



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Biostratigraphy)

Dynamics of East European modern amphibian and reptile species distribution areas and their potential use in Quaternary stratigraphy



Dynamiques des aires de distribution des espèces d'amphibiens et reptiles d'Europe orientale et potentiel pour leur utilisation en stratigraphie du Quaternaire

Viatcheslav Yu. Ratnikov

Geological Faculty, Voronezh State University, University sq., 1, Voronezh 394006, Russia

ARTICLE INFO

Article history:

Received 10 February 2015

Accepted after revision 24 August 2015

Available online 26 October 2015

Handled by H.A. Blain

Keywords:

Quaternary

Biostratigraphy

Amphibians

Reptiles

East European plains

ABSTRACT

The last appearance dates and especially occurrences of amphibian and reptile species have a rather limited stratigraphic potential in Quaternary deposits. However, changes in their areas of distribution against the background of climate variations open some possibilities for biostratigraphy. Based on fossil assemblages of amphibians and reptiles, interglacial or periglacial conditions can be distinguished. Substitution of forest associations by those typical for forest-steppes or steppes within the limits of the modern forest zone can be attributed to climate aridization at the onset of a glaciation. Therefore, during paleogeographic reconstructions, it is important to determine a natural zone, instead of an assortment of possible biotopes. Glacial intervals for modern steppe zones can theoretically be visualized by the emergence of desert taxa. Distribution areas of amphibians and reptiles during interglacial optima show different outlines. They usually varied slightly, but sometimes the range of some species expanded (*Bufo viridis*) or species disappeared (*Strauchbufo raddei*) from a large part of their original distribution. Such changes can be used to define large age intervals within a regional biostratigraphy.

© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Mots clés :

Quaternaire

Biostratigraphie

Amphibiens

Reptiles

Possibilités

Plaines d'Europe de l'Est

Les dates de dernière apparition, et plus spécialement, de présence d'espèces d'amphibiens et de reptiles ont plutôt un potentiel stratigraphique limité pour les sédiments quaternaires. Néanmoins, les changements de leurs aires de distribution liées aux variations climatiques offrent quelques possibilités pour la biostratigraphie. Basées sur les assemblages fossiles d'amphibiens et de reptiles, les conditions interglaciaires ou périglaciaires peuvent être distinguées. Les remplacements d'associations forestières par des associations de steppe arborée, puis steppiques, à l'intérieur des limites actuelles des zones boisées peuvent être attribués à une aridification du climat liée au début d'une glaciation. Par conséquent, lors de reconstructions paléogéographiques, il est important de déterminer un seul environnement naturel au lieu d'un assortiment de possibles biotopes. Les intervalles glaciaires pour les zones steppiques actuelles peuvent théoriquement être visualisés par l'émergence

E-mail address: vratnik@yandex.ru<http://dx.doi.org/10.1016/j.crpv.2015.08.003>

1631-0683/© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

de taxons désertiques. Les aires de distribution des amphibiens et reptiles durant les optima interglaciaires montrent des schémas différents. Généralement, elles varient peu, mais parfois certaines espèces s'étendent (*Bufo viridis*) ou disparaissent (*Strauchbufo raddei*) d'une grande part de leur distribution originelle. De tels changements peuvent être alors utilisés pour définir de larges périodes chronologiques dans le cadre d'une biostratigraphie régionale.

© 2015 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

In biostratigraphy, the relative age of sedimentary rocks is determined on the basis of changes in a species or a species complex over time (Kholmovoy et al., 2008; Stepanov and Mesezhnikov, 1979). Thus, the duration of stratigraphic divisions can, at least, not be shorter than the time of a species' existence, and the occurrence or extinction of species is assumed to be simultaneous throughout the entire distribution area. This method is widely used in the stratigraphy of Pre-Quaternary sediments.

But, this provides a problem for the biostratigraphic subdivision of Quaternary deposits. One of their specific features is the relatively short duration of assignable intervals, which is shorter than the duration of a species' existence. Modern morphological species of East European amphibians and reptiles already appeared in the fossil record prior to the Quaternary glaciations. Note that we are considering "morphological species". There is a recent tendency to increase the number of species in herpetology, as, in particular, subspecies are converted to species (compare Bannikov et al., 1977 with Ananjeva et al., 1998, then with Ananjeva et al., 2006 and Kuzmin, 2012). The species level is based on genomic features, karyotypes, and reproductive isolation, while the morphology, especially of the skeleton, can be close or even similar (Borkin et al., 2003; Pisanets, 2010; Stöck et al., 2008; Wielstra et al., 2013 and others). Such species probably have a shorter temporal duration, but because these differences cannot be seen in the fossil material, this classification is absolutely inapplicable in stratigraphy. Thus, it is impossible to determine the stratigraphic intervals within the limits of the last million years on the basis of modern amphibian and reptile species occurrences. However, some boundaries can be established on the basis of the disappearance of extinct forms. For example, representatives of Palaeobatrachidae lived in territory of the East Europe up to the Muchkapien (MIS 15, 621–568 kyr BP according to lossifova et al., 2009) interglacial (Ratnikov, 1997; Wuttke et al., 2012).

However, there are other opportunities to use modern amphibian and reptilian species for stratigraphic purposes within the limits of the Quaternary period, connected with the dynamics of the distribution areas of modern herpetofauna species. Here, we shall focus on the Pleistocene herpetofaunal assemblages from the East European plain.

2. Modern natural zones and distribution areas of amphibians and reptiles from Eastern Europe

East Europe extends from north to south about 3000 km. We can observe consecutive meridional change of natural

zones named on the basis of their vegetation type: tundra, forest-tundra, zone of coniferous forests (taiga), zone of mixed and deciduous forests, forest-steppe, steppe, desert and mountain zones (Fig. 1).

Distributions of modern amphibians and reptiles cover at present almost the whole of Eastern Europe, and their limits of distribution are determined by different factors: presence of sufficiently long seasons with positive temperatures, the degree of water warming during amphibian larval development, and so on (Bannikov and Denisova, 1956). Notably, the distribution boundaries closely coincide with natural zone transitions (Fig. 2).

