

# Methods of Paleogeographic Reconstructions Based upon Fossil Remains of Amphibians and Reptiles of the Late Cenozoic of the East European Platform

V. Yu. Ratnikov

Voronezh State University, Voronezh, 394893 Russia

Received May 24, 1994

**Abstract—Theoretical prerequisites and possibilities for the application of the fossil remains of the Late Cenozoic amphibians and reptiles to paleogeographic reconstructions are discussed.**

Remains of amphibians and reptiles have come into use, along with the remains of mammals, in reconstructions of Cenozoic paleogeographic situations. Thus, specialists who work on such reconstructions must be familiar with the peculiarities of these organisms and with the methodological aspects of herpetofauna analysis. An article on paleogeographic reconstruction based on anurans was earlier published [19]. However, it went unnoticed and certain details of the analysis were unclear in papers summarizing paleogeographical situations [21]. The present article discusses the theoretical prerequisites of such reconstructions.

A list of fossil herpetofauna provides a basis for analysis and we would like to pay particular attention to the form of the list. So far it is widely believed by both zoologists and paleontologists that landscapes of the past are evaluated by the species composition, of a locality. Therefore, species identified in taphocoenoses are the only ones used for paleoenvironment reconstruction [9-11, 14-16], but the analysis itself is restricted to a list of plausible habitats of the listed forms. It is our opinion that a paleoenvironment reconstruction should be maintained using a quantitative ratio between fossil species that belong to different ecological groups to provide an idea about the particular biotope dominance and, therewith, the climatic zone. A similar procedure has long been used by students of small mammals [13].

Most of Late Cenozoic amphibians and reptilians of the East European Platform have been assigned to recent species, which allows us to reveal their habitat conditions by analogy with the Recent representatives. Areas of the latter forms spread now over almost the entire East European Platform, and their boundaries are determined by different factors: long standing seasons with positive temperatures, the degree to which the water warms during amphibian larvae development, etc. It is observed as well, that the area boundaries strongly depend on landscape zone transition [2, 17]. The northern boundaries of the distribution of terres-

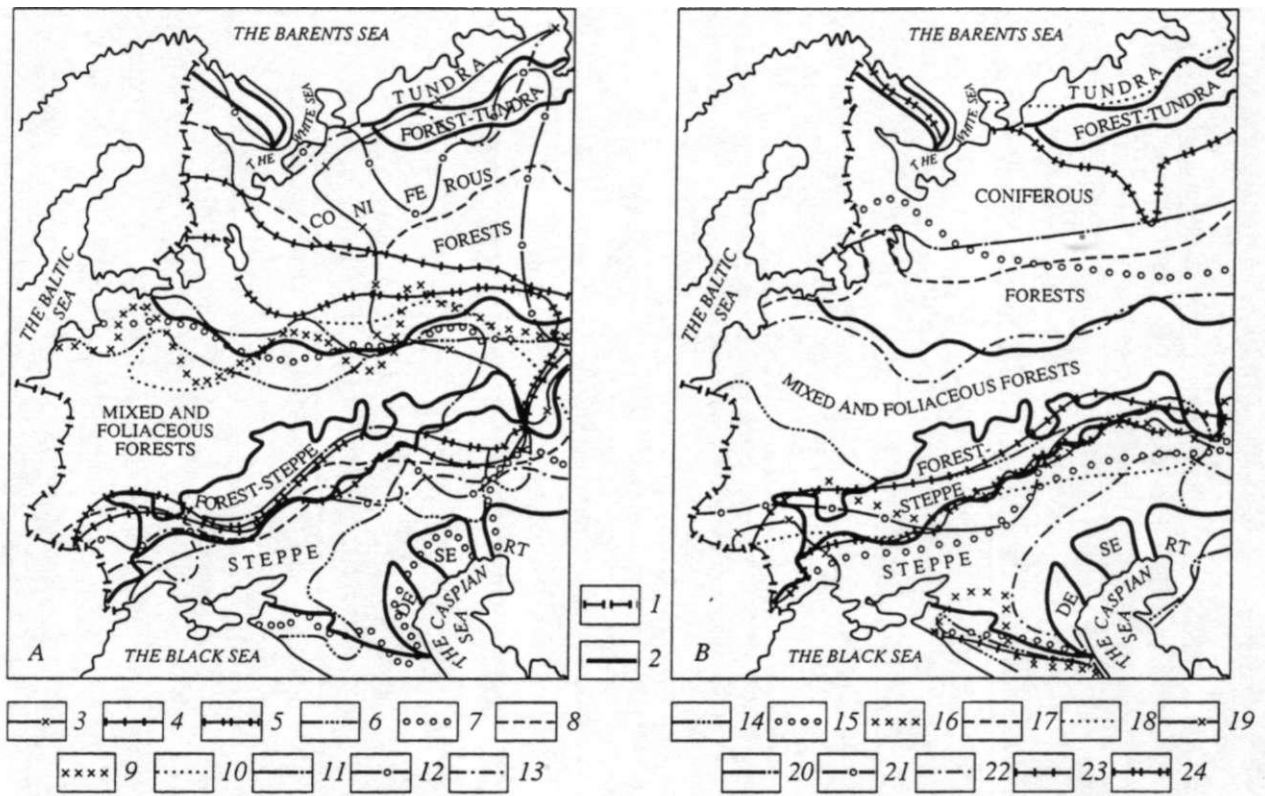
trial cold-blooded vertebrates are almost restricted to the limits of forest-tundra and are commonly located far to the south (areas of *Salamandrella keyserlingii* Dybowski, *Rana arvalis* Nilsson, and *Lacerta vivipara* Jacquin only spread over the dumetous and sedge tundra zones) (see figure). So the occurrence of amphibians and/or reptiles even identified to the class level (Amphibia or Reptilia) in a locality, signifies that the locality is well off the ice cover.

