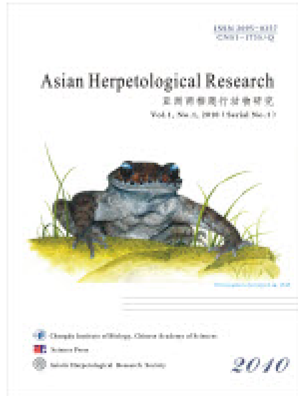

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Complete List of Authors:	Ratnikov, Viatcheslav; Voronezh State University Maslova , Irina ; FSBIS Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences Omelko, Valeriya; FSBIS Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences Tiunov, Mikhail; FSBIS Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences
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Middle Holocene Herpetofauna and Paleogeographic Conditions Based on Fossil Remains from Medvezhiy Klyk Cave (Lozovy Ridge, Southern Sikhote-Alin, Primorsky Krai, Russia)

Viatcheslav Yu. RATNIKOV[1], Irina V. MASLOVA[2*], Valeriya E. OMELKO[2] and Mikhail P. TIUNOV[2]

[1] Voronezh State University, Voronezh 394018, Russia

[2] Federal Scientific Centre of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences, Vladivostok 690022, Russia

[*] Corresponding author: Senior Researcher Irina V. MASLOVA, Federal Scientific Centre of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences, Vladivostok, Russia, with her research focusing on biology and ecology of Russian Far Eastern herpetofauna

E-mail: irinarana@yandex.ru

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Abstract The study was based on material from the Medvezhiy Klyk Cave, located in the Southern Sikhote-Alin range in the Russian Far East. The aim of this research was to assess the taxonomic composition and changes in the species diversity of the Southern Primorye herpetofauna over geological time in response to environmental changes. In the fifth layer of sedimentary deposits in Medvezhiy Klyk Cave (horizons 15–11), corresponding to the Middle Holocene, remains of sixteen extant species of amphibians and squamate reptiles were identified: *Bombina orientalis*, *Bufo sachalinensis*, *Dryophytes japonicus*, *Rana amurensis*, *R. dybowskii*, *Pelophylax nigromaculatus, Takydromus amurensis*, *T. wolteri*, *Zootoca vivipara*, *Elaphe dione*, *E. schrenckii*, *Lycodon rufozonatus*, *Hebius vibakari*, *Rhabdophis lateralis*, *Gloydius intermedius*, and *G. ussuriensis*. *Salamandrella* sp. was identified only to the genus level due to difficulties in distinguishing species within this genus based on the preserved skeletal elements. Additionally, among the snake remains, some bones could not be assigned to any species in the comparative osteological collection. These remains are classified as *Lycodon* sp. and Serpentes gen. et sp. indet. They most likely also belong to extant species that currently inhabit regions south of the Russian border.

The faunal assemblages of amphibians and reptiles indicate that forest vegetation predominated around the cave during the Middle Holocene, with the most extensive forest cover occurring during the accumulation of horizon 14. This period was also the most favorable for thermophilic and moisture-dependent species, including those whose current ranges lie further south. The climate throughout the deposition of the fifth layer is reconstructed as warmer and more humid than present-day conditions, consistent with other Middle Holocene climate reconstructions. Only horizon 11 corresponds to a relative climatic cooling.

Keywords East Asia, amphibians, reptiles, paleogeography, climate, Holocene

1. Introduction

The Pleistocene–Holocene history of the herpetofauna of the Russian Far East remains poorly studied due to the limited number of discovered and described fossil remains. There are only two brief publications on herpetofauna from the deposits of the Bliznets Cave (Lozovy Ridge, southern Sikhote-Alin). The first study (Alexeeva and Chkhikvadze, 1987) reports the discovery of the Red-banded Snake *Lycodon rufozonatus* Cantor, 1842. The second (Alexeeva and Chkhikvadze, 1998) provides a general list of 12 species of amphibians and reptiles found in the cave, dating from 12,000 years ago to the present. Although their remains are abundant, they have not yet been fully studied. The absence of detailed bone descriptions and illustrations in these publications makes comparison with new collections impossible.

The Medvezhiy Klyk Cave, located in southern Sikhote-Alin in the Lozovy Ridge, 2 km from the Bliznets Cave, is a unique site due to the abundance of bone remains. Numerous remains of mammals, birds, and terrestrial and soil-dwelling mollusks of Holocene and Late Pleistocene age have been discovered there, as reported in several studies (Omelko and Kholin, 2017; Omelko *et al.*, 2020; Panasenko and Kholin, 2011, 2013; Panasenko and Tiunov, 2010; Prozorova *et al.*, 2006; Tiunov, 2016; Tiunov and Panasenko, 2010; Tiunov *et al.*, 2016). A significant portion of the bone assemblage consists of amphibians and reptiles, with their number reaching tens of thousands of specimens.

This vertical karst cave served as a natural trap for animals that lived nearby and occasionally fell in. The vertical walls of the shaft prevented escape, and after death, the animals' bones accumulated at the bottom of the cave (Omelko *et al.*, 2020). The presence of fish bones and remains of semi-aquatic species (*Neomys fodiens* (Pennant, 1771)) and valley species (*Myospalax psilurus* (Milne-Edwards, 1874) and *Tscherskia triton* (de Winton, 1899)) suggests that some animals were brought into the cave by birds of prey. However, their role in the accumulation of bones was likely secondary (Omelko *et al.*, 2020).

Layer-by-layer analysis of amphibian and reptile remains from the Medvezhiy Klyk Cave will enable an assessment of the taxonomic composition and changes in the species diversity of the herpetofauna of southern Primorye over geological time in relation to environmental changes.

2. Description of the Location, Vegetation, and Herpetofauna of the Vicinity of Medvezhiy Klyk Cave

Medvezhiy Klyk Cave is located on the Lozovy Ridge in the southern Sikhote-Alin Mountains (43°01’43’’ N, 133°01’23’’ E) at an elevation of 465 meters above sea level (Figure 1).

The Lozovy Ridge is a small isolated range stretching 7 km in length and 2 km in width (Bersenev, 2021). It serves as a watershed between the Partizanskaya and Litovka river basins and extends from northeast to southwest (Figure 1C). The terrain is characterized by steep slopes on the northwest side and more gradual slopes on the south and southeast. The ridge crest is narrow and ridgelike in some places, and plateau-like in others. Rocky screes and cliffs are common.

Limestone outcrops occupy extensive areas of the ridge, particularly in its southern part. In the north, the outcrops are also significant but largely concealed beneath forest canopy. The rocky terrain results in a distinct vegetation structure and the presence of rare species. The vegetation includes oak woodlands, shrub and herbaceous thickets, broadleaf forests, and mixed conifer-broadleaf forests (Dudkin, 1998).

At the foot of the southeastern slopes, *Quercus dentata* Thunb. forms well-developed forest communities together with other deciduous species such as *Q. mongolica* Fisch. ex Ledeb., *Tilia amurensis* Rupr., *Ulmus japonica* (Rehd.) Sarg., and *Fraxinus rhynchophylla* Hance. Common shrubs include *Lespedeza bicolor* Turcz., *Corylus heterophylla* Fisch. ex Trautv., and *Rubus* species. Vines such as *Actinidia kolomicta* (Maxim.) Maxim. and *Vitis amurensis* Rupr. are also present (Dudkin, 1998).

