Russian Geology and Geophysics
Vol 38, No. 9, pp. 1493-1500, 1997

Geobgiya i Geofizika
UDC 567.8:551.79(571.54)

TAILLESS AMPHIBIANS AND LANDSCAPE SETTINGS OF THE LATE CENOZOIC IN WESTERN TRANSBAIKALIA

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Bone remains of tailless amphibians from the localities Beregovaya, Dodogol, and Tologoi in Western Transbaikalia are described. Remains of *Bufo raddei* toads are the most abundant Species diagnosis of tree frogs is difficult, and they are determined as *Hyla* aff. *japonica* and *Hyla* sp. The frog remains are identified as *Rana* aff. *chensinensis, R.* aff. *asiatica,* and *R.* aff. *amurensis,* but they may also belong to an extinct form. The landscape in the vicinity of the localities seems to be steppe, occasionally, with forest massifs along the banks of water reservoirs.

Tailless amphibians, Late Cenozoic, Transbaikalia

INTRODUCTION

Several years ago Dr. L. I. Khozatskii gave me, for investigation, numerous collections of bone remains of vertebrates, which he received from M. A. Erbaeva as early as the 1960s. They contained lower tetrapods from the localities Tologoi, Dodogol, and Beregovaya, which are well studied now. The geology and mammal fauna of these localities have been described in many papers [1-6]. No attention has yet been given to their amphibians and reptiles.

Examination of the received collections showed that the bulk of the bone remains belonged to tailless amphibians, to which this article is devoted. Tailed amphibians and reptiles are to be considered in future papers.

MATERIAL

Several samples with amphibian remains were collected from each locality. The systematic composition of the batrachofauna is shown in Table 1. In the Beregovaya locality all samples were taken from bed 4 [2] and were of the same age (Lower Eopleistocene), whereas samples from Tologoi and Dodogol were of different ages.

The section of the Dodogol locality has been described by Erbaeva [5]. According to her report, sample 15 was taken from bed 7, and the sample "horizon 4" was taken from the upper part of the same bed, dating from the Middle Eopleistocene. The sample "horizon 3-4" was taken from the boundary between beds 6 and 7, that is, at the Middle/Upper Eopleistocene boundary. Sample "horizon 3" was taken from bed 6 and, therefore, dates from the Upper Eopleistocene. The sample "krasnotsvety (redrocks)" seems to be of the same origin. The sample "horizon 3" was taken from bed 5, the Upper Eopleistocene.

Raevskii et al. [6] presented a complete description of the Tologoi section. Samples 38x, No. 88, and 35xx were taken from the upper part of the middle rock mass (beds 16 and 17) of Upper Eopleistocene age; the sample "upper horizon" was taken from the upper part of the upper rock mass (beds 3, 4) of Lower Eopleistocene age.

Thus, the amphibian remains collected from the three localities cover a time range from the upper Lower Eopleistocene (Beregovaya) to the Lower Pleistocene (Tologoi).

Examination of the material involved systematic determination of each bone, but the levels of the determinations were different (Table 1). Some remains, the most important for systematics, are described below. The terms used in [7] are invoked.

Table 1

Systematic Composition of Tailless Amphibians in Localities and Quantitative Proportions of Remains in Samples

Age	Eopleistocene										Lower Pleistocene
	Lower	Middle		Upper							
Locality	Beregovaya	Dodogol						Tologoi			
Samples		No. 15	Hor. 4	Hor. 3-4	Hor. 3	Red-rocks	Hor. 2	38x	No. 88	35xx	Upper horizon
Bufo raddei	63	140	8	5	16	41	189	624	103		122
Bufo viridis complex	30	96	3	2	4	8	212	617	182		73
Bufo sp.	46	181	7	9	14	37	406	1677	320		88
Hyla aftjaponica								11			
Hyla sp.							1	13	1		
Rana aff. *asiatica*		287		1		1	50				
Rana aff. *amurensis*							10	10			1
Rana aff. *chensinensis*		85	1				14				
Rana temporaria complex		1277		1			277	143			2
Rana sp.		2148		4		5	482	298	6	20	5
Anura	9	709		1	3	5	116	3500	500		100