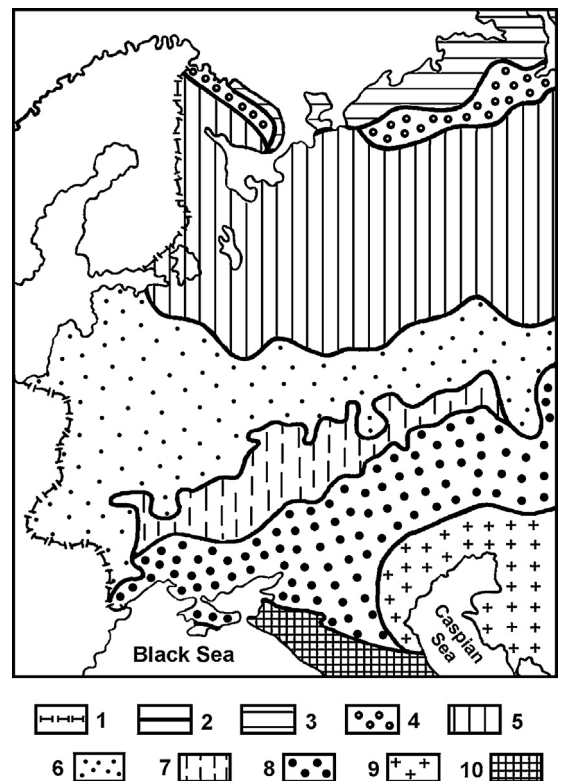


Fig. 1. Natural zones of Eastern Europe (according Nikolaeva, 1986, simplified). Symbols: 1 – western boundaries of Russia, Latvia, Belarus, Ukraine and Moldova; 2 – natural zone boundaries; 3 – tundra; 4 – forest-tundra; 5 – coniferous forests; 6 – mixed and deciduous forest; 7 – forest-steppe; 8 – steppe; 9 – desert; 10 – mountain zones.

Fig. 1. Zones naturelles d'Europe orientale (simplifié de Nikolaeva, 1986). Symboles : 1 – frontières occidentales de l'ex-Union soviétique ; 2 – limites des zones naturelles ; 3 – toundra ; 4 – toundra arborée ; 5 – forêts de conifères ; 6 – forêts mixte et à feuilles caduques ; 7 – steppe arborée ; 8 – steppe ; 9 – désert ; 10 – zones montagneuses.

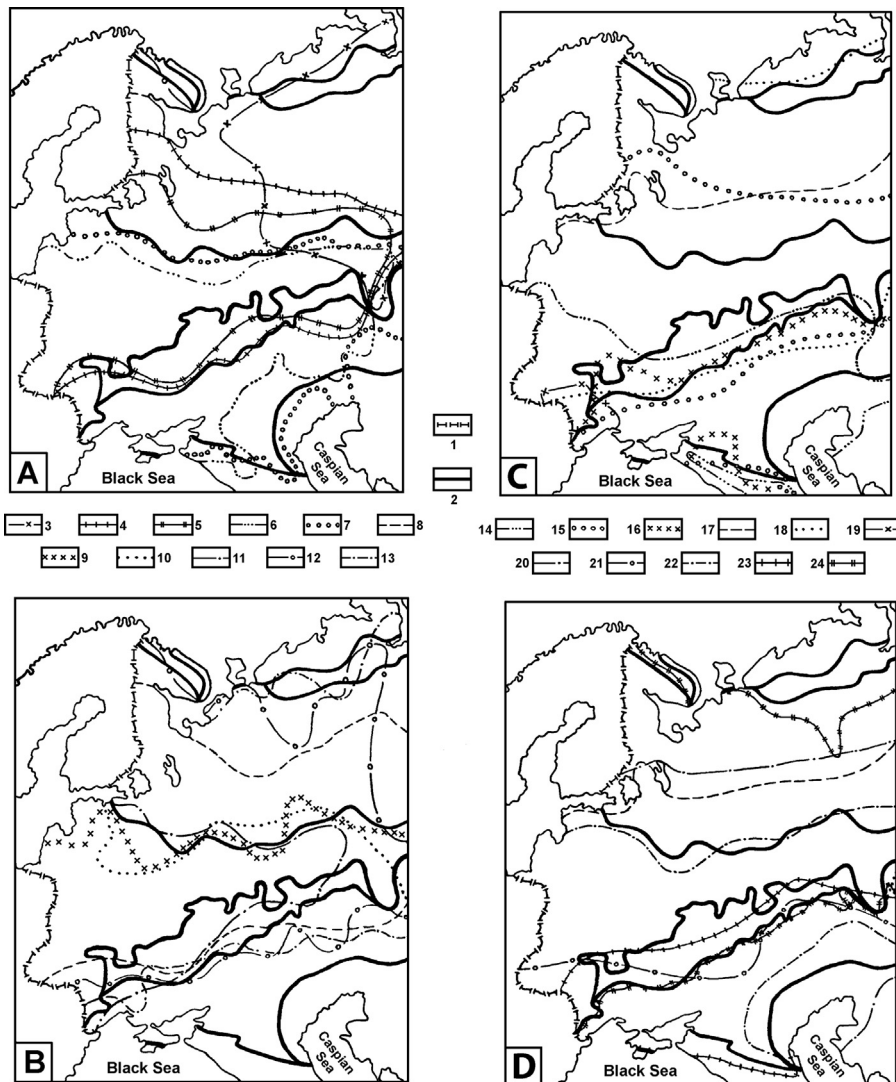


Fig. 2. Boundaries of natural zones (simplified) and distribution areas of modern species (according Bannikov et al., 1977): A – tailed amphibians, Firebellied Toad and Spadefoot; B – toads and frogs; C – turtle and lizards; D – snakes. Symbols: 1 – western boundaries of Russia, Latvia, Belarus, Ukraine and Moldova; 2 – natural zone boundaries; 3–13 – amphibian distribution area boundaries: 3 – *Salamandrella keyserlingii*, 4 – *Lissotriton vulgaris*, 5 – *Triturus cristatus*, 6 – *Bombina bombina*, 7 – *Pelobates fuscus*, 8 – *Bufo bufo*, 9 – *Bufo viridis*, 10 – *Pelophylax ridibundus*, 11 – *Pelophylax lessonae*, 12 – *Rana temporaria*, 13 – *Rana arvalis*; 14–24 – reptile distribution area boundaries: 14 – *Emys orbicularis*, 15 – *Anguis fragilis*, 16 – *Eremias arguta*, 17 – *Lacerta agilis*, 18 – *Zootoca vivipara*, 19 – *Lacerta viridis*, 20 – *Natrix natrix*, 21 – *Natrix tessellata*, 22 – *Coronella austriaca*, 23 – *Vipera renardi*, 24 – *Vipera berus*.