Manchurian-type polydominant broadleaf forests dominate the northwestern slope and southeastern foothills of the ridge. The main tree species include *Quercus mongolica*, *Fraxinus rhynchophylla* Hance, *Acer pseudosieboldianum* (Pax.) Kom., *A. mono* Maxim., *Tilia amurensis* Rupr., *Carpinus cordata* Blume, *Fracsinus mandshurica* Rupr., *Ligustrina amurensis* Rupr., *Aralia elata* (Miq.), *Kalopanax septemlobus* (Thunb.) Koidz., *A. barbinerve* Maxim., *A. mandshuricum* Maxim., and *Betula davurica* Pall. (Dudkin, 1998).

Conifer-broadleaf forest patches are limited to the ridge summit and the upper part of the southwestern slope in the southern half of the ridge. Treeless areas are covered by forb-rich meadows dominated by meadow-steppe vegetation. Rocky areas support either sparse plant groupings or distinct plant communities. Plant colonization is strongly influenced by microtorelief (Dudkin, 1998).

Currently, nine species of amphibians and fourteen species of reptiles are known from Primorsky Krai (Table 1) (Borzée, 2024; Maslova, 2016). Their distribution is influenced by various factors, including temperature, humidity, elevation, vegetation type, soil characteristics, presence of leaf litter, mobility, dependence on water bodies, and others. The habitat preferences and geographic distribution of these species within the region are shown in Table 1. In the southeastern part of Primorsky Krai, in the vicinity of Medvezhiy Klyk Cave, eight amphibian and eight reptile species have been recorded (marked with an asterisk in Table 1). The nearest confirmed records of *Strauchbufo raddei* (Strauch, 1876) are from the Razdolnaya River near of Ussuriysk City. *Pelodiscus maackii* (Brandt, 1857) and *Oocatochus rufodorsatus* (Cantor, 1842) are found in the western part of the region — the former inhabiting stagnant or slow-flowing water bodies of lowland areas, and the latter favoring open habitats along water bodies.

The single local population of *Orientocoluber spinalis* (Peters, 1866) is recorded in the southwest of Primorsky Krai (Pemzovaya Bay, Sea of Japan, Far Eastern Marine Reserve, Khasansky District). In the Russian Far East, *Lycodon rufozonatus* inhabit only in two locations: the Chernye Mountains (Nadezhdinsky District) and the Siny Ridge (Yakovlevsky District). *Zootoca vivipara* (Lichtenstein, 1823) and *Vipera berus sachalinensis* Tzarevsky, 1917 inhabit to the northern part of Primorsky Krai (Emelianov, 2018; Kharin and Akulenko, 2008; Kuzmin and Maslova, 2003; Maslova, 2016; Maslova *et al.*, 2021; Sundukov, 2025).

It is noteworthy that the endemic of the southern Sikhote-Alin, the *Onychodactylus fischeri* (Boulenger, 1886), is currently absent from the Lozovy Ridge but lives in neighboring ridges. We also did not find any of its remains in the cave. This is likely due to *O. fischeri*'s high habitat requirements, preferring shallow, cold mountain streams with a thick layer of gravel on the bottom (Kuzmin and Maslova, 2003), which are not present on the Lozovy Ridge. The ridge has a different geological origin compared to the neighboring mountains and is composed of late Permian reef limestone of the Chandalaz suite (Bersenev, 2021; Bersenev and Alexeeva, 2024).

The entrance to the Medvezhiy Klyk Cave is located on the watershed ridge in the northeastern part of the Lozovy Ridge, with a narrow crack-shaped opening (1.0 m in length, 0.55 m in width), elongated from northwest to southeast and facing upwards (Figure 2A). The cave is a vertical karst cavity (Figure 2B). The original depth of the cave is 17.4 m, while the depth of the shaft (thickness of extracted deposits) is 5.4 m, with a total (final) depth of 22.8 m.

The excavation for paleontological material was initiated along the boundary of the existing speleological shaft (Figure 2C-e). The initial excavation area was 100x50 cm, divided into two squares – A1 and A2. The width of the trench changes with depth from 100 to 62 cm due to the curvature of the well's walls. The soil was removed in conditional horizons with a thickness ranging from 5 to 10 cm, depending on the nature of the soil. In total, 108 horizons were excavated with a cumulative thickness of 5.4 m (Panasenko and Tiunov, 2010).

During the excavations, 13 lithological layers were identified (Panasenko and Tiunov, 2010; Omelko *et al.* 2020). In 2010-2011, the absolute age of bone samples from layers 3, 5, 7, 9, 11, and 13 was determined using radiocarbon dating. Specifically, for layer 3 (at a depth of 13-18 cm), a dating of 2116 ± 86 cal BP was obtained, and for layer 5 (at a depth of 63-68 cm), a dating of 5815 ± 57 cal BP was determined (Omelko *et al.* 2020).

To date, collections of amphibians and reptiles from five upper more or less horizontal layers and 15 conditional horizons have been identified (Figure 2D):

Layer 1 – densely compacted dark brown clay and humus, with small bone fragments, small gravel, and inclusions of anthropogenic debris. Depth: 0.03-0.06 m. Horizon 1.

Layer 2 – dense humus with bone fragments and gravel inclusions. Depth: 0.04–0.11 m. Horizons 1 and 2.

Layer 3 – stone debris filled with black-brown humus soil, containing voids and wood remains. Depth: 0.1–0.45 m. Horizons 2 to 8.

Layer 4 – black humus soil with gravel inclusions and many small bones. Depth: 0.38-0.51 m. Horizons 8 and 9.

Layer 5 – dark brown loam with small and large gravel inclusions. Depth: 0.45–0.83 m. Horizons 10–15 (Panasenko and Tiunov, 2010). The concentration of bone material in this layer is very high and peaks at a depth of 63–68 cm (Horizon 12).

Samples were collected for spore-pollen analysis; however, laboratory examination revealed an absence of pollen in the samples, most likely due to its poor preservation in the cave deposits.

3. Materials and Methods

More than 42,000 isolated amphibian and reptile bones have been collected from the five upper layers (15 stratigraphic horizons). The results of the study of materials from the top four layers (nine upper stratigraphic horizons) have already been published (Ratnikov *et al.*, 2023, 2024). The material from the tenth horizon was lost and, accordingly, was not processed or included in the analysis. In this work, we will focus primarily on the material from the fifth layer (15th to 11th stratigraphic horizons), from which more than 25,000 bones were recovered.

The identification of the majority of the bones was based on morphological characteristics provided in several publications (Chen, 2020; Chen *et al*., 2021; Ikeda, 2007; Ratnikov, 1994, 2001, 2003, 2004, 2012, 2022, 2024; Ratnikov and Litvinchuk, 2007, 2009; Shi *et al*., 2023; Szyndlar, 1984, 1991a, 1991b). Part of the material was identified by comparison with bones from the author's osteological collection. It should be noted that Ikeda (2007) points out the absence of a hypapophysis on the trunk vertebrae of two species of water snakes of the genus *Amphiesma* (now *Hebius*), contrary to the description of the subfamily Natricinae (Szyndlar, 1991a), including *Amphiesma (=Hebius) vibakari*. All eight specimens of this species in our comparative collection possess hypapophyses. Chen (2020) also shows a photograph of a trunk vertebra of *Hebius vibakari* with a hypapophysis. It is possible that Ikeda used incorrectly identified material. In this study, we present photographs of fossil remains of *Hebius vibakari* (Boie, 1826) and *Rhabdophis lateralis* (Berthold, 1859) from the Medvezhiy Klyk Cave (Figure 3).