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SYSTEMATIC DESCRIPTION

ORDER ANURA
FAMILY BUFONIDAE
Genus *Bufo* Laurenti, 1768

Bufo raddei Strauch, 1876

Material. Beregovaya: frontoparietale — 4, nasale — 1, maxillare — 2, parasphenoideum — 2, sphenethmoideum — 2, scapula — 2, humerus — 5; ilium — 25, femur — 20. Dodogol, No. 15: frontoparietale — 12, nasale — 6, maxillare — 8, parasphenoideum — 7, squamosum — 10, sphenethmoideum — 6, scapula — 18, clavicula — 10, humerus — 14, ilium — 32, femur — 17; "horizon 4": scapula — 1, ilium — 3, femur — 4; "horizon 3-4": humerus — 1, femur — 4; "horizon 3": maxillare — 1, parasphenoideum — 1, scapula — 2, humerus — 2, ilium — 8, femur — 2; "redrock": parasphenoideum — 3, scapula — 5, humerus — 5, ilium — 21, femur — 7; "horizon 2": frontoparietale — 13, maxillare — 3, parasphenoideum — 5, squamosum — 1, sphenethmoideum — 3, scapula — 36, clavicula — 6, humerus — 17, Шит - 80, femur — 25; Tologoi, 38x: frontoparietale — 41, nasale — 20, maxillare — 37, parasphenoideum — 21, squamosa — 47, sphenethmoideum — 15, scapula — 88, clavicula — 82, humerus — 22, ilium — 189, femur — 62; No. 88: frontoparietale — 10, maxillare — 5, parasphenoideum - 4, squamosa — 5, sphenethmoideum — 6, scapula — 17, clavicula — 15, humerus — 1, ilium — 30, femur — 10; "upper horizon": frontoparietale — 5, maxillare — 2, parasphenoideum — 4, sphenethmoideum — 2, scapula — 8, humerus — 3, ilium — 64, femur — 30.

Frontoparietale (Fig. 1, *A)*. Fairly thick elongated bones with flat dorsal surface. All intact or almost intact samples have strongly narrowed frontal parts characteristic of modern species *Bufo raddei* and *B. calamita*. However, the latter has a pronounced crest bordering the flat surface of the parietal part of the bone and spreading to the frontal part in bigger individuals. This crest is weakly pronounced or absent from the fossil material. Accretion of the frontoparietale bone with the anterior otic bone is often observed. In bigger individuals the exoccipitale is also accreted to them.

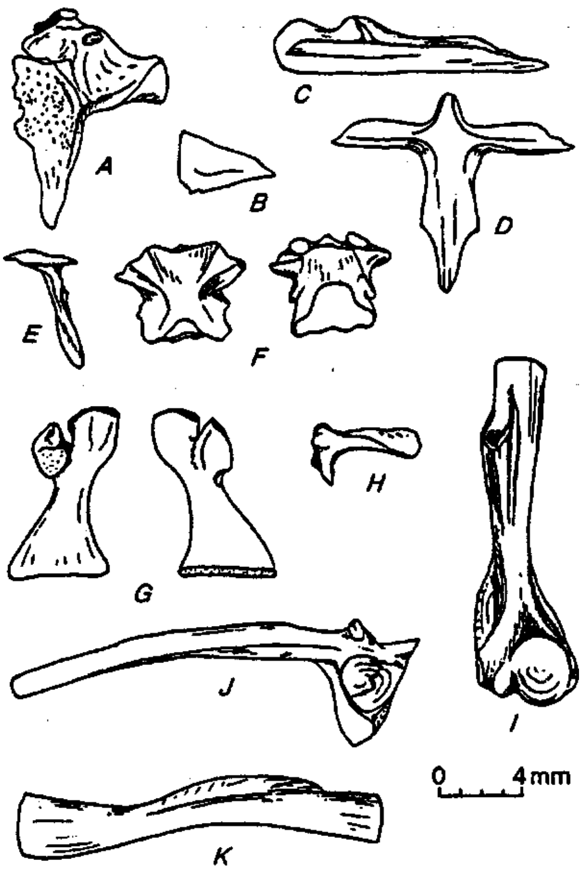

Fig. 1. Bone remains of the toad *Bufo raddei*. *A* — specimen from the collection of Voronezh State University (VSU) No. 590-1/1, accreted frontoparietale, exoccipitale, and anterior otic bone (dorsal view); *B* - VSU No. 590-1/2899, nasale (dorsal view); C - VSU No. 590-1Д234, maxillare (interior view); *D* — VSU No. 590-1/93, parasphenoideum (ventral view); *E* — VSU No. 590-1/1163, squamosum (exterior view); *F* — VSU No. 590-1/922, sphenethmoideum (dorsal and ventral views) ;G — VSU No. 590-1/545, scapula (interior and exterior views); Я — VSU No. 590-1/1818, clavicula (interior view); / - VSU No. 590-1/177, humerus (ventral view);/ - VSU No. 590-1/688, ilium (exterior view); *K* - VSU No. 590-1/378, femur (dorsal view).