Northern areal boundaries of *Bombina bombina* (L.), *Pelobates fuscus* (Laur.), *Bufo viridis* Laur., *Rana lessonae* Camerano, *R. ridibunda* Pall., *Emys orbicularis* (L.), and *Coronella austriaca* Laur. roughly coincide with the transition from coniferous taiga to mixed forest.

Southern areal boundaries of *Salamandrella keyserlingii* Dybowski, *Triturus cristatus* (Laur), *T. vulgaris* (L.), *Bufo bufo* (L.), *Rana lessonae* Camerano, *Anguis fragilis* L., *Lacerta vivipara* Jacquin, *Vipera berus* (L.), and northern areal boundaries of *Eremias arguta* (Pall.) and *Vipera ursini* (Bonaparte) generally coincide with the forest-steppe.

Every species is associated with a certain type of biotope. Both density population and the number of individuals inhabiting the given territory display biotope distribution dependence. Since the adjacent climatic zones can also include common biotops, certain amphibian and reptilian species turn out to inhabit two or more zones. On the other hand, each zone is distinct for a specific set of species (table). That is, environmental conditions in the vicinity of a locality can be reconstructed from a fossil assemblage.

Amphibians and reptiles are controlled to a variable degree by ponds, whereas amphibians are totally water dependent and do not go far from it (maximum distance registered for a green toad is 10 km) [3]; reptiles have lost such a dependence. That is, fossil amphibian fauna denotes the situation in valleys, and reptilian fauna basically indicates the situation on placores, and for



Boundaries of natural zones (simplified) and boundaries of recent species areas: (A) amphibians; (B) reptiles. Legend: (1) former USSR boundaries; (2) natural zone boundaries; (3-13) amphibian areal boundaries: (3) *Salamandrella keyserlingii*, (4) *Triturus vulgaris*, (5) *T. cristatus*, (6) *Bombina bombina*, (7) *Pelobates fuscus*, (8) *Bufo bufo*, (9) *B. viridis*, (10) *Rana ridibunda*, (11) *R. lessonae*, (12) *R. temporaria*, (13) *R. arvalis*; (14-24) reptilian areal boundaries: (14) *Emys orbicularis*, (15) *Anguis fragilis*, (16) *Eremias arguta*, (17) *Lacerta agilis*, (18) *L. vivipara*, (19) *L. viridis*, (20) *Natrix natrix*, (21) *N. tessellata*, (22) *Coronella austriaca*, (23) *Vipera ursini*, (24) *V. berus*.

ases of joint occurrence they should be considered separately as complementary elements.