Fig. 2. Limites des zones naturelles (simplifiée) et aires de distribution d'espèces modernes (selon Bannikov et al., 1977) : A – amphibiens à queue ; B – crapauds et grenouilles ; C – tortues et lézards ; D – reptiles. Symboles : 1 – frontières occidentales de l'ex-Union Soviétique ; 2 – limites des zones naturelles ; 3–13 – limites de l'aire de distribution des amphibiens : 3 – *Salamandrella keyserlingii*, 4 – *Lissotriton vulgaris*, 5 – *Triturus cristatus*, 6 – *Bombina bombina*, 7 – *Pelobates fuscus*, 8 – *Bufo bufo*, 9 – *Bufo viridis*, 10 – *Pelophylax ridibundus*, 11 – *Pelophylax lessonae*, 12 – *Rana temporaria*, 13 – *Rana arvalis* ; 14–24 – limites de l'aire de distribution des reptiles : 14 – *Emys orbicularis*, 15 – *Anguis fragilis*, 16 – *Eremias arguta*, 17 – *Lacerta agilis*, 18 – *Zootoca vivipara*, 19 – *Lacerta viridis*, 20 – *Natrix natrix*, 21 – *Natrix tessellata*, 22 – *Coronella austriaca*, 23 – *Vipera renardi*, 24 – *Vipera berus*.

The northern boundaries of the distribution of terrestrial ectothermic vertebrates almost never transverse the limits of forest-tundra and are commonly located far to the south (only the areas of *Salamandrella keyserlingii*, *Rana arvalis* and *Zootoca vivipara* rarely extend into low bush and sedge tundra). Northern distribution boundaries of *Bombina bombina*, *Pelobates fuscus*, *Bufo viridis*, *Pelophylax lessonae*, *Pelophylax ridibundus* and *Coronella austriaca* roughly coincide with the transition from coniferous taiga

to mixed forest. The southern distribution limits of *S. keyserlingii*, *Triturus cristatus*, *Lissotriton vulgaris*, *Bufo bufo*, *P. lessonae*, *Rana temporaria*, *Anguis fragilis*, *Z. vivipara*, *Vipera berus* and northern distribution limits of *Emys orbicularis*, *Eremias arguta* and *Vipera renardi* generally coincide with the location of the forest-steppe zone (Bannikov et al., 1977; Nikolaeva, 1986).

Every species is associated with certain types of biotopes (Ananjeva et al., 1998; Bannikov et al., 1977;

Table 1

Distribution of modern species of amphibians and reptiles through different natural zones.

Tableau 1

Distribution des espèces modernes d'amphibiens et de reptiles selon les différentes zones.

Species	Tundra	Forest-tundra and coniferous forests	Mixed and deciduous forest	Forest-steppe	Steppe	Desert
<i>Salamandrella keyserlingii</i>	+	++	++	+		
<i>Lissotriton vulgaris</i>		+	++	+		
<i>Triturus cristatus</i>		+	++	+		
<i>Bombina bombina</i>			++	++	++	
<i>Pelobates fuscus</i>			+	++	++	
<i>Bufo bufo</i>		++	++	++		
<i>Bufo viridis</i>			+	++	++	++
<i>Pelophylax ridibundus</i>			+	++	++	++
<i>Pelophylax lessonae</i>			++	++		
<i>Rana temporaria</i>		++	++	++		
<i>Rana arvalis</i>	+	++	++	++	+	
<i>Emys orbicularis</i>			++	++	++	
<i>Anguis fragilis</i>		+	++	++	+	
<i>Eremias arguta</i>				++	++	++
<i>Lacerta agilis</i>		+	+	++	++	
<i>Lacerta viridis</i>			++	++	+	
<i>Zootoca vivipara</i>	+	++	++			
<i>Natrix natrix</i>		++	++	++	+	
<i>Natrix tessellata</i>				+	++	+
<i>Coronella austriaca</i>			++	++	+	
<i>Vipera berus</i>		++	++	++		
<i>Vipera renardi</i>					++	+

According to Ratnikov, 1996a.

++: species is common; +: species is scarce.

Garanin, 1983; Kuzmin, 2012). Both population density and the number of individuals inhabiting a given territory depend on the distribution of biotopes (Ratnikov, 1996a). Since adjacent natural zones can include identical biotopes, every amphibian or reptilian species may inhabit two or more zones; on the other hand, each zone is characterized by a specific association of species (Table 1). Therefore, the environmental conditions and possibly the natural zone in the vicinity of a locality can be reconstructed on the base of a fossil assemblage.

The following ecological types can be marked out among modern terrestrial ectothermic vertebrates of Eastern Europe (Ratnikov, 1996a):

- species of closed biotopes typical for the forest zone are: the Siberian Salamander *S. keyserlingii*, the Smooth Newt *L. vulgaris*, the Crested Newt *T. cristatus*, the Common Toad *B. bufo*, the Grass Frog *R. temporaria*, the Pool Frog *P. lessonae*, the Slow Worm *A. fragilis*, the Viviparous Lizard *Z. vivipara* and the Adder Viper *V. berus*. The Moor Frog *R. arvalis* is more characteristic for the forest zone, but also inhabits tall grass wet meadows and, therefore, has a very broad area, extending from steppes to forest-tundra. The distribution of the Smooth Snake *C. austriaca* also extends from forests to steppes, although this species prefers closed biotopes as well;
- species of open spaces, including deserts, are: the Green Toad *B. viridis*, the Marsh Frog *P. ridibundus*, the Sand Lizard *Lacerta agilis*, the Eastern Green Lizard *L. viridis*, the Steppe Runner *E. arguta* and the Steppe Viper *V. renardi*. They penetrate to some extent into the forest zone;
- intrazonal species, the distribution of which is not connected directly with changes of natural zones. The

distribution of the Fire-bellied Toad *B. bombina* is primarily related to the dynamics and temperature regimen of the inhabited ponds (it prefers small, well-warmed up ponds with lentic or slowly moving waters) (Bannikov et al., 1977; Kuzmin, 2012; Pisanets, 2007). The Common Spadefoot *P. fuscus* inhabits the territories with dry and sufficiently soft soils suitable for digging (Ananjeva et al., 1998; Garanin, 1983; Kuzmin, 2012). The distribution areas of both species slightly extend into the coniferous forest zone in the north, but probably have an indirect connection to natural zones (they are most numerous in steppe and forest-steppe zones). Concerning the semi-aquatic snakes, the Grass Snake *Natrix natrix* is more characteristic for closed biotopes, whereas the Dice Snake *N. tessellata* has a preference for open spaces. The European Pond Terrapin *E. orbicularis* does not extend to the north further than the mixed forest zone (Bannikov and Denisova, 1956; Bannikov et al., 1977; Garanin, 1983; Pikulik, 1985).