Nasale (Fig. 1, *B),* The shape of the fossil nasal bones is close to triangular, unlike the nasal bones of gray toads, in which an S-shaped horizontal bend is clearly observed. Their proportions correspond to those of *B. raddei,* much narrower than in *B. viridis* and somewhat wider than in *B. calamita.*

Maxillare (Fig. 1, C). Elongated massive toothless bones differing from the corresponding bones of gray toads and *B. viridis* in having no strongly elongated process in the rear part of the palatal plate and rounded, not protruding forward, anterosuperior end of the facial plate. Unlike *B. calamita,* they have no fold in the anterior part of the bone and are similar in shape to *B. raddei.*

Parasphenoideum (Fig. 1, *D).* Cross-like bones, whose body width is markedly more than widths of lateral processes. Parasphenoidea of the Mongolian toad differed strikingly from those of gray toads and *B. viridis* in the relief of the ventral surface and body width; they resemble most of all the corresponding bone of *B. calamita* but have a less bent corpus parasphenoidei, less distinct sculpture where lateral processes branch off, wider lateral processes, a usually narrower posterior process, and stepwise converging lateral edges of the bone body.

Squamosum (Fig. 1, *E).* The narrow ramus zygomaticus indicates that the bones belong to the group of green toads. These bones differ from *B. viridis* by the pars horizontals not widening in the middle part and from *B. calamita* by ramus retrozygomaticus narrowing more gently.

Sphenethmoideum (Fig. 1, *F).* Sphenethmoidea of the fossil toads are distinguished by their strongly folded ventral surfaces characteristic of green toads. Their morphology is similar to that of *B. raddei* but differs

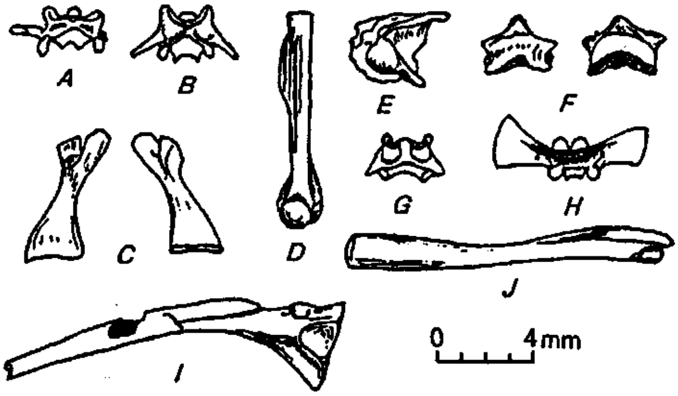

Fig. 2. Bone remains of Hylidae. *A-D: Hyla* aff. *japonica: A* - VSU No. 590-1/2936, third thoracic vertebra (dorsal view); *B* — VSU No. 590-1/2938, ventral vertebra (dorsal view); *C* — VSU No. 590-1/2924, scapula (exterior and interior views); *D* - VSU No. 590-1/2929, humerus (ventral). *E—Ji Hyla* sp.: *E* - VSU No. 591-6/98, exoccipitale (posterior view); *F* - VSU No. 590-1/2942, sphenethmoideum (ventral and dorsal views); *G* - VSU No. 590-1/2934, atlas (dorsal view); *Я* - VSU No. 590-1/2931, sacrum (dorsal view), J - VSU No. 590-1/2919, ilium (exterior view);/ - VSU No.590-1/2927, femur (dorsal view).

from *B. viridis* in the width of the ventral flattened area and from *B. calamita* in the relative length of the dorsal area of the bone.

Scapula (Fig. 1, *G).* The fossil scapulae differ markedly from *B. viridis* and *B. calamita;* they are longer and have narrower necks. Unlike scapulae of gray toads, they have narrower acromial parts and are most of all similar to scapulae of *B. raddei.*

Clavicula (Fig. 1, *H).* This bone is variable in its relative width in various toad species, but the fossils differ from all species, except for *B. raddei,* in a marked widening of the bone toward the medial end and, in most cases, by greater thickness.