Species of enclosed biotopes characteristic of the forestzone can be discerned among recent species of amphibians and reptiles of temperate latitudes on the East European Platform: Siberian salamander *Salamandrella keyserlingii* Dybowski, common newt *Triturus vulgaris* (L.), crested newt *T. cristatus* (Laur.), gray toad *Bufo bufo* (L.), brown frog *Rana temporaria* L., edible frog *R. lessonae* Camerano; *Anguis fragilis* L., common lizard *Lacerta vivipara*, and common viper *Vipera berus* (L.). Sharp-faced frog *Rana arvalis* Nilsson is most characteristic of the forest zone, but is also found in tall-grass wet meadows and, therefore, inhabits a very broad area, extending from steppes to forest-tundra. The area of smooth snake *Coronella austriaca* Laur. also extends from forests to steppes, although the species prefers enclosed biotopes. Green toad *Bufo viridis* Laur., lake frog *Rana ridibunda* Pall., sand lizard *Lacerta agilis* L., green lizard *L. viridis* Laur., *Eremias arguta* (Pall.), and steppe viper *Vipera ursini* (Bonaparte) are typical inhabitants of open spaces, including deserts. They penetrate to some extent into the forest zone. The distribution of fire-bellied toad

*Bombina bombina* (L.) is primarily related to the dynamics and heat mode of the ponds inhabited (it prefers small, well-warmed up ponds with lentic or slowly moving waters), and the distribution of spade-footed toad *Pelobates fuscus* (Laur.), to the availability of dry and sufficiently soft soils. Both species extend, but not too far, into the coniferous forest zone along the northern boundary of areas, although probably have an indirect connection to natural zones. Of the aquatic snakes, the grass snake *Natrix natrix* (L.) is the most characteristic of the enclosed biotopes, and water snake *N. tessellata* (Laur.), of the open biotopes, but fresh-water turtle *Emys orbicularis* L. does not expand to the north of the mixed forest zone [2, 3, 6, 18].

The forest-steppe zone is the most species-rich for it is inhabited by representatives of both forest and steppe biotopes. Forest-tundra is inhabited by woodland forms due to its lack of typical tundra species.

Thus, we may evaluate a relative number of fossils typical of open and enclosed biotops from the study of fossil assemblages consisting of Recent species. The resulting ratio allows us to reconstruct the environmental conditions of the herpetofauna. The resulting quantitative ratios, however, can be inconsistent with past

Distribution of recent species of amphibians and reptiles through different zones: (++) species is common, (+) species is scarce

Species	Tundra	Forest-tundra and coniferous forests	Mixed and deciduous forest	Forest-steppe	Steppe	Desert
<i>Salamandrella keyserlingii</i>	+	++	++	+		
<i>Triturus vulgaris</i>		+	++	+		
<i>T. cristatus</i>		+	++	+		
<i>Bombina bombina</i>			++	++	++	
<i>Pelobates fuscus</i>			+	++	++	
<i>Bufo bufo</i>		++	++	++		
<i>B. viridis</i>			+	++	++	++
<i>Rana ridibunda</i>			+	++	++	++
<i>R. lessonae</i>			++	++		
<i>R. temporaria</i>		++	++	++		
<i>R. arvalis</i>	+	++	++	++	+	
<i>Emys orbicularis</i>			++	++	++	
<i>Anguis fragilis</i>		+	++	++	+	
<i>Eremuas arguta</i>				++	++	++
<i>Lacerta agilis</i>		+	+	++	++	
<i>L. vivipara</i>	+	++	++			
<i>L. viridis</i>			++	++	+	
<i>Natrix natrix</i>		++	++	++	+	
<i>N. tessellata</i>				+	++	+
<i>Coronella austriaca</i>			++	++	+	
<i>Vipera berus</i>		++	++	++		
<i>V. ursini</i>				++	++	+

ratios. So, the herpetofauna analysis requires the appropriate corrections. First of all, burial conditions, that is, the taphonomic type of locality, affects the composition of the herpetofauna fossils.

The greatest amount of localities is associated with alluvial channel deposits. Fossil amphibians and reptiles from a significant part of a river basin are commonly accumulated and, therefore, they somewhat adequately reflect the composition of herpetofauna that inhabited this territory in the past. This allows us to reconstruct the paleogeographic situation that existed within the given basin with sufficient accuracy.

