOV & VELICHKO 1982). This means that the whole East European Plain and a major part of the West Siberian Plain were frozen lands.

In the territory of European Russia, a sophisticated complex of surface structures of cryogen origin with dominating large 20-30 m long and 4-5 m broad crack systems had evolved at this time. To the east of the Ural Mountains, in the territory of the South Trans-Urals and West Siberia "...cryogen transformations like involutions and ice clines occurred frequently and served .... as an indicator of long-term frozen ground and severely cold climate" (STEPHANOVSKY & MALEEVA 1977). On the other hand, in some microhabitats on the western slopes of the South Ural Mountains the nemoral forest vegetation and broad-leafed floras managed to survive even during the very cold periods. Despite this fact as well as the evidence of fossil findings of underground dwellers like the mole-rat *Myospalax myospalax* LAXMANN, 1773, the poikilothermic reptiles did not survive these cold climate conditions, and disappeared from most parts of Siberia, the Urals and the Russian Plain (NIKOLSKY 1947), as well as North Europe.

The impact of Pleistocene climatic changes on the fauna of Europe was substantial: The low temperatures during the glacials displaced most thermophilic groups: Reptile life was heavily affected; many species became extinct or lost large parts of their former ranges (LENK et al. 1998). The situation was aggravated by the existence of natural barriers, preventing the animals from escaping to the South. Such barriers were the Mediterranean, Black and Caspian Seas, the Balkans, Caucasus and Central Asian mountain chains as well as arid areas in Central Eurasia. Only species that could survive in one of various restricted however climatically favoured areas ("glacial refugia") in the southern extremities of Europe and adjacent regions were saved from extinction (LATTIN 1949; HEWITT 1996). After analyzing data on birds' paleontology and biogeography, ornithologists proposed the existence of several such refugia in Central and Eastern Asia (KRIVENKO 1991).

Hence, the recent presence of reptiles in Eurasia north to a line which is roughly represented by the 42nd parallel must have been caused by postglacial migration/colonization events (STUGREN & KOHL 1980; COOPER et al. 1995; TABERLET et al. 1998). The sequence of glaciations and interglacials made the animal's geographic ranges repeatedly shrink and expand. However, the fact that fossil reptilian's remnants have been found in temperate Eurasia sediments support the idea of relatively warm local climate during Pleistocene interglacial periods (RATNIKOV 1996).

For the Eastern European herpetofauna the most crucial refugia must have been those in the Balkans, Caucasus, Asia Minor and probably in Central Asia (KHABIBULLIN 2001a, 2002). From these refugia started the inter- and postglacial dispersion into the present day distribution areas.

As to originally widespread species, practically each refugium gave origin to its own subspecies. The diverse subspecies structure of several modern European reptile species with vast geographic range like *Lacerta agilis* (see KALYABINA et al. 2001) or *Emys orbicularis* (see FRITZ 1998) supports this idea.

The dispersion from glacial refugia was induced when glaciers melted and climate became warmer some 12,000 to 8,000 years ago in the Pre-Boreal period of the Holocene (KRIVENKO 1991). This expansion significantly accelerated during the Holocene climate optimum. The main migratory flow of reptiles that now inhabit Central and North Europe and Siberia, was directed from refugia in the Caucasus, and South and South-Eastern Europe towards North and Northeast through the East-European Plain and Ural Mountains as far as Siberia. Analysis of the clinal variability of several morphological parameters in reptilian species of the temperate zone supported this hypothesis (YABLOKOV 1976; ANISIMOVA 1981).

In the Sub-Boreal and Sub-Atlantic Holocene periods, after slight cooling of the climate and subsequent retreat of most animals' geographical ranges, the climate conditions became relatively stable (KRIVENKO 1991).

As one can see from atlases of reptilian geographical ranges, all reptile species inhabiting the western slopes of the Urals, can also be found on their eastern slopes. So the mountainous landscapes of the Urals as a physical phenomenon did not globally influence the reptilian post-glacial dispersion and colonization process in North Eurasia, though mountain landscapes do play a significant role on the microhabitat level.

Great forest complexes remained unchanged only in the mountainous part of the South Urals, unlike the steppe regions that are mainly agriculture lands now. The mountains of the South Urals and, consequently, their forests extend southwards into the steppe zone. This fact favors the southward dispersion of boreal species like *Zootoca vivipara* and *Vipera berus*. However, because of human activities, these conditions favorable for forest species evolved only in the most recent past. Intensive agricultural, farming and forestry activities mainly affected the plain regions, not the mountains. On the other hand, the Ural Mountains form the northern border of the geographic range of several reptile species like *Emys orbicularis*, *Elaphe dione* and *Vipera ursinii*. For these species montane temperate zone environmental conditions are unfavorable. The Ural Mountains are barriers between the water basins of Volga River, Ob River and Ural River, and from this point of view they influenced the distribution patterns and played a particular role in the post-glacial colonization process of hydrophilous reptiles (i.e. *N. natrix* dispersion from the Caspian sea northward along the Ural river).

The first humans arrived at the South Urals not before the Late Holocene. In Bashkortostan the earliest known archeological camp is Mysovaya near Lake Karabalykty in the Trans-Urals that dates back to the Early Paleolithic (SHAKUROV 1996). During the Paleolithic and Mesolithic the so-called "consuming" economy (i. e. hunting, fishing and foraging) dominated. In the Neolithic (6,000-4,000 years BC) in the South Urals the transition from "consuming" to "productive" economy (i. e. agriculture, cattle breeding and fish farming) took place. The intensive colonization of the South Urals territories dates back to the Bronze Age when the first stationary settlements were established. Until the 17th-18th century the main activities of semi-nomadic local Bashkir people remained the cattle breeding and early apiculture. Only by the end of nineteenth century the thoroughly settled way of life spread over the whole South Urals. The whole sum of anthropogenic impacts on environment and local biota is very diverse, aprogressively increasing and by nowadays very intense. This primarily results in natural landscape transformations, habitat fragmentation, diminished biodiversity and reduction of number of suitable environments.

At least in some reptile species, the recent range regression has been caused and, possibly, post-glacial colonization process in Central and North Europe has been influenced not only by suboptimal conditions of their natural environment but also, more important, direct and indirect disturbances by man (e. g. *Emys orbicularis* – see FRITZ 1998). As a consequence the northern distribution limit of reptiles in Europe is not a natural one. Instead, it reflects impacts over the course of thousands of years in a heavily disturbed environment. The patterns of larger-scale Holocene reptile colonization (for example, migratory routes) were less affected by man in Eastern Europe because it is much less populated as compared to Western Europe. However, the local distributional "mosaic" is to a considerable degree the result of human, mostly agricultural, activities.

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