Of the above-mentioned natural zones, the forest-steppe zone is the richest in species number because it is inhabited by representatives of both closed and open biotopes. Since typical tundra species of amphibians and reptiles are absent in Eastern Europe, the forest-tundra is inhabited only by woodland taxa.

3. Dynamics of distribution areas

It is obvious that the covering glaciers, periodically coming from Scandinavia, have had an influence on the distribution areas of animals. First of all, ectothermic animals evidently disappeared from the territories covered by

glaciers. But changes also occurred in the periglacial territories.

Not so long ago, all natural zones in the Quaternary period were considered to have been displaced under the influence of decreasing temperature across the glacier edge, and the animals within the zones migrated as the zones were displaced. The spatial location of ecosystems was believed to constantly fluctuate from the north to the south and back. However, experts on small mammals noted the occurrence during glacials of so-called “mixed faunas”, consisting of fossil assemblages of taxa (genera and species) that in the present day do not occur in the same biotopes; this concerns in particular steppe and tundra species (Agadzhanian, 1972; Markova, 1994, 2004; Markova and Puzachenko, 2008; Rekovets, 1995). Formation of such assemblages is possible if the forest zone is eliminated as a barrier between tundra and steppe. Therefore, the hypothesis of zones migration does not explain the available data. We need a hypothesis that explains both the formation of the “mixed faunas” and the restoration of a forest zone after a glaciation.

Importantly, temperature decrease is not the only influence of a glacier on an environment. Condensation of water in ice leads to the aridization of the climate and is accompanied by the reduction of forest and by the predominance of grassy vegetation (Velichko, 1973). Thus, the distribution of tundra during continental glaciations moved towards the south, whereas the steppe zone moved towards the north. At the same time, the forested area was divided into ever decreasing areas that were gradually reduced to rather small massifs. As a result, unique periglacial landscapes were formed. They were populated by original therioecocomplexes that included tundra and steppe representatives. Analogues for them do not exist today (Baryshnikov and Markova, 2002; Markova and Puzachenko, 2008; Rekovets and Nadachowski, 2007). That means that glacial ecosystems differed in their structure both from interglacial ecosystems from the past and from all ecosystems existing nowadays, which are also interglacial. In the background of these periglacial landscapes, refuges of forest vegetation persisted in river valleys.

Natural zones restored gradually after the retreat of glaciers. Forests did not come from the south, but appeared as a result of expansion of tree taxa in the refuges as humidity increased in the watersheds (Ratnikov, 2013).

Against the background of vegetation change, the distribution areas of “ectothermic” animals constantly varied. The distribution areas of two ecological types, the inhabitants of closed and opened biotopes, also changed (Ratnikov, 2009). The splitting of forests into a mosaic, with the subsequent reduction into refuges, led to the corresponding distribution fragmentation and area reduction of species in closed biotopes. Most likely, amphibians and reptiles did not survive in all refuges of forest vegetation. Then, after the retreat of glaciers and subsequent expansion of forests, the distribution areas of the populations inhabiting these refuges widened and eventually united.

During the fragmentation of forest areas at the beginning of glacial periods, the steppe species had opportunities to advance toward the north along the “corridors” of steppe between the “islands” of forests, and then to widen their

distribution as these “islands” reduced in sizes. This expansion was bounded by the limits of glaciers distribution. During a deep subsequent penetration of continental ice toward the south, especially at the time of Don or Moscovian (= Dnieper) glaciations (MIS 16, 659–621 kyr BP and MIS 6, 186–127 kyr BP, respectively, according to Iossifova et al., 2009), areas of steppe species became smaller still. Then, during glacial retreat, the restoration of forest area reduced the open spaces and consequently, the range of their associated species.

In contrast with mammals, East European species of amphibians and reptiles do not include typical tundra forms, and “mixed” herpetofaunal complexes have not been observed. Only the degree of herpetofaunal diversity distinguishes assemblages from the different climatic periods (Ratnikov and Mebert, 2011).

4. Possibilities for biostratigraphy

The use of the herpetological information for biostratigraphical purpose has been detailed in Table 2. First of all, the presence of “ectothermic” animal remains strongly suggests the absence of ice cover in a given place. Such situations existed either between glaciations, or outside of glacier distribution.

As forest-linked herpetofauna within the limits of periglacial hyperzone were concentrated in a few refuges, fossil associations of amphibians and reptiles at glacial intervals show poor species diversity, consisting mainly of steppe elements. Change from forest associations to forest-steppe or steppe assemblages within the limits of modern forest zone is attributed to climate aridization as a result of the coming glaciation. Therefore, during paleogeographic reconstructions, it is important to determine what is a natural zone, as opposed to an assortment of possible biotopes. For this purpose, it is necessary to consider quantitative ratios of the remains of various ecological types (Ratnikov, 1996a, 2002).

Ratios in a fossil assemblage can be different from the original ratios and require appropriate corrections. First of all, we must consider burial conditions, which have an influence on the composition of the fossil herpetofauna. The taphonomic type of locality regulates the area from which fossils are derived. Alluvial channel deposits contain remains of amphibians and reptiles from a significant part of a river basin and, therefore, they mostly reflect the composition of herpetofauna that inhabited this territory during the locality formation. Inundated, dead channel, limnetic, marsh, proluvial, deluvial, karst and cave deposits contain the herpetofauna remains from the close vicinity of the pond or locality (Ratnikov, 1996a, 2002). Another correction is the degree of preservation. Agadzhanian (1979) pointed out that the destruction rate of organic remains is higher in forest conditions than in steppes, due to the slower burial rate, the abundance of scavengers, and the presence of humic acids in soils. Therefore, even a few forest animal fossils can indicate a wide distribution of forest and bush biotopes. An equal ratio of forest and steppe animal fossils may be interpreted as a significant predominance of closed biotopes over open ones. Glacial intervals

Table 2

Theoretical possibilities of using of amphibians and reptiles finds in the Quaternary stratigraphy of Eastern Europe.

Tableau 2

Possibilités théoriques d'utilisation des découvertes d'amphibiens et de reptiles pour la stratigraphie du Quaternaire d'Europe orientale.