Humerus (Fig. 1, *Г).* The fossil humeri have flattened dorsal surfaces indicating that they belong to green toads. They differ from *B. viridis* in thickness and more distinct sculpture of the proximal part. Their differences from *B. calamita* are less pronounced: the fossil bones, like those of modern *B. raddei,* have a wider distal head, a less developed lateral crest, a generally wider and convex medial crest, and more pronounced ventral crests, usually coming closer to the distal head.

Ilium (Fig. L *J).* The fossil ilia have a thin wing and well-pronounced precetabular fossa, unlike *B. calamita* and gray toads. They differ from *B. viridis* by a high, nearly symmetrically located tuber superior, bearing a large, clearly seen lump. In most specimens the lump is clearly divided into two apices, like in specimens from the locality Bural-Obo, Mongolia, described by Hodrova [8]. In some specimens, however, the lump is smooth or has a pit at its summit. Such specimens are rare but occur nearly in all samples. Interestingly, our modern reference collections contain no specimens with such a clear division of the lump into two apices.

Femur (Fig. 1, *K).* This bone is of diagnostic significance for toads owing to crista femoris. The development of the latter varies among species, thus allowing their determination. Comparison between the fossil and the modern material shows that such a long, high, and thin crest is present in *B. raddei.* Species *B. calamita* has such a long crest, too, but it is lower and thicker.

Family Hylidae
Genus *Hyla* Laurenti, 1768

Our reference material on tree frogs is scarce and represented by only two species, *H. arborea* and *H. japonica,* with which the fossil remains can be compared. Gutieva's abstract [9] is the only communication describing the osteology of the two tree frog species. Some differences from the available specimens of modern species in almost all tree frog bones call for their description, because the remains may belong to a novel species. But the extent of differences of various bones (particularly, from *H. japonica)* is variable, so that some of them are determined as *H.* aff. *japonica* and the others, as *Hyla* sp.

Hyla aff. *japonica* Gunther, 1859

Material. Tologoi, sample 38x: vertebrae — 6, scapulae — 3, humeri — 2.

Vertebra III (Fig. *2, A).* Procelous vertebrae with a short neural arch, wide neural canal, and small body weakly separated from the vertical plates. They differ from *H. arborea* by narrower vertical plates of the neural arch and its shorter horizontal plate; from *H. japonica* only by a more sharpened cut in the front of the neural arch.

Vertebrae V-VIII (Fig. 2, *B).* Procelous ventral vertebrae have characteristic forward-directed diapophyses and differ from *H. arborea* by narrower vertical plates of the neural arch and its shorter horizontal plate; from *H. japonica* by somewhat thicker bodies.

Scapula (Fig. 2, C). A very long, narrow bone, which can be readily taken for small specimens of *Bufo raddei* but differs in having a clearly convex posterior edge of corpus scapulae, smoother bending of this edge before facies lunata, more straightened edge of facies lunata in the dorsal view, and acromial process longer and rounded at the end.

The fossil tree frog scapulae differ from *H. arborea* in having less diverging acromial and glenoidal processes and relatively greater width of the former.

H. japonica of our reference collections is somewhat variable in the proportions of scapulae. Two specimens have narrower necks and acromial processes than the fossil material, and the processes are slightly more diverging. One specimen is thicker and similar to the fossil scapulae.

Humerus (Fig. 2, *D).* The fossil humeri differ from *H. arborea* by a smaller length and a well-pronounced crista ventralis secundaria. In the relative length and proportions of distal crests they are closer to *H. japonica* but differ in having a clearly pronounced second ventral crest.

Hyla sp.

Material. Dodogol, "horizon 2": exoccipitale — 1. Tologoi, 38x: sphenethmoideum — 1, atlas — 2, sacrum — 3, ilium — 5, femur — 2. "No. 88": ilium — 1.

Exoccipitale (Fig. 2, *E).* The bone belongs to a small individual and strongly differs from exoccipitalia of genera *Bufo, Rana, Pelobates,* and *Bombina* in having a short and wide (nearly isometrical) condylus occipitalis. It differs from both species present in the reference collection in some structural features, but the differences may be explained by underdeveloped skeletal elements of the young animal.

Sphenethmoideum (Fig. 2, *F).* Unlike sphenethmoidea of other tailless amphibians, in tree frogs this bone is very wide and short. The species diagnosis of this element is difficult.