Inundated, dead channel, and limnetic deposits are more favorable for the burial of amphibians, since those ponds supported concentrations of live amphibians. The bones of animals that inhabit these ponds and the immediate vicinity, are buried here, along with remains that were transported by overland flows. The composition of the fossil herpetocomplex thus reflects the situation mostly in the pond vicinity. It is possible that the formation of pure autochthonous anuran burials is in an inundated and dead channel, and in limnetic deposits. These are the burials of frogs that starved during hibernation, as in the Upper Pleistocene Rudnyi locality in Belgorod Region [20]. In such cases, most of the bones

belong to individuals of one genus and only partly reveal the composition of the fossil herpetocomplex.

The composition of herpetocomplexes in helobious deposits presumably agrees with the set of forms that inhabited the marsh and its immediate vicinity, that is, the immediate neighborhood of the locality.

Diluvial, proluvial, and solifluctional deposits contain, at times, a great many bones. It turns out that the material was accumulated mostly by temporal overland flows from a small area and thus denotes the situation in the immediate vicinity. Typical aquatic forms (such as green frogs) lack in oryctocoenosis.

Burials in the cover overlying deposits (classification of A.K. Agadzhanian [1]) are generally associated with mole casts. They probably occur most commonly after channel alluvium burials. Borrowers (such as spadefoots) may fall there more often, but rarely for animals using burrows as coverts (toads, snakes, etc.). Although other forms, even aquatic [20], can be found in localities, a real quantitative relationship of species inhabiting a given territory in the past is severely wrong in value.

Bones in karst crevice fillings were accumulated by underground waters that circulated in fractures. Fossil

herpetocomplexes in such localities contain forms that inhabited the vicinity of karst sinks and that served as collectors of dead bodies.

Accumulations of fossil vertebrates in caves, different grottos, and niches, according to I.M. Gromov [8], along with accumulations in river alluvium deposits, constitute the major part of known localities. However, they are all associated with mountain regions and unknown on the East European Platform. Primary accumulations of bones in localities discussed are formed as a result of the hunting activity of carnivorous birds and mammals. The composition of fossil animals association is inconsistent with the true ratio of animals and determined by the food choice of the carnivore.

The rate of bone destruction also requires correction. Agadzhanian [1] pointed out that the destruction rate of organic remains is higher in forest conditions than in steppes, due to the slower tempo of overland flows, abundance of scavengers, and the presence of humid acids in soils. Therefore, the difficulty of locating even a few forest animal fossils testifies to the wide distribution of woodland and dumetous biotopes. An equal ratio of wood and steppe animal fossils is interpreted as signifying a significant predominance of enclosed biotopes over open.

When analyzing faunas of small mammals, correction coefficients are primarily introduced to account for the quantity of skeletal elements of teeth [13], which is indicative of the species and thus a quantitative ratio of species is obtained which is closer to the real one. Contrary to rodents, the identification of amphibians and reptiles is based on bones. Having species with an equal amount of distinctive skeletal elements of both the enclosed and open biotopes within every recent genus of amphibians and reptiles, the coefficients need not be introduced for the reconstruction of paleogeographic conditions. Furthermore, the convection between osteologic features of anurans and their ecology permits one to distinguish paleogeographic conditions, in a number of cases, based only on specific assemblages and groups, and even without a precise species identification. Representatives of the *Bufo bufo* assemblage and the group of frog species *Rana ex gr. temporaria*, as examples, are inhabitants of enclosed biotopes and representatives of the *Bufo viridis* assemblage are confined to open biotopes.

In most localities of fossil herpetofauna, anurans are either the only group found, or they prevail over reptiles. This can probably be explained by the burial advantage of amphibians, because with all factors being equal, the overland flows are the major agent of bone accumulation, and the most known localities have aquatic origins. The rarely occurring salamander fossil is probably due to their small size and bone fragility. However, in some occurrences, reptilian fossils exceed amphibian fossils in number.

The highest percentage of reptilian fossils is comprised of snake vertebrae, the lowest, of lizard bones.

This can be explained by osteologic features: snakes have as many as a few hundred skeletal vertebrae. Fragments of turtle carapaces may constitute the majority of reptilian remains (although bad for identification). In temperate latitudes, such occurrences are rare.