Stratigraphic subdivisions of West Europe			MIS	Stratigraphic subdivisions of East European central part		A	B	C	D	E
Holocene			1	Holocene		+	f			
Pleistocene	Upper	<i>Devensian (= Weichsel) glaciation</i>	2	Upper Neopleistocene			s			
			3	<i>Upper valdai</i>		+	f			
			4–5d	<i>Middle valdai</i>			s			
		Ipsvich (= Eemian) Interglacial	5e	<i>Lower valdai</i>		+	f	+?		
			Mikulín							
Middle	Vollstonian (= Saalian) glaciation	<i>Warta</i>	6	Middle Neopleistocene			s			
			7	<i>Moscovian (= Dnieper)</i>		+	f			
			8	<i>Gorkino</i>			s			
			9	<i>Vologodsk</i>		+	f			
			10	<i>Chekalin</i>			s			
	Hoxnian (= Holsteinian) Interglacial	<i>Fuhne</i>	11	<i>Kaluga</i>		+	f			
				Likhvin						
Lower	<i>Anglian (= Elsterian) glaciation</i>	"Cromerian complex"	12	<i>Oka</i>			s			
			13	Lower Neopleistocene		+	f		+	
			14	<i>Ikoretsk</i>			s			
			15	<i>Navlin</i>		+	f		+	
			16	<i>Muchkap</i>			s			
	Interglacial I	<i>Glaciation B</i>	17	<i>Don</i>		+	f			
			18	<i>Moiseevo</i>			s			
			?	<i>Setun'</i>		+	f		+	
				<i>Il'inka</i>		+			+	
				Upper Eopleistocene		+			+	
Pliocene				Pliocene		+			+	
				Lower Eopleistocene		+			+	

A: intervals of possible herpetofaunal remains discoveries in the territories which were covered by glaciers; B: possible changes of herpetofaunal ecological associations within the limits of modern forest territories; f: forest; s: steppe or forest–steppe; C: stratigraphic interval of authentic presence of Mongolian Toad (*Strauchbufo raddei*) in Eastern Europe; D: stratigraphic interval of authentic presence of Green Toad (*Bufo viridis*) in Eastern Europe; E: occurrence of Siberian Salamander (*Salamandrella* sp.) in central areas of Eastern Europe. Comparison of Western and Eastern European stratigraphic divisions is given according to recently published works (Markova and van Kolschoten, 2012; Shik, 2014). Glacial intervals are typeset by italic.

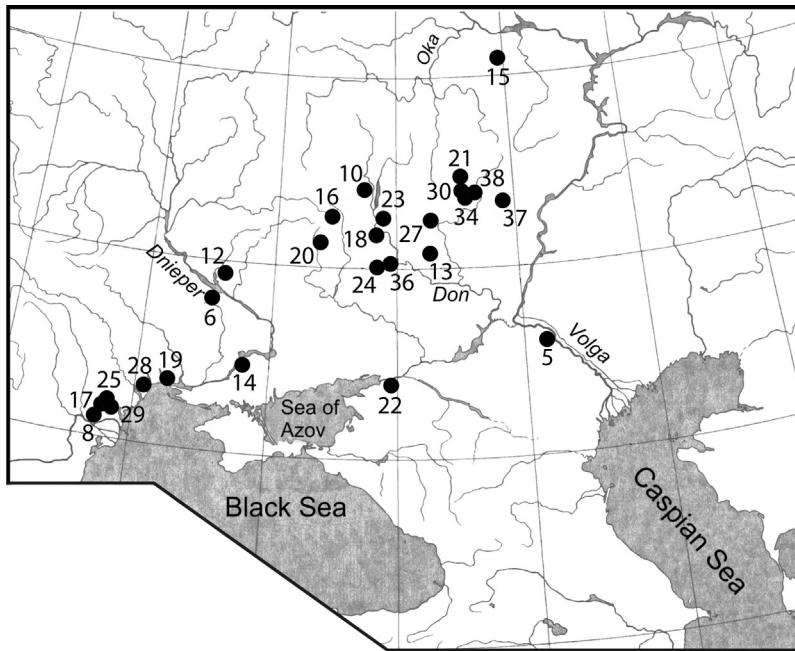


Fig. 3. Pliocene – Middle Pleistocene localities of Mongolian Toad (*Strauchbufo raddei*) in territory of the Eastern Europe (Ratnikov, 2009). Here and on Figs. 4 and 5 the numbers means the following sites: 1 – Antselovich (Upper Neopleistocene–Holocene), 2 – Bol'shie Tigany (Upper Neopleistocene), 3 – Brod (Holocene), 4 – Chernianka (Upper Neopleistocene), 5 – Cherny Yar (Middle Neopleistocene), 6 – Chigirin (Middle Neopleistocene), 7 – Devich'i Skaly (Holocene), 8 – Dolinskoe (Pliocene), 9 – Domashkinskie Vershiny (Upper Neopleistocene), 10 – Donskaya Negatchevka (Middle Neopleistocene), 11 – Gadiach (Upper Neopleistocene), 12 – Gun'ki (Middle Neopleistocene), 13 – Iliinka-2 (Lower Neopleistocene), 14 – Karai-Dubina (Eopleistocene), 15 – Kashpir (Middle–Upper Neopleistocene), 16 – Kholki (Lower Neopleistocene), 17 – Kotlovina (Pliocene), 18 – Kozii Ovrag (Lower Neopleistocene), 19 – Kryzhanovka (Eopleistocene), 20 – Kupino (Lower Neopleistocene), 21 – Kuznetsovka (Lower Neopleistocene), 22 – Liventsovka (Pliocene), 23 – Mastyuzhinka (Lower Neopleistocene), 24 – Morozovka (Middle–Upper Neopleistocene), 25 – Nagornoe-1 (Lower Neopleistocene), 26 – Nizhnee Krivche (Upper Neopleistocene), 27 – Novotroitskoe (Lower Neopleistocene), 28 – Odessa (Pliocene), 29 – Ozernoe-1 (Middle Neopleistocene), 30 – Posevkinno (Lower Neopleistocene), 31 – Repnoe (Lower Neopleistocene), 32 – Sergeevka-2 (Lower Neopleistocene), 33 – Shikhabylovo (Upper Neopleistocene), 34 – Soglasie-Korostel'ovo (Lower Neopleistocene), 35 – Srednyaya Akhtuba (Holocene), 36 – Staraya Kalitva-2 (Lower Neopleistocene), 37 – Trostnianska (Lower Neopleistocene), 38 – Vol'naya Vershina (Lower Neopleistocene), 39 – Voroncha (Holocene), 40 – Zmeevka-2 (Holocene).