The names of modern genera and species are given according to the nomenclature used in the latest reports from leading international herpetological databases: Amphibian Species of the World: an Online Reference (Frost, 2024) and The Reptile Database (Uetz *et al.*, 2025).

The primary identification of fossil material and its distribution across horizons and excavation squares are presented in Table 2. A large number of bones have been identified with open nomenclature. This can be explained by two reasons. First, not all skeletal elements can be identified to the species level due to the similarity in morphology among different species, genera, families, and even orders. For example, in frogs, only the scapulae, frontal, parietal, iliac, and humeral bones of males can be identified to the species level. Secondly, bone degradation prevents species identification of elements that have species-specific characteristics in an undamaged state.

The analysis of the obtained data requires selecting an optimal method for bone counting. For amphibians and reptiles, it is impossible to choose a single bone for statistical calculations and subsequent conclusions, as the differential preservation of skeletal elements precludes this. Therefore, various skeletal elements must be considered. Basing counts solely on species-level identifications risks excluding taxa whose bones could not be identified to the species level. Consequently, all bones identified below the order level were included in the analysis, following a prior calibration. Since the bones that could not be identified to species level most likely belong to the same species as those identified by other bones, we perform calibration, meaning that all identifications are attributed to species. We assume that bones identified, for example, to genus level, belong to the same species of that genus identified by other bones. Therefore, we distribute them among the species in the same proportion. Bones identified to subfamily level are distributed among the identified genera of this subfamily. Bones identified only to order level are excluded from calculations, as they do not affect the relative proportions of subordinate taxa. The calibrated number of bones for each species was converted into percentages. These were calculated for each stratigraphic horizon, with data from different samples of the same horizon being combined (Table 3).

In previous publications (Ratnikov *et al*., 2023, 2024), we assumed that if a genus was identified in the sample but species identifications were missing, it referred to a species currently inhabiting the vicinity of the cave. In particular, the remains of *Salamandrella sp.* are more likely to belong to the species *Salamandrella tridactyla* Nikolskii, 1905, which inhabits the Primorye region and nearby areas (the plain part of the Jewish Autonomous Region, southern Khabarovsk Krai, eastern Manchuria, and northern Korea), rather than *Salamandrella keyserlingii* Dybowski, 1870, which has a wider range but is not found in Primorye (Kuzmin, 2012). The transition to older deposits revealed the appearance of both southern and northern forms, which are no longer present in the vicinity of the cave. Therefore, we left the identification of *Salamandrella* sp. unchanged, assuming that at different times, different representatives of this genus may have inhabited the area, possibly even coexisting.

When analyzing and interpreting our materials, we must assume that the quantitative ratio of the found bones reflects the numerical relationship of individuals of the corresponding species that perished in the cave. However, this ratio does not correspond to the distribution of species living in the immediate or distant surroundings of the cave. There are several reasons for this:

1. The number of bones in the skeleton of snakes is several times higher than that of lizards and amphibians. Since lizards, tailed, and tailless amphibians have approximately the same number of bones, and lizards and tailed amphibians are represented minimally in the samples, thus having little impact on the conclusions, we treat amphibians and reptiles separately, considering the total number of bones in each class as 100%.

2. The cave entrance is located on the summit of the mountain ridge at an elevation of 465 m above sea level, which significantly reduces the possibility of species from open lowland biotopes, those living in or near water bodies (such as *Rana amurensis* Boulenger, 1886 and *Pelophylax nigromaculatus* (Hallowell, 1861), falling into the cave "trap."

3. Species from lowland areas, like all others, could enter the cave as prey for predators, especially birds. It is clear that the species composition and the number of bones of each species are related to the diet of the predators.

4. Due to structural features, some species have a better chance of escaping upwards after falling into the cave (e.g., *Dryophytes japonicus* (Günther, 1859)), compared to others.

Because the cave's taphocenosis does not correspond to the paleobiocenosis of the surrounding area, our assumptions about the paleoenvironment are quite schematic. Paleoenvironment reconstructions were made based on the quantitative ratios of remains from various ecological groups (Ratnikov 1996, 2016).

Changes were traced across the stratigraphy for the following parameters:

1. The ratio of the remains from species of open biotopes (*Pelophylax nigromaculatus*, and *Rana amurensis*), closed (forest) biotopes (*Bombina orientalis* (Boulenger, 1890), *Rana dybowskii* (Günther, 1859), *Takydromus amurensis* Peters, 1881, *Elaphe schrenckii* Strauch, 1873, *Lycodon rufozonatus* and *Gloydius intermedius* (Strauch, 1868)), eurytopic species (species of the genus *Salamandrella*, *Bufo sachalinensis* Nikolskii, 1905, *Dryophytes japonicus*, *Zootoca vivipara* (Lichtenstein, 1823), *Elaphe dione* (Pallas, 1773), *Rhabdophis lateralis*, and *Gloydius ussuriensis*). We selected a group that inhabits complex biotope systems (*Takydromus wolteri* and *Hebius vibakari*).

2. The ratio of the remains from moisture-adapted reptiles (*Lycodon rufozonatus*, *Rhabdophis lateralis*, and *Gloydius ussuriensis*), thermophilic amphibians and reptiles (*Bombina orientalis*, *Dryophytes japonicus*, *Pelophylax nigromaculatus*, *Takydromus amurensis*, *T. wolteri* Fischer, 1885, *Elaphe schrenckii*, *Hebius vibakari*, *Rhabdophis lateralis*, and *Lycodon rufozonatus*), and cold-resistant species (*Bufo sachalinensis*, *Rana amurensis*, *R. dybowskii*, *Zootoca vivipara*, *Elaphe dione*, *Gloydius intermedius*, and *G. ussuriensis* (Emelianov, 1929)).

3. Attention was given to the presence of species that no longer inhabit the vicinity of the cave.

4. Results

In the Middle Holocene deposits of the Medvezhiy Klyk Cave, remains of six amphibian species (*Bombina orientalis*, *Bufo sachalinensis*, *Dryophytes japonicus*, *Rana amurensis*, *R. dybowskii*, and *Pelophylax nigromaculatus*), ten reptile species (*Takydromus amurensis*, *T. wolteri*, *Zootoca vivipara*, *Elaphe dione*, *E. schrenckii*, *Hebius vibakari, Rhabdophis lateralis*, *Lycodon rufozonatus*, *Gloydius intermedius* and *G. ussuriensis*), as well as three taxa in open nomenclature – *Salamandrella* sp., *Lycodon* sp., and Serpentes gen. et sp. indet. (Table 3) were discovered.

Some of these specimens could not be matched with any analogs from our comparative collection. Primarily, this pertains to vertebrae that we previously (Ratnikov *et al.*, 2024) identified as *Lycodon* sp. The reason for this identification was the horizontally directed prezygapophyseal processes (Figure 4). *L. rufozonatus* currently inhabits areas closer to the Medvezhiy Klyk site than other species with similar processes, so we initially identified our fossil findings with this species. However, our comparative collection contains a single juvenile specimen of *L. rufozonatus*, and its vertebrae show morphological differences compared to the fossil vertebrae. Since we are unable to observe the intraspecific variability of *L. rufozonatus* vertebrae, we cannot conclusively associate the fossil material with this species, nor can we completely rule out this possibility.