Atlas (Fig. 2, *G)* with a convex condylus has a strongly flattened thin body, thereby differing from toads, frogs, and spade-footed toads. They differ from *H. arborea* in having a convex space between the cotyli (it is nearly straight in *H. arborea),* from *H. japonica* in having closer located cotyli, a longer neural arch, and greater convexity of the space between the cotyli.

Sacrum (Fig. 2, *H).* The transverse dorsal crest in the reference material of both species is somewhat variable, hampering the species identification. However, in the fossil specimens this crest is clearly sloped forward, which is not observed in the reference collection. The bone differs from toad sacra in having a strong backward slope of the diapophyses.

Ilium (Fig. 2, i). The wing of the bone is rather thick, tuber superior is long, but its sculpture is not the same in various specimens: some are smooth, and some have tubercles on the lateral side. Strong variability in shape and size of the elements of the ilia is also observed in the reference material, so, the species identification is difficult.

Femur (Fig. 2,7). These bones of tree frogs are thin, long, with well-developed crista femoris. It is difficult to assign them to any particular species.

Family Ranidae
Genus *Rana* Linnaeus, 1758

Species identification of frogs is more difficult than that of toads. Modern species of brown frogs can be reliably enough determined from two bones only: frontoparietale and ilium. Some species can be determined from scapulae. Determination of fossil material is even more difficult because of brittleness of these bones. The available fossil bones from Transbaikalia are similar to three modern species.

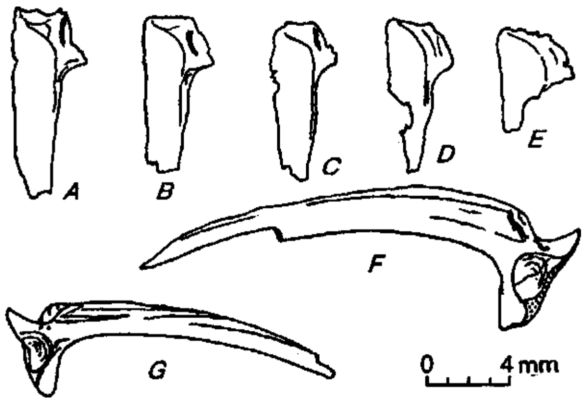

Fig. 3. Bone remains of frogs. *Rana* aff. *chensinensis,* VSU Nos. 590-1/501,502, and 591-6/28, frontoparietaiia (dorsal view); *D, E, G: Rana* aff. *amurensis: D,E* — VSU Nos. 590-1/2943,2944, frontoparietaiia (dorsal view); *G* - VSU No. 590-1/2949, ilium (exterior view); *F — Rana* aff. *asiatica,* VSU No. 591-1/40, ilium (exterior view).

Rana aff. *chensinensis* David, 1875

Material. Dodogol, No. 15: frontoparietale — 85; "horizon 2": frontoparietale — 14.

Frontoparietale. Flattening of the dorsal surface of the specimens of sample No. 15 (Fig. 3, *A*, *B)* is bordered by linea transversalis and 1. medialis, located at the lateral bend of the bone and sometimes weakly pronounced. A short 1. prooticalis is sometimes observed. Processus occipitalis is well developed. Most specimens have a weakly or clearly pronounced groove between processus prooticalis and p. occipitalis. The sagittal edge of the bone is fairly even, with few hollows in the parietal stretch; it deflects laterally near the anterior edge of the bone. The fossils frontoparietaiia differ most of all from the corresponding bones of *R. arvalis* and *R. asiatica* in their flattened dorsal surface. Such flattening is observed in four species of Russian brown frogs: *R. amurensis,* R. *chensinensis, R. macrocnemis,* and *R. temporaria.* The described specimens are morphologically closer to *R. chensinensis,* but have some minor differences: they differ from Kurile specimens of the same species in the shape of the parietal part of the bone and from Primorye species by a relatively wider dorsal flattening.

The specimens of "horizon 2" (Fig. 3, ***C)*** demonstrate principally the same traits, but processus occipitalis is less pronounced, and the parietal part of the bone seems to be shorter. Some bones demonstrate a smoother transition of the lateral margin to processus prooticalis.

Rana alt. *asiatica* Bedriaga, 1898

Material. Dodogol, No. 15: ilium — 287; "horizon 4": ilium - 1; "horizon 3-4": ilium - 1; "horizon 2": ilium — 50.