Fig. 3. Localités Pliocène à Pléistocène moyen du crapaud mongol (*Strauchbufo raddei*) dans les territoires d'Europe orientale (Ratnikov, 2009).

for modern steppe zones can theoretically be recognized by the emergence of desert species.

Interglacial herpetofaunas are characterized by an increased diversity and the presence of thermophile southern forms. Interglacials differed from each other in their climatic parameters (Bolikhovskaya, 1995; Ratnikov, 2013). Therefore, distribution areas of amphibians and reptiles in interglacial optimums may also have had different outlines. Such fluctuations may depend not only on changes in climate and borders of natural zones, but also on other factors, such as the assortment of forming biotopes, the presence of competitors, predators, food, etc. The cumulative pressure of these factors could lead to initially inexplicable distributions. As a result, distribution areas sometimes varied only slightly, but sometimes they expanded, or even disappeared within significant territories. Some species of amphibians show changes of distribution that can be used in regional stratigraphy for defining of large age intervals. For example, the Mongolian Toad (*Strauchbufo raddei*) living nowadays in Eastern Russia, Mongolia, Manchuria, Korea, North and central China (Kuzmin, 2012), lived in Eastern Europe from the Pliocene up to and including the Middle Pleistocene (Ratnikov, 1996b, 2002, 2009) (Fig. 3). Numerous reliable findings of the Green Toad (*B. viridis*) appear here only from the Late

Pleistocene onwards. Only two bones of this species have been found in more ancient sediments together with *S. raddei*: one comes from the Pliocene of the locality of Dolinskoe and another from the il'inka horizon of the locality of Staraya Kalitva (Ratnikov, 1996b, 2002, 2009) (Fig. 4). Two bones, one of *S. raddei*, and another of *B. viridis*, have been found in Morozovka. This site has been estimated by various experts as either Late or Middle Pleistocene. Assuming that the bone of *S. raddei* was not redeposited, both species would have coexisted at the beginning of the Late Pleistocene. The finding of the Mongolian Toad therefore points to a sediment age of that is older than the Late Pleistocene, whereas the Green Toad remains can, most likely, be attributed to a younger age. The distribution area of the Siberian Salamander (*Salamandrella* sp.) at the end of the Early Neopleistocene covered most of the East European plain (Fig. 5).

As an example of an analysis of an amphibian-reptile association, I will now discuss the herpetofauna of the Mastyuzhinka site, located in the basin of the river Ikorets (a tributary of the river Don) near of the town of Liski in the Voronezh area. Characteristic of the association is that more than half the anuran bones belong to small (juvenile) individuals. The site was probably a shallow pool with quiet, warm water in which young amphibians developed.

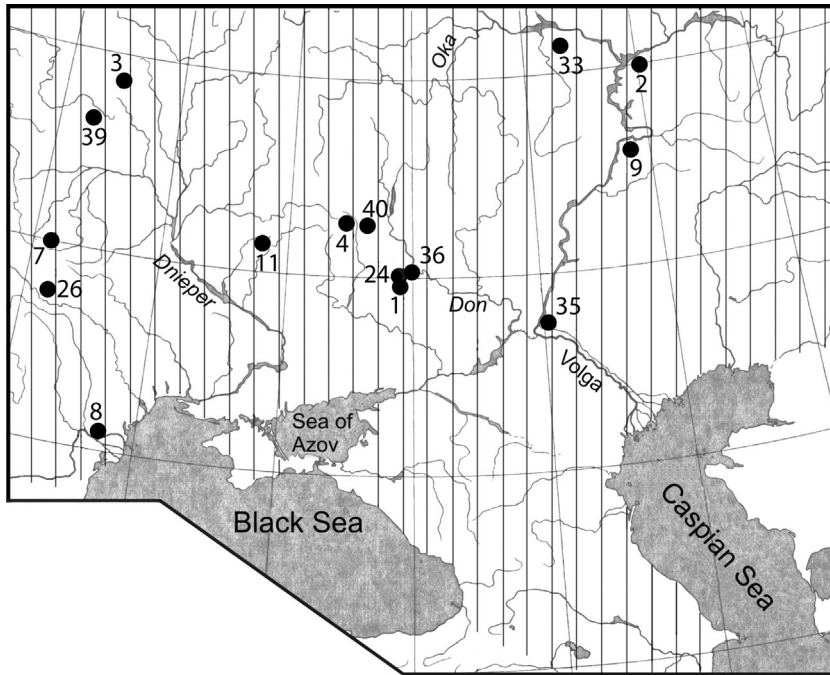


Fig. 4. Localities of Green Toad (*Bufotes viridis*) in territories of Eastern Europe (Ratnikov, 2009). The area of modern distribution of the species is hatched.
Fig. 4. Localités du crapaud vert (*Bufotes viridis*) dans les territoires d'Europe orientale (Ratnikov, 2009). L'aire de distribution actuelle de l'espèce est représentée par des traits verticaux.

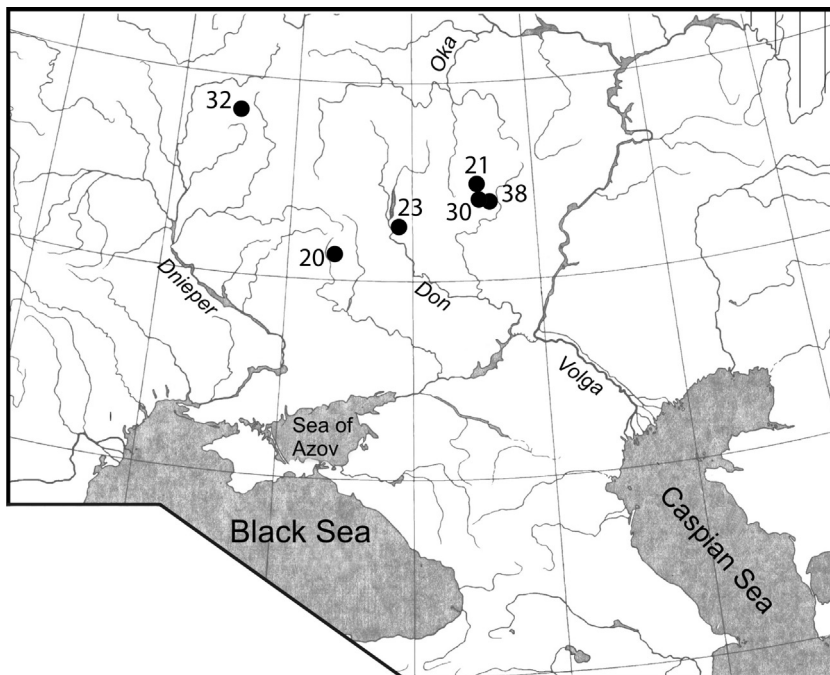


Fig. 5. Localities of Siberian Salamander (*Salamandrella* sp.) in territories of Eastern Europe (Ratnikov, 2009). The area of modern distribution of the species is hatched.
Fig. 5. Localités de la Salamandre de Sibérie (*Salamandrella* sp.) dans les territoires d'Europe orientale (Ratnikov, 2009). L'aire de distribution actuelle de l'espèce est représentée par des traits verticaux.