In horizon 12, we found skull bones that showed no differences from *L. rufozonatus* (Figure 5). However, in horizons 11–15, we discovered other bones that we could not match with any of the species in the collection (Figures 6, 7). Vertebrae with horizontal prezygapophyseal processes also proved to be inconsistent. The most notable difference is the shape of the zygosphene (either straight or convex from the front view) and the zygantrum (Figure 8). However, the lack of comparative samples prevents us from determining whether this represents intraspecific variability or different species. All bones initially identified in open nomenclature as *Lycodon* sp., *Lycodon* sp.1 (large), cf. *Lycodon* sp.1 (large), *Lycodon* sp. 2 (small), *Lycodon* sp. 3 (large) have been grouped with *L. rufozonatus* for ease of interpretation under the name *Lycodon* sp. Bones initially identified in open nomenclature as Colubrinae forma1, Natricinae forma1, Viperidae forma1, and Serpentes forma1 were grouped into another category under the name Serpentes gen. et sp. indet. We believe that the modern ranges of *Lycodon* sp. and Serpentes gen. et sp. indet.are located southern then Primorsky krai, Russia.

In all horizons, remains of *Rana dybowskii*, *Bufo sachalinensis*, *Elaphe dione*, *E. schrenckii*, *Hebius vibakari*, *Rhabdophis lateralis*, *Gloydius intermedius*, as well as groups of *Lycodon* sp.

and Serpentes gen. et sp. indet. were found. The remains of other species were found in some horizons but not in all (Table 3, Figure 9).

Horizon 15 (depth – 83–78 cm). The majority of amphibian bones in this horizon belong to *Rana dybowskii* (78.29%). The abundant species is *Bufo sachalinensis* (19.57%), while *Bombina orientalis* accounts for 2.14%. Among reptiles, the most numerous species is *Elaphe dione*, with remains accounting for 64.65%. Two other species are relatively numerous: *Hebius vibakari* (17.56%) and *E. schrenckii* (13.85%). The remains of *Gloydius intermedius* (1.97%), *Takydromus wolteri* (0.30%), and *Rhabdophis lateralis* (0.23%) are less frequent. The total number of *Lycodon* sp. and Serpentes gen. et sp. indet. is 1.44%.

Horizon 14 (depth – 78–73 cm). The number of bones in this horizon is minimal, but it seems not to have affected species diversity. The percentage of *Rana dybowskii* increased to 82.64%, while *Bufo sachalinensis* decreased to 13.68%. The relative amount of *Bombina orientalis* slightly increased to 2.63%, and a fourth amphibian species appeared in the faunal complex of this horizon – *Pelophylax nigromaculatus* (1.05%).

The most numerous reptile species remains *Elaphe dione*, although its proportion decreased significantly (54.45%). The relative number of *E. schrenckii* increased (29.89%), while *Hebius vibakari* decreased (17.56%). The relative number of *Gloydius intermedius* decreased slightly (1.42%), and *Rhabdophis lateralis* increased (0.36%). Lizards are absent in this horizon, but the relative number of *Lycodon* sp. (3.88%) and Serpentes gen. et sp. indet. (0.39%) significantly increased, reaching their highest values across the five horizons.

Horizon 13 (depth – 73–68 cm). The amphibian faunal complex of this horizon is again represented by only three species. The percentage of *Rana dybowskii* decreased to 79.14%, while *Bufo sachalinensis* increased to 19.22%. The number of the third species, *Bombina orientalis*, also decreased (1.64%). The number of definitively identified reptile species increased: *Takydromus wolteri* (0.70%) and *Gloydius ussuriensis* (0.09%) appeared. The proportion of *Elaphe* species became the lowest among the five horizons: *E. dione* (52.93%) and *E. schrenckii* (13.74%). The proportion of *Hebius vibakari* and *G. intermedius* increased, reaching their maximum values: 27.41% and 3.21%, respectively. The number of *Rhabdophis lateralis* (0.32%) remained roughly the same, while the proportion of *Lycodon* sp. and Serpentes gen. et sp. indet. decreased significantly (1.33% and 0.27%, respectively).

Horizon 12 (depth – 68–63 cm). The largest number of both bone remains and species of amphibians and reptiles were found here. Two bones of *Salamandrella* sp. account for 0.1% of the amphibian remains. The same percentage was assigned to *Rana amurensis*. The proportion of *R. dybowskii* continues to decrease (72.27%), while *Bufo sachalinensis* increases (25.61%). The second species, which appeared along with *Salamandrella* sp. only in this horizon, *Dryophytes japonicus*, constitutes 0.15%.

The proportion of *Elaphe dione* increased (56.88%), as did *E. schrenckii* (17.37%). Conversely, the proportion of *Hebius vibakari* decreased (20.74%). The relative numbers of *Takydromus wolteri* (1.60%) and *Gloydius ussuriensis* (0.39%) increased, while *Rhabdophis lateralis* (0.15%) and *G. intermedius* (1.71%) decreased. The number of *Lycodon* sp. and Serpentes gen. et sp. indet., although at their highest levels in terms of quantity, decreased further in percentage terms (1.02% and 0.14%, respectively). Notably, it was in this horizon that skull bones were identified as *Lycodon rufozonatus*.

Horizon 11 (depth – 63–58 cm). In this horizon, the number of amphibian species decreases again to three. The proportion of *Rana dybowskii* reaches a minimum (56.51%), while *Bufo sachalinensis* reaches its maximum (43.28%). The third species remains *R. amurensis* (0.21%).

The diversity of reptiles in this horizon reaches its peak, as all previously noted forms are added to by a small number of *Zootoca vivipara* (0.05%). Both species of *Takydromus* are present: *T. wolteri* (1.29%) and *T. amurensis* (0.05%). The proportion of *Elaphe dione* continues to increase (61.07%). The proportions of *E. schrenckii* and *Hebius vibakari* decreased and nearly equalized (16.89% and 17.98%, respectively). The proportion of *Rhabdophis lateralis* remains at about the same level (0.13%), while the amount of *Gloydius intermedius* increased (2.17%) and *G. ussuriensis* decreased (0.05%). The relative proportions of *Lycodon* sp. and Serpentes gen. et sp. indet. continue to decrease (0.29% and 0.03%, respectively).

5. Discussion

The faunal complexes of amphibians from the Middle Holocene include both forest species and species of open landscapes. The relative abundance of forest species in all horizones exceeds half, while species of open landscape, such as meadow forms, are only present in the horizones 14 and 11 (Figure 10). From this, we can conclude that forest biotopes were predominant in the southern Sikhote-Alin during this time period.

In the reptile faunal complex, typical species of open biotopes are absent, but instead, species from complex biotopes — ranging from scrubland and shrubs to open rocky areas — are present, such as *Takydromus wolteri* and *Hebius vibakari*. The latter species was previously considered a forest dweller in an earlier paper (Ratnikov *et al*., 2024), but we now reconsider its classification, which influences our interpretation. As a result, the trend in changes of forest species among reptiles is similar to that of amphibians, with a peak in the horizon 14 (Figure 10). Reptiles of complex biotopes are in antiphase with forest species, and their minimum numbers appear in the horizon 14 (Figure 10). The number of eurytopic amphibian and reptile species changes little overall in horizons.