Ilium (Fig. 3, *F).* The dorsal crest is higher than ala, its height at a certain stretch is equal to that of tuber superior, then slightly decreases. Tuber superior's elongated, clearly pronounced, laterally bent, with or without small tubercles on the surface. The subacetabular zone is usually narrow, seldom wider. The specimens are closer to the modern species *R. asiatica* but differ by having a more pronounced tuber superior and narrow subacetabular zone.

The fossil specimens show a considerable similarity to another modern species, *R. arvalis,* differing in the bent tuber superior as well as in lower and differently shaped dorsal crest.

Rana aff. *amurensis* Boulenger, 1886

Material. Dodogol, "horizon *2":* ilium — 10; Tologoi, 38x: frontoparietale — 8, ilium — 4; "upper horizon": ilium — 1.

Frontoparietale (Fig. 3, *D, E).* Flattening of the dorsal surface is bordered by weakly pronounced linea transversalis and 1. medialis; 1. prooticalis is absent. Processus occipitalis is moderately or weakly developed. No groove is observed between p. prooticalis and p. occipitalis. The sagittal edge of the bone is even, without hollows. These specimens have a relatively shorter parietal part than those of Dodogol and are similar in shape to *R. amurensis,* differing in the absence of linea prooticalis and, probably, in a relatively greater width of the flattened part.

Ilium (Fig. 3, *G).* The height of the dorsal crest is close to that of ala and very smoothly decreases to the front. Tuber superior is elongated, with or without small complicating tubercles. The subacetabular zone is narrow. The morphology of these fossils is similar to that of *R. amurensis,* differing in somewhat larger size of the bone body and less bent shape of ala.

DISCUSSION

As seen from Table 1, the Mongolian toad, *Bufo raddei,* is the most common and abundant species in the Transbaikalian localities. Its remains are found in all beds with the fauna of tailless amphibians, from the Lower Eopleistocene throughout the Lower Pleistocene. This species is quite reliably identified, although it has a specific feature — presence of a clearly visible tubercle on tuber superior, divided into two apices. Differing in this trait from the modern *B. raddei,* the Transbaikalian fossil specimens are similar to remains of East-European *B. raddei,* having the same peculiarity [10]. The fossil form might be an extinct subspecies and be, therefore, of stratigraphic value.

Findings of tree frogs are very scarce and occur in only three samples, which points to a minor role of these forms in biocenoses of that time. The materials available, both modern and ancient, are not sufficient to conclude whether Transbaikalian tree frogs are remains of an extinct or of a modern form.

Frogs are more common than Hylidae in ancient faunas. They account for a considerable part of some samples. Morphological traits revealed a close similarity of various bone remains to three modern species. Existence of just three species, though, appears doubtful. The species *Rana* aff. *chensinensis* was determined in two samples on frontoparietaiia only, whereas ilia from these samples were closer to another species. Such selectivity of burial does not seem natural, and this brings up the conclusion that all the remains in these samples belong to a single extinct form.

Comparison of morphology of frog remains between samples reveals another interesting phenomenon: both frontoparietaiia and ilia tend to become more similar to *R. amurensis* up the stratigraphic scale. The same tendency is demonstrated by scapulae, although the author omits their description in the systematic description. The matter is that scapulae of the modern species *R. asiatica* and *R. amurensis* in the extreme variants differ in width of collum scapulae: It is wider in tie former. There is, however, an overlapping range of this index observed in both species. Such scapulae were found in the Dodogol (No. 15) and Tologoi samples, but the bulk of the material in the former is made up of wide-necked scapulae absent from the latter.

Hence it may be suggested that we deal with a gradual morphological change of the species. This requires a better understanding; for the time being, the material is described by referring to similarity to the closest modern species.

Let us imagine the landscapes of that time, taking into account the taphonomic peculiarities of the localities. Most bone-bearing sediments are of proluvial origin, except for bed 7 in Dodogol, which formed in a lake [5]. So, the reasoning concerns only the proximal neighborhood of the localities [7]. Remains of *Bufo raddei,* a typical steppe inhabitant, are the most abundant in all samples but No. 15. This is indicative of the presence of open spaces when the sediments were deposited. The presence of frogs with a wide scope of ecological adaptation (forest-steppe) suggests an elevated humidity in the region and proximity to water reservoirs. Shrub and forest biotopes might be present within the steppe landscape (samples No. 15 and "horizon 2"). Rare remains of tree frogs appear to be indicative of the presence of high grass or shrubs.

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Recommended by S. A. Arkhipov 18 October 1995