The quantity of amphibian and reptilian fossils in most occurrences is not abundant when compared to small mammal remains. This is primarily explained by the fact that rodents significantly outnumber cold-blooded vertebrates, and secondly, by the superior preservation of enameled mammal teeth. However, the number of species of amphibians and reptiles inhabiting the East European Platform is not big and, therefore, even with a small number of identified species, the reconstruction of the landscape is adequately reliable. In some occurrences, the number of fossils of cold-blooded terrestrial vertebrates exceeds the number of mammals [20].

The reconstruction of the paleolandscape in a few localities will be considered as examples. The following taxa were identified from the Holocene taphocenosis in channel alluvium near Voroncha village, Korelichi District, Grodno Region (data from P.F. Kalinovskii): Amphibia: *Bufo viridis* Laur., 1; *B. bufo* complex, 5; *B. sp.*, 7; *Rana temporaria* L., 15; *R. ex gr. temporaria*, 3; *R. temporaria* complex, 2; *R. lessonae* Camerano, 1; *R. sp.*, 57; Anura fam. indet., 54; Reptilia: *Anguis fragilis* L., 1; and *Lacerta cf. agilis* L., 2. The majority of fossils belongs to inhabitants of enclosed biotopes testifying to the existence of woodland in the river basin. A single find of green toad that spreads north to the mixed forest zone, as well as of edible frog and blind worm fossils, tells about the mixed or deciduous forest. Furthermore, one can suggest the existence of open woodlands and clearings based on the presence of sand lizard fossils.

The following amphibians from the Lower Pleistocene locality near Kuznetsovka village, Uvarovo District, Tambov Region are associated with an inundated and dead channel, and limnetic deposits (reptiles have not been identified yet in the personal collection and partial material of Agadzhanian): *Bombina bombina* (L.), 4; *Pelobates fuscus* (Laur.), 5; *P. sp.*, 38; *Pelobatidae* gen. indet., 5; *Bufo raddei* Str., 2; *B. viridis* complex, 8; *B. bufo* complex, 1; *B. sp.*, 10; *Rana arvalis* Nilsson, 5; *R. cf. arvalis* Nilsson, 13; *R. ex gr. temporaria* L., 2; *R. lessonae* Camerano, 3; *R. sp.*, 61; and Anura fam. indet., 42. The number of forms typical of open biotopes (*B. raddei*, *B. viridis* complex) is notably larger than that of enclosed biotopes (*B. bufo* complex, *R. ex gr. temporaria*, *R. lessonae*), which indicates a roughly equal propagation of steppe and woodland areas in the vicinity of the locality. A large number of spade-footed toads is also associated with the wide development of steppe areas. The sharp-faced frog inhabits both woodlands and wet tall-grass meadows and confirms the presence of these situations. Fire-bellied toad fossils suggests the availability of shallow

well-warmed ponds, which agrees with a taphonomic type of locality.

The following taxa, associated with mole casts, were identified in the Lower Pleistocene occurrence near Troitskoe village, Novokhopersk District, Voronezh Region (material was put by Agadzhanian): Amphibia: *Pelobates* sp., 2; *Bufo raddei* St., 5; *B.* sp., 12; *Anura* fam. indet., 9; Reptilia: *Lacerta* cf. *agilis* L., 23; *L.* sp., 8; *Vipera ursini* (Bonaparte), 1; and *V.* sp., 1. Both amphibians and reptiles depict open biotopes, which confirm the presence of steppe in the vicinity of the locality.

An important feature of terrestrial vertebrates is their varying sizes over a stretch of area having varying habitat conditions [7, 22]. Theoretically, the determination of the sizes of buried individuals by their fossil bones will increase the scope of a paleoenvironment reconstruction. It is essential that the sizes that are determined for identified bones are large enough, when compared to body sizes; otherwise, the error will be too great. Anurans comprise the only group of terrestrial vertebrates that satisfies the outlined conditions. Their body length is easily derived from the following equation:  $L^* = L \times 1^*/1$ , where  $L^*$  is the length of the fossil body;  $L$  is the length of an individual of a corresponding species from the standard collection;  $1^*$  is the length of the fossil bone; and  $1$  is the length of a corresponding bone from the standard collection. Iliac bones of anurans are the most convenient for calculations: they are definable to a specific level and their length constitutes about one third of their body length.