Heat-loving reptiles are represented by both modern inhabitants of the study area (*Takydromus amurensis*, *T. wolteri*, *Elaphe schrenckii*, *Hebius vibakari*, *Rhabdophis lateralis*, and *Lycodon rufozonatus*) and species currently living farther south (Serpentes gen. et sp. indet.). The remains of this group are abundant in all Middle Holocene horizones, but especially so in the horizones 13 and 14 (Figure 10). In the horizon 14, the proportion of *E. schrenckii*, *L.rufozonatus*, and Serpentes gen. et sp. indet. increases significantly (Figure 9). This aligns with the radiocarbon dating for the horizon 12 (depth 63–68 cm) of 5815 ± 57 cal. BP and paleogeographical reconstructions for that time — mean annual temperatures were 3–5°C higher than today, the climate was more humid, and forests were dominated by broadleaf species such as *Juglans*, *Carpinus cordata*, *Ulmus*, *Quercus dentate*, *Q. omorica*, *Phellodendron*, *Tilia*, *Acer*, *Fraxinus*, *Syringa*, and *Corylus* (Korotky *et al*., 1997, 2005; Evstigneeva *et al*., 2025).

Although the remains of heat-loving amphibians are few, their numbers also peak in the horizon 14 (Figure 10).

For those reptile species whose diet primarily consists of amphibians and fish (e.g., *Rhabdophis lateralis*, *Lycodon rufozonatus*, and *Gloydius ussuriensis*), there is a clear connection with humid biotopes, which include various types of water bodies. It is possible that the relative abundance of these species corresponds to the degree of humidity in the climate. Their maximum abundance also coincides with the horizon 14, just like that of the heat-loving species (Figure 10).

We hypothesize that the horizon 11 corresponds to a period of cooling and reduced humidity. The number of drought- and cold-resistant species such as *Bufo sachalinensis* and *Elaphe dione* increases, while the number of heat- and humidity-loving species like *Lycodon* sp. and *Rhabdophis lateralis* decreases. For the first time, remains of *Zootoca vivipara* is recorded, a species that is currently distributed north of the study area. Its southern range boundary passes approximately 500 km from the Medvezhiy Klyk Cave (Maslova and Seryodkin, 2016). Interestingly, the number of cold-resistant amphibian remains nearly constant throughout the depth of the stratigraphy (Figure 10). These findings further confirm significant changes in the distribution areas of modern species even during the Holocene.

The herpetofaunal species composition of the Middle Holocene exhibits several differences compared to the Late Holocene. Notably, the Late Holocene assemblages lack remains of Serpentes gen. et sp. indet. and *Zootoca vivipara*, while remains of *Strauchbufo raddei* appear (Ratnikov et al., 2023, 2024). Furthermore, *Elaphe rufodorsatus* (=*Oocatochus rufodorsatus*), which was identified in the Holocene herpetofauna from the Bliznets Cave located 2.5 km from

Medvezhiy Klyk Cave (Alexeeva and Chkhikvadze, 1998), was not found in either the Middle or Late Holocene layers at this site.

Quantitative analysis shows a decrease in the number of remains of moisture- and heat-loving species from the Middle to the Late Holocene, alongside an increase in species inhabiting open landscapes. Additionally, more significant shifts in the quantitative ratios of specific amphibian and reptile groups were observed between the different horizons within the Late Holocene itself (Ratnikov et al., 2023, 2024).

Data on insectivores, bats, lagomorphs, and rodents from Medvezhiy Klyk Cave indicate that Layer 5 contains remains of both typical forest species and species of open landscapes (Omelko *et al*., 2020; Panasenko and Tiunov, 2010; Tiunov, 2016). This pattern is consistent with findings from other caves in Primorsky Krai, namely Bliznets and Perspektivnaya, which also yield remains of both forest and open-habitat mammals (Alexeeva, 1986; Danukalova *et al*., 2025).

Studies have established that the remains of rodents and insectivores in Medvezhiy Klyk Cave are dominated by eurytopic species (Omelko *et al*., 2020). Notably, among rodents in the Middle Holocene, the eurytopic vole *Craseomys rufocanus* became mono-dominant, accounting for up to 79% of the remains (Panasenko and Tiunov, 2010).

Data from Bliznets and Perspektivnaya Caves provide evidence for the presence of the warmth-loving greater horseshoe bat (*Rhinolophus nippon*) in the Middle Holocene, a species whose current range is centred in Central China (Alekseeva and Tiunov, 1987; Danukalova *et al*., 2025). Furthermore, the remains of the semi-aquatic Eurasian water shrew (*Neomys fodiens*) are recorded specifically in Layer 5 of Medvezhiy Klyk Cave (Omelko *et al*., 2020).

The data suggest that several mammal species have shifted their geographical ranges since the Middle Holocene. Some species now reside to the west or north of Medvezhiy Klyk Cave, while *R. nippon* is found substantially further south (Omelko *et al*., 2020). Additionally, the teeth of three extinct pika species—*Tonomochota khasanensis*, *T. sikhotana*, and *T. khinganica*—have been identified in Middle Holocene deposits of Far Eastern caves (Danukalova *et al*., 2025; Gusev, 2024).

Summing up the data from our research on the late Holocene herpetofauna from the Medvezhiy Klyk Cave deposits (Ratnikov *et al*., 2023, 2024), we conclude that representatives of the group Serpentes gen. et sp. indet. disappeared from the studied area, likely at the boundary between the Middle and Late Holocene, and have not reappeared since. In contrast, representatives of the group *Lycodon* sp. were present during the Late Holocene, though in smaller numbers (Ratnikov *et al*., 2024). On local sites in southern Primorye, isolated finds of *L. rufozonatus* are recorded even today (Sundukov, 2025). Other species have persisted in this area to the present day, despite climatic and landscape changes throughout the Middle and Late Holocene.

6. Conclusions

In the fifth layer of sedimentary deposits in the Medvezhiy Klyk Cave (horizons 15–11), corresponding to the Middle Holocene, the remains of sixteen modern species of amphibians and squamate reptiles were found: *Bombina orientalis*, *Bufo sachalinensis*, *Dryophytes japonicus*, *Rana amurensis*, *R. dybowskii*, *Pelophylax nigromaculatus*, *Takydromus amurensis*, *T. wolteri*, *Zootoca vivipara*, *Elaphe dione*, *E. schrenckii*, *Hebius vibakari*, *Rhabdophis lateralis*, *Lycodon rufozonatus*, *Gloydius intermedius*, and *G. ussuriensis*. The genus level was determined for *Salamandrella* sp. due to the difficulty in identifying species within this genus based on the preserved skeletal elements. In addition, among the remains of snakes, bones were found that could not be associated with any species in our comparative osteological collection. These have been grouped as *Lycodon* sp. and Serpentes gen. et sp. indet. These remains are likely also from modern species currently found south of the study region, outside Russia.

In all horizons, *Bufo sachalinensis*, *Rana dybowskii*, *Elaphe dione*, *E. schrenckii*, *Hebius vibakari*, *Rhabdophis lateralis*, *Gloydius intermedius*, as well as the groups *Lycodon* sp. and Serpentes gen. et sp. indet., are present. The remains of other species are not found in all horizons. The greatest number of bones belong to *R. dybowskii*, *B. sachalinensis*, *E. dione*, *E. schrenckii*, and *H. vibakari*.

The faunal complexes of amphibians and reptiles in horizons 15–11 suggest that in the Middle Holocene, the surroundings of the cave were predominantly forested, with the greatest development of forests during the accumulation of horizon 14. This time was also the most favorable for thermophilic and hygrophilic species, including those whose ranges are currently located south of the study region, and whose relative abundance in the corresponding deposits was highest. Although their presence in all horizons allows for the assumption of a warmer and wetter climate than present during the entire accumulation of the fifth layer, this is well aligned with other climate reconstructions for the Middle Holocene (Korotky *et al*., 1997, 2005; Evstigneeva *et al*., 2025).