The animals, which died either here or on the nearby land, were buried in this reservoir.

According to modern classification (Frost, 2015), of the composition of the fossil amphibians and reptiles fauna from the Mastyuzhinka site is as follows: *Salamandrella* sp. – 114, Caudata indet. – 3; *Bombina* cf. *variegata* – 6, *Bombina* sp. – 3, *P. fuscus* – 1, *P. cf. fuscus* – 3, *Pelobates* sp. – 115, *S. raddei* – 32, Bufonidae indet. (not *Bufo*) – 26, Bufonidae indet. – 32, *R. arvalis* – 21, *R. cf. arvalis* – 6, *Rana* sp. – 8, Ranidae indet. – 71, Anura indet. – 63; *L. agilis* – 10, *L. cf. agilis* – 3.

At least six species present in this association are indicative of favorable (warm and damp) conditions at the time of burial. Three species (*Bombina variegata*, *Salamandrella* sp., *S. raddei*) do not live in the Voronezh area today. Remains of *S. raddei* exclude a Late Pleistocene age for the herpetofauna. *Salamandrella* sp. reduces the age interval further as this form is only found in after-Don deposits of the Early Neopleistocene in central Eastern Europe, suggesting the Muchkap or Ikoretsk interglacial.

The prevailing quantity of *Salamandrella* sp. remains (the species of closed biotopes) testifies to the existence of forest conditions in vicinities of the site. Moreover, species of open biotopes (*S. raddei*, *L. agilis*) are also present, suggesting that this forest is within the limits of the forest-steppe zone. The numerous remains of Spadefoot would seem to confirm this hypothesis. As the site is within the limits of the modern forest-steppe zone, we can conclude that conditions during deposition were not necessarily drier than today, so it was, most likely, an interglacial optimum.

It is obvious that use of such methodology requires knowledge of the history of the species inhabiting the study region. Potential candidates for this purpose are *B. variegata*, *Bufo verrucosissimus*, *E. arguta*, *Elaphe dione* and *Zamenis longissimus*, the remains of which are also discovered in localities distant from their modern distribution areas (Ratnikov, 2009).

5. Conclusion

The dynamics of past distribution areas of modern amphibian and reptilian species, based on fossil remains recovered in archaeological and/or palaeontological localities, allows the following stratigraphical inferences:

- the presence of the “ectothermic” animal remains suggests the absence of ice cover in a given place at the time of burial of the herpetofauna;
- change of forest associations to forest-steppe and steppe associations, within the limits of modern forest zone, can be attributed to climate aridization as a result of increasing glacial conditions;
- some species of amphibians (like *S. raddei*, *B. viridis*, *Salamandrella* sp.) that show changes in their past distribution areas, can be used in regional stratigraphy for the definition of comparatively large age intervals.

Nevertheless, it is necessary to consider each case carefully within the framework of the history of the locality.

Acknowledgements

The author thanks Hugues-Alexandre Blain (Tarragona) and two anonymous experts for reading the manuscript and useful recommendations and Anne Blair Gould (Delft) and Lars van den Hoek Ostende (Leiden) for correction of English.

References

- Agadzhanian, A.K., 1972. Lemming fauna of the Middle and Late Pleistocene. *Bull. Comm. Study Quat.* 39, 67–81 (in Russian).
- Agadzhanian, A.K., 1979. A study of the history of small mammals. In: Sokolov, V.E., Dinesman, L.G. (Eds.), *Chastnye metody izucheniya istorii sovremennykh ekosistem* [Special Methods of the Historical Study of Recent Ecosystems]. Nauka, Moscow, pp. 164–193 (in Russian).
- Ananjeva, N.B., Borkin, L.Y., Darevsky, I.S., Orlov, N.L., 1998. *Amphibians and Reptiles. Encyclopedia of the Russian Nature* [Zemnovodnye i presmykayushchiesya. Entsiklopediya prirody Rossii]. ABF, Moscow (576 p. [in Russian]).
- Ananjeva, N.B., Orlov, N.L., Khalikov, R.G., Darevsky, I.S., Ryabov, S.A., Barabanov, A.V., 2006. *The Reptiles of Northern Eurasia: Taxonomic Diversity, Distribution, Conservation Status*. Pensoft Publishers, Sofia (247 p.).
- Bannikov, A.G., Darevskii, I.S., Ishchenko, V.G., Rustamov, A.K., Shcherbak, N.N., 1977. *Handbook of Amphibians and Reptiles of the USSR* [Opredelitel' zemnovodnykh i presmykayushchikh fauna SSSR]. Prosveshchenie, Moscow (414 p. [in Russian]).
- Bannikov, A.G., Denisova, M.N., 1956. *Essays on Amphibian Biology* [Ocherki po biologii zemnovodnykh]. Uchpedgiz, Moscow (166 p. [in Russian]).
- Baryshnikov, G.A., Markova, A.K., 2002. Fauna (Theriodomplexes of the Late Pleistocene). In: Velichko, A.A. (Ed.), *Dynamics of Landscape Components and Internal Sea Basins of Northern Eurasia for Last 130,000 Years*. GEOS, Moscow, pp. 123–138.
- Bolikhovskaya, N.S., 1995. *The Evolution of the loess-paleosol Formation of Northern Eurasia* [Evolutsiya lessovo-pochvennoi formatsii Severnoi Evrazii]. Moscow University Press, Moscow (270 p. [in Russian]).
- Borkin, L.J., Litvinchuk, S.N., Rosanov, J.M., Khalturin, M.D., Lada, G.A., Borissovsky, A.G., Faizulin, A.I., Kotsershinskaya, I.M., Novitsky, R.V., Ruchin, A.B., 2003. *New data on the distribution of two cryptic forms of the common spadefoot toad (Pelobates fuscus) in Eastern Europe*. *Russ. J. Herpetol.* 2, 111–118.
- Frost, D.R., 2015. *Amphibian Species of the World: an Online Reference*. Version 6. 0 (Date of access). American Museum of Natural History, New York, USA (Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>).
- Garanin, V.I., 1983. *Amphibians and Reptiles of the Volga-Kama Region* [Zemnovodnye i presmykayushchiesya Volzhsko-Kamskogo kraya]. Nauka, Moscow (175 p. [in Russian]).
- Iossifova, Y.I., Agadzhanian, A.K., Ratnikov, V.Y., Sycheva, S.A., 2009. *On the Ikoretsian svita and horizon in the top of the Lower Neopleistocene in the Mast'uzhinka section (Voronezh region)*. *Bull. Reg. Mezhdvedom. Stratigraf. Kom. Cent. Jugu Rus. Platf.* 4, 89–104 (in Russian).
- Kholmovoy, G.V., Ratnikov, V.Yu., Spull, V.G., 2008. *Theoretical Bases and Methods of Stratigraphy* [Teoreticheskie osnovy i metody stratigrafii]. Voronezh state university Publishing house, Voronezh (154 p. [in Russian]).
- Kuzmin, S.L., 2012. *Amphibians of the Former USSR* [Zemnovodnye of former USSR]. KMK, Moscow (370 p. [in Russian]).
- Markova, A.K., 1994. *Pleistocene landscapes of Russian plain on the base of small mammals' fauna*. *Bull. Soc. Imp. Nat. Mosc. Dep. Geol.* 1, 64–68 (in Russian).
- Markova, A.K., 2004. *Eastern European Pleistocene mammal faunas*. In: Konishchev, V.N., Safianov, G.A. (Eds.), *Structure, Dynamics and Evolution of Natural Geoecosystems*. Gorodets Press, Moscow, pp. 583–598 (in Russian).
- Markova, A.K., van Kolschoten, T., 2012. *Middle Pleistocene small mammal faunas of Eastern and Western Europe: chronology, correlation*. *Geogr. Environ. Sustain.* 4, 17–23.
- Markova, A.K., Puzachenko, A.Yu., 2008. *Mammal assemblages during the Last Glacial Maximum (LGM) (≤ 24 – ≥ 17 kyr BP)*. In: Markova, A.K., van Kolschoten, T. (Eds.), *Evolution of the European Ecosystems during Pleistocene-Holocene transition (24–8 kyr BP)*. KMK Scientific Press Ltd, Moscow, pp. 91–116 (in Russian).