An attempt to establish the relationship between frog sizes and their habitat conditions has already been made [5]. The bone sizes of even-aged individuals from three populations in Europe were used for the comparison. In our opinion, dimensional characteristics of populations, and not of single individuals, should be analyzed. The variations for every species are individual, and some display a trend. For example, the maximum sizes of brown frog individuals increase to the north along the western boundary of the former USSR [2].

Zoologists pointed to variations in three parameters: minimum, median, and maximum sizes of individuals in populations. After the determination of corresponding measurements for a fossil population, one can conclude that past climatic conditions are similar to habitat conditions for recent populations with identical sizes. Unfortunately, data on minimum body sizes are inoperable for fossil material, since this value is measured for mature animals. The remains of mature individuals are impossible to separate from juvenile ones, and, thus, the value of the minimum size will be undervalued when compared to real. By the same token, the medium size does not suffice. Therefore, only the maximum sizes of individuals can be used for the analyses.

The term "maximum sizes" is worthy of consideration. Very large individuals, that reached outstanding sizes, due to extremely favorable conditions or longer

lifespans, can be found in any population. However, by analogy, atypically sized individuals cannot be preserved as well due to their rarity [4]. That is, the maximum size is considered to be the dimension that many individuals (or almost every) of a generation of amphibians achieves. It is this index that will be reflected by abundant fossil material and such individuals in Recent populations, if observed by zoologists, will be easily determined statistically.

The above mentioned locality near Rudnyi can be used as an example. About 2800 bones of brown frogs were collected from this locality and maximum sizes approached as much as 78-81 mm. Brown frogs of that size currently inhabit area between St. Petersburg and Moscow. One can suggest, based on this similarity, the existence of a past climatic situation in the past that was analogous to the present-day one south of St. Petersburg.

Variations in the maximum size of individuals over areas are not alone unique to intraspecific populations, but are also typical of higher taxa. Thus, the largest anurans primarily inhabit tropical regions. The largest species of toads from the former USSR (*Bufo verrucosissimus* Pall.) occurs in the Caucasus. Therefore, the finds of unusually large forms in a given territory can nowadays be interpreted as a credible indicator of a past warmer and wetter climate. The Lower Pleistocene Kholki locality of the Belgorod Region exemplifies a situation in which the remains of individuals of toads were found with a body length reaching 110-115 mm, compared to 85 mm for recent representatives of that genus inhabiting the same region [2].

Extinct amphibian and reptilian forms are few in number in Pleistocene localities and it is unlikely that neglecting them will adversely affect the accuracy of paleogeographical reconstructions in herpetofauna analysis. In the Pliocene deposits, extinct forms occupy a reasonably conspicuous, if not leading, position in extinct communities and should be considered in their analyses.

In summary, the following traits can be pointed out.

(1) The number of fossils of low terrestrial vertebrates in localities is commonly less than that of mammals; nonetheless, they can be used for paleoenvironmental reconstruction. Besides, in some cases, they can outnumber other vertebrates.

(2) Identification of the systematic composition of herpetofauna is carried out on skeletal bones, and specific identifications are not alone used for drawing conclusions about past environments.

(3) By virtue of their hematocryality, amphibians and reptiles react readily to climatic variations and are probably a more reliable climatic indicator than mammals.

(4) Only anurans have bones that are distinguishable to a specific length and size, so that animals can be determined with sufficient accuracy. This enables one to make conclusions regarding the paleoclimate through the correlation of the maximum sizes of extinct

population with Recent representatives of the same species. Unfortunately, despite the fact that some species have notable variations in maximum sizes over an area, the quantitative characteristics and pattern of those variations are not sufficiently studied. Some experts even wholly deny the presence of a directional pattern. It would be a good idea to study this problem in detail. For now, our comparison can be based on the scant data of the brown frog [2, 12].

(5) The rate of evolution of cold-blooded terrestrial vertebrates is slower than for mammals, which, of course, is problematic when using data on herpetofauna for Anthropogene stratigraphy. However, the same factor is advantageous for paleogeographic reconstructions, since it allows us to draw conclusions regarding paleoenvironments with Recent amphibian and reptile species for time intervals even though Recent taxa of rodents have not yet appeared or are few in number.

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