The horizon 11 corresponds to a period of cooling and a decrease in humidity. The number of drought- and cold-resistant species increased, and the number of thermophilic groups, primarily *Lycodon* sp., significantly decreased.

Overall, the Middle to Late Holocene interval saw the persistence of forest vegetation throughout its duration, with fluctuating levels of heat and humidity. However, there was no global climate shift toward cooling during this period, as the deposits of the Middle Holocene contain a greater number of species that are likely of southern origin.

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Table 1 Distribution of amphibian and reptile species of Primorsky Krai across ecological groups

Species	Biotopic distribution	Geographical distribution
Amphibian		
*Far East Salamander – *Salamandrella tridactyla* (Nikolsky, 1905)	E	A
*Russian Clawed Salamander – *Onychodactylus fischeri* (Boulenger, 1886)	F	S (the southern part of the Sikhote-Alin Ridge)
*Sakhalin Toad – *Bufo sachalinensis* Nikolskii, 1905	E	A
Mongolian Toad – *Strauchbufo raddei* (Strauch, 1876)	O	L (the coast of Khanka Lake, the valley of Razdolnaya River; the basin of Ussuri River; the mouth of Tumannaya River)
*Oriental Fire-bellied Toad – *Bombina orientalis* (Boulenger, 1890)	F (*B. orientalis silvatica* Korotkov, 1972) / O (*B. orientalis praticola* Korotkov, 1972)	A (forest) / S – (meadow)
*Japanese Tree Frog – *Dryophytes japonicus* (Günther, 1859)	E	A
*Siberian Wood Frog – *Rana amurensis* Boulenger, 1886	O	L (the coast of Khanka Lake, the valley of Razdolnaya River; Muravyov-Amursky Peninsula; the basin of Ussuri River)
*Dybowski's Frog – *Rana dybowskii* Guenther, 1876	F	A
*Black-spotted Frog – *Pelophylax nigromaculatus* (Hallowell, 1861)	O	L (the coast of Khanka Lake, the valley of Razdolnaya River; Muravyov-Amursky Peninsula; the coast of the Sea of Japan from Khasansky District to Lazovsky

		District; the basin of Ussuri River)
Reptiles		
Amur softshell turtles – *Pelodiscus maackii* (Brandt, 1857)	O	L (Khanka Lake, Razdolnaya River; the basin of Ussuri River)
*Mountain Grass Lizard – *Takydromus wolteri* Fischer, 1885	B, OF, SC	L (the coast of the Sea of Japan in the S-W and S-E of Primorsky Krai; the Prikhankaiskaya Lowland; the valley of the Razdolnaya River; the basin of Arsenyevka and Ussuri Rivers to the north to the Bolshaya Ussurka River. Inhabits small hills)
*Amur Grass Lizard – *Takydromus amurensis* Peters, 1881	F	A
Viviparous Lizard – *Zootoca vivipara* (Lichtenstein, 1823)	F	N
*Steppes Ratsnake – *Elaphe dione* (Pallas, 1773)	E	A
*Amur Ratsnake – *Elaphe schrenckii* Strauch, 1873	F	A
Red-backed Rat Snake – *Oocatochus rufodorsatus* (Cantor, 1842)	O, B, OF, SC	L (the S-W of Primorsky Krai; the Prikhankaiskaya Lowland; the valley of the Razdolnaya River; the basin of Arsenyevka, Ussuri, Bolshaya Ussurka and Bikin Rivers. Inabits near water bodies)
*Tiger Keelback – *Rhabdophis lateralis* (Berthold, 1859)	E	A (it is common in the southern and central regions of Primorsky Krai, rare in the north of the region, absent in the upper part of the mountain systems – in dark conifers forests and barrens. Habitats are confined to

		reservoirs)
*Japanese Keelback – *Hebius vibakari* (H. Boie, 1826)	F, OF, SC	A
Red-banded Snake – *Lycodon rufozonatus* Cantor, 1842	F	S, L (two populations on the Malaya Ananyevka River, Nadezhdinsky District and near Bel'tsovo Settl., Yakovlevsky District)
Slender Racer – *Orientocoluber spinalis* (Peters, 1866)	SC	S, L (a single population in the Pemzovaya Bay of the Sea of Japan, Far Eastern Marine Reserve, Khasansky District)
*Ussuri Pitviper – *Gloydius ussuriensis* (Emelianov, 1929)	E	A (tends to inhabit wet areas)
*Central Asian Pitviper – *Gloydius intermedius* (Strauch, 1868)	F, SC	A (in forest biotopes inhabits upper levels of mountain ranges)
Adder – *Vipera berus* sachalinensis Tzarevsky, 1917	E	N

Note: E — eurytopic species, O — species inhabiting open biotopes, F — species inhabiting forest biotopes, B — species inhabiting shrubs, OF — species inhabiting sparse forests, SC — species inhabiting seashore (rocky habitats); A — throughout the Primorsky Krai, L — locally, N — in the north of the Primorsky Krai, S — in the south of the Primorsky Krai.

*Species inhabiting at present the south-east of Primorsky Krai near Medvezhiy Klyk Cave

Table 2 Distribution of herpetofaunal remains from the Medvezhiy Klyk Cave across stratigraphic conditional horizons and sampling squares.

Taxa	15A1	14A1	13A1	13A2	12A1	12A2	12 A1+ A2	11A1	11A2
Salamandrella sp.	–	–	–	–	–	1	1	–	–
Bombina orientalis	5	–	4	7	–	3	5	–	–
Bombina sp.	1	5	1	4	5	19	4	–	–
Bufo sachalinensis	38	17	50	66	56	75	88	80	48
Bufo sp.	–	–	–	4	57	60	–	28	75
Bufonidae indet.	17	9	40	28	56	36	93	122	56
Dryophytes sp.	–	–	–	–	–	2	1	–	–
Pelophylax nigromaculatus	–	1	–	–	–	–	–	–	–
Rana amurensis	–	–	–	–	–	–	–	1	-
Rana cf. amurensis	–	–	–	1	–	–	1	–	–
Rana dybowskii	68	48	83	73	104	79	242	63	55
Rana sp.	32	13	42	98	22	145	28	27	47
Ranidae indet.	120	97	208	270	265	291	295	187	156
Anura indet.	26	16	52	37	69	49	78	72	40
Takydromus amurensis	–	–	–	–	–	–	–	–	1
Takydromus cf. *amurensis*	–	–	–	–	–	–	–	–	2
Takydromus wolteri	1	-	2	1	13	16	4	6	6
Takydromus cf. *wolteri*	–	–	–	–	–	–	–	–	2
Takydromus sp.	3	–	6	15	6	45	3	-–	4
Zootoca vivipara	–	–	–	–	–	–	–	–	1
Lacertidae indet. (small formes)	–	–	–	–	42	1	9	24	10
Elaphe dione	838	132	587	1170	1060	1524	2103	1055	1170
Elaphe cf. *dione*	–	–	–	–	–	–	12	2	3
Elaphe schrenckiii	180	73	154	300	279	487	659	284	331
Elaphe cf. *schrenckii*	–	–	–	–	2	–	6	–	2
Elaphe sp.	2	6	8	19	32	23	11	1	30
Lycodon rufozonatus	–	–	–	–	–	5	-	–	–