- Nikolaeva, A.S. (Ed.), 1986. Geographical Atlas for Students of the 7th Grade [Geograficheskii atlas SSSR dlya sed'mogo klassa]. GUGK, Moscow (32 p.).
- Pikulik, M.M., 1985. Zemnovodnye Belorussii [Amphibians of Byelorussia]. Nauka Tekh, Minsk (191 p. [in Russian]).
- Pisanets, Y.M., 2007. Amphibians of Ukraine [Amfibii ukrainy]. Zoological Institute NAN of Ukraine, Kiev (312 p. [in Russian]).
- Pisanets, Y.M., 2010. Annotated list of Eastern European amphibians. Collec. Artic. Zool. Mus. 41, 77–110 (in Russian).
- Ratnikov, V.Yu., 1996a. Methods of Paleogeographic reconstructions based upon fossil remains of amphibians and reptiles of the Late Cenozoic of the East European platform. Paleontol. J. 1, 75–80.
- Ratnikov, V.Yu., 1996b. On the Finds of Green Toads (*Bufo viridis* complex) in the Late Cenozoic of the East European platform. Paleontol. J. 2, 225–231.
- Ratnikov, V.Yu., 1997. On the Finds of *Pliobatrachus* (Anura, Palaeobatrachidae) in Eastern Europe. Paleontol. J. 4, 70–76.
- Ratnikov, V.Yu., 2002. Late Cenozoic Amphibians and Squamate Reptiles of the East European Plain. Voronezh state university Publishing house, Voronezh (138 p. [in Russian]).
- Ratnikov, V.Yu., 2009. Fossil Remains of Modern Amphibian and Reptile Species as the Material for Studying of their Areas History. Voronezh state university Publishing house, Voronezh (91 p. [in Russian]).
- Ratnikov, V.Yu., 2013. Dynamics of paleogeographic conditions in territory of the East Europe in Pleistocene. Proc. Voronezh State Univ. Geol. 2, 188–190 (in Russian).
- Ratnikov, V.Yu., Mebert, K., 2011. Fossil remains of *Natrix tessellata* from the Late Cenozoic deposits of the East European plain. Mertensiella 18, 337–342.
- Rekovets, L.I., 1995. Periglacial micromammal faunas from the Late Pleistocene of Ukraine. Acta Zool. Cracov. 1, 129–138.
- Rekovets, L.I., Nadachowski, A., 2007. The evolution of biocoenoses of the Periglacial zone in Late Pleistocene Eastern Europe. Vestnik Zool. 3, 197–206 (in Russian).
- Shik, S.M., 2014. Neopleistocene of the European Russia Center: modern representations about stratigraphy and paleogeography. Stratigr. Geol. Correl. 2, 108–120 (in Russian).
- Stepanov, D.L., Mesezhnikov, M.S., 1979. General Stratigraphy [Osnovy stratigrafii]. Nedra, Leningrad (424 p. [in Russian]).
- Stöck, M., Dubey, S., Klütsch, C., Litvinchuk, S.N., Scheidt, U., Perrin, N., 2008. Mitochondrial and nuclear phylogeny of circum-Mediterranean tree frogs from the *Hyla arborea* group. Mol. Phylogenet. Evol. 49, 1019–1024.
- Velichko, A.A., 1973. The Natural Process in the Pleistocene. Nauka Press, Moscow (256 p. [in Russian]).
- Wielstra, B., Litvinchuk, S.N., Naumov, B., Tzankov, N., Arntzen, J.W., 2013. A revised taxonomy of crested newts in the *Triturus karelinii* group (Amphibia: Caudata: Salamandridae), with the description of a new species. Zootaxa 3682 (3), 441–453.
- Wuttke, M., Pfikryl, T., Ratnikov, V.Yu., Dvořák, Z., Roček, Z., 2012. Generic diversity and distributional dynamics of the Palaeobatrachidae (Amphibia: Anura). Palaeobiodivers. Palaeoenviron. 3, 367–395.