Lycodon sp.	11	10	1	1	-	–	–	3	8
Lycodon sp.1 (large)	5	–	16	24	11	19	29	–	–
cf. *Lycodon* sp.1 (large)	–	–	–	–	–	12	5	–	–
Lycodon sp. 2 (small)	-	–	–	4	4	1	–	–	–
Lycodon sp. 3 (large)	2	–	–	–	–	–	–	–	–
Colubrinae forma1	1	-	7	–	–	1	5	–	–
Colubrinae indet.	-	–	–	5	89	17	10	29	47
Hebius vibakari	228	24	276	646	700	667	393	382	299
Rhabdophis lateralis	3	1	2	9	1	3	9	5	–
Natricinae forma1	–	–	–	–	–	2	-	1	–
Natricinae indet.	–	–	–	–	2	1	–	–	–
Colubridae indet.	21	30	–	62	–	34	164	–	–
Gloydius intermedius	26	3	28	73	26	60	56	40	37
Gloydius ussuriensis	–	–	–	3	–	15	16	2	–
Gloydius sp.	–	1	–	5	–	–	2	–	5
Viperidae forma1	–	–	1	–	–	–	1	–	–
Viperidae indet.	–	–	–	4	2	2	2	–	–
Serpentes forma1	–	1	–	–	–	1	1	–	–
Serpentes indet.	14	17	29	87	764	215	266	802	405
Total	1642	504	1626	3016	3669	3911	4602	3215	2840

Table 3 Calibrated distribution of herpetofaunal remains from the Medvezhiy Klyk Cave by arbitrary stratigraphic horizons.

Taxa	15		14		13		12		11	
	Spec.	%	Spec.	%	Spec.	%	Spec.	%	Spec.	%
Salamandrella sp.	–	–	–	–	–	–	2	0.10	–	–
Bombina orientalis	6	2.14	5	2.63	16	1.64	36	1.77	–	–
Bufo sachalinensis	55	19.57	26	13.68	188	19.22	521	25.61	409	43.28
Dryophytes japonicus	–	–	–	–	–	–	3	0.15	–	–
Pelophylax nigromaculatus	–	–	2	1.05	–	–	–	–	–	–
Rana amurensis	–	–	–	–	–	–	2	0.10	2	0.21
Rana dybowskii	220	78.29	157	82.64	774	79.14	1470	72.27	534	56.51
Total amphibians	281	100	190	100	978	100	2034	100	945	100
Takydromus amurensis	–	–	–	–	–	–	–	–	2	0.05
Takydromus wolteri	4	0.30	-	-	24	0.70	139	1.60	49	1.29
Zootoca vivipara	–	–	–	–	–	–	–	–	2	0.05
Elaphe dione	854	64.65	153	54.45	1815	52.93	4953	56.88	2314	61.07
Elaphe schrenckii	183	13.85	84	29.89	471	13.74	1512	17.37	640	16.89
Hebius vibakari	232	17.56	27	9.61	940	27.41	1806	20.74	681	17.98
Rhabdophis lateralis	3	0.23	1	0.36	11	0.32	13	0.15	5	0.13
Gloydius intermedius	26	1.97	4	1.42	110	3.21	149	1.71	82	2.17
Gloydius ussuriensis	–	–	–	–	3	0.09	34	0.39	2	0.05

Lycodon sp.	18	1.36	11	3.88	47	1.33	90	1.02	11	0.29
Serpentes gen. et sp. indet.	1	0.08	1	0.39	8	0.27	11	0.14	1	0.03
Total reptiles	1321	100	281	100	3429	100	8707	100	3789	100
Total	1602	–	471	–	4407	–	10741	–	4734	–

Figure legends

Figure 1 Location of the Medvezhiy Klyk Cave (Primorsky Krai, Russia). A: in the Primorsky Krai; B: in the Lozovy Ridge; C: in the northeastern spurs of the Lozovy Ridge. The arrow indicates the location of the Medvezhiy Klyk Cave.

Figure 2 Medvezhiy Klyk Cave (the Southern Sikhote-Alin, Primorsky Krai, Russia). A: cave entrance; B: vertical profile of the cave and horizontal sections of the cave (i – original cave floor, ii – excavation area, iii – spoil heaps); C: excavation profile along the southwestern wall (1 – excavated deposits; 2 – limestone; 3 – limestone blocks; 4 – unexcavated deposits).

Figure 3 Fossil remains of *Hebius vibakari* (A–J) and *Rhabdophis lateralis* (K–R) (Medvezhiy Klyk Cave, the Southern Sikhote-Alin, Primorsky Krai, Russia). Trank vertebra (A–E): A – anterior view, B – dorsal view, C – lateral view, D – posterior view, E – ventral view; Caudal vertebra (F–J): F – anterior view, G – dorsal view, H – lateral view, I – ventral view, J – posterior view; Palatinum (K–M): K – lateral view, L – medial view, M – ventral view; Trank vertebra (N–R): N – anterior view, O – dorsal view, P – posterior view, Q – lateral view, R – ventral view.

Figure 4 Fossil trank vertebra of *Lycodon* sp. (Medvezhiy Klyk Cave, the Southern Sikhote-Alin, Primorsky Krai, Russia). A: anterior view; B: dorsal view; C: lateral view; D: posterior view; E: ventral view.

Figure 5 Fossil remains of *Lycodon rufozonatus* (Medvezhiy Klyk Cave, the Southern Sikhote-Alin, Primorsky Krai, Russia). Basiparasphenoid (A–B): A – dorsal view, B – ventral view; Maxilla (C–D): C – lateral view, D – medial view; Left palatine (E–F): E – lateral view, F – medial view; Right pterygoid (G–H): G – dorsal view, H – ventral view.

Figure 6 Fossil remains of unidentificated forms from 12 horizone (Medvezhiy Klyk Cave, the Southern Sikhote-Alin, Primorsky Krai, Russia). Compound bone of Natricinae forma 1 (A–C): A – dorsal view, B – medial view, C – lateral view; Dentary of Serpentes (D–F): D – dorsal view, E – lateral view, F – medial view; Compound bone of Serpentes forma 1 (G–I): G – dorsal view, H – lateral view, I – medial view; Compound bone of Viperidae forma 1 (J–L): J – dorsal view, K – medial view, L – lateral view; Dentary 1 of Colubrinae forma 1 (M–O): M – dorsal view, N – lateral view, O – medial view; Dentary 2 of Colubrinae forma 1 (P–R): P – dorsal view, Q – lateral view, R – medial view.

Figure 7 Fossil remains of unidentificated forms from 13–14 horizone (Medvezhiy Klyk Cave, the Southern Sikhote-Alin, Primorsky Krai, Russia). Basiparasphenoid of Viperidae forma 1 (13 horizone) (A–B): A – dorsal view, B – ventral view; Epistropheum of Colubrinae forma 1 (13 horizone) (C–G): C – anterior view, D – dorsal view, E – lateral view, F – posterior view, G –

ventral view; Maxilla of *Lycodon* sp. (14 horizone) (H–J): H – lateral view, I – medial view, J – ventral view.

Figure 8 Different morphology of vertebrae, intendent to *Lycodon* (Medvezhiy Klyk Cave, the Southern Sikhote-Alin, Primorsky Krai, Russia). A–B, E–F: vertebrae with straight zigosphene; C–D, G–H: vertebrae with convex zigosphen; A–D: cervical vertebrae; E–H: trank vertebrae; A, C, E, G: anterior view; B, D, F, H: posterior view.

Figure 9 Relative abundance of amphibian and reptile remains from the deposits of Medvezhiy Klyk Cave (the Southern Sikhote-Alin, Primorsky Krai, Russia).

Figure 10 Relative abundance of amphibians and reptiles from different ecological groups (the deposits of Medvezhiy Klyk Cave the Southern Sikhote-Alin, Primorsky Krai, Russia).

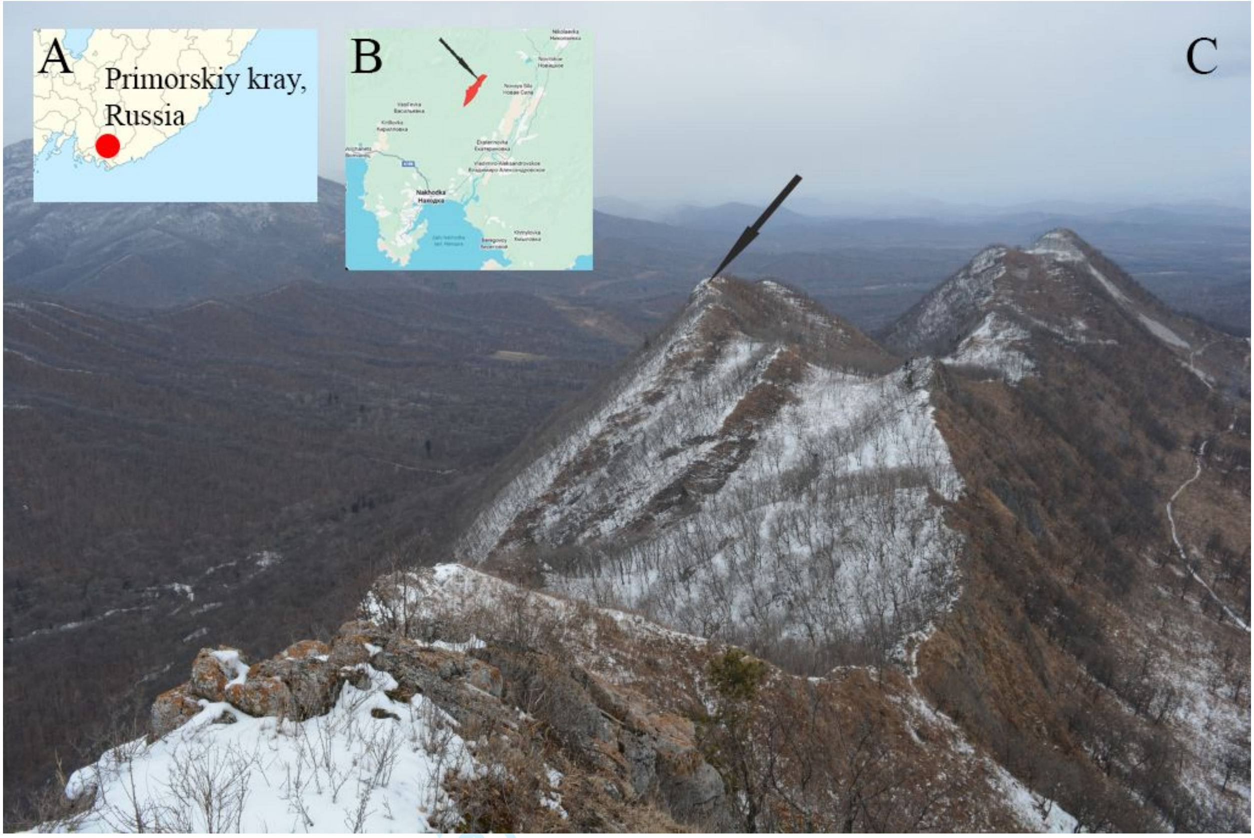
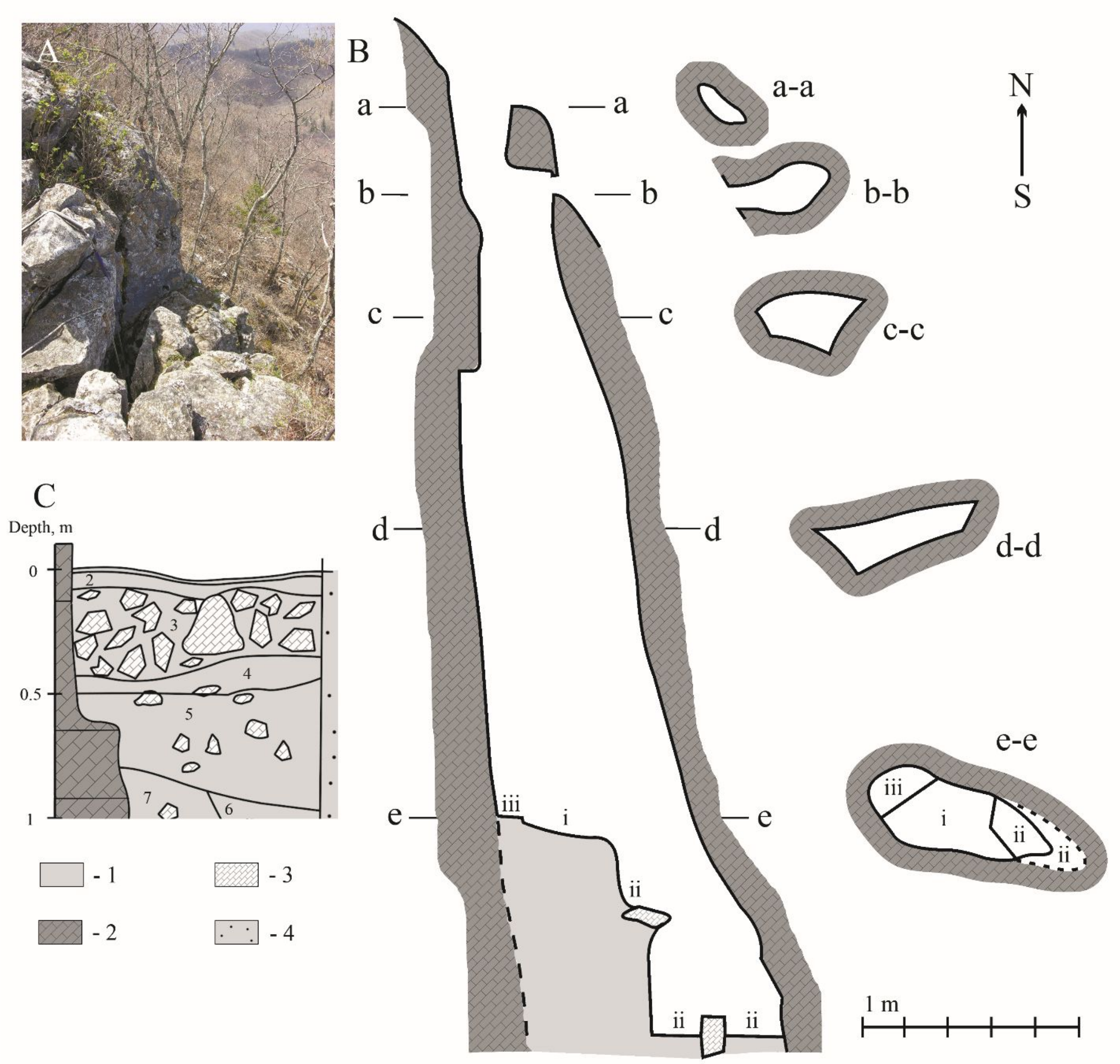


Figure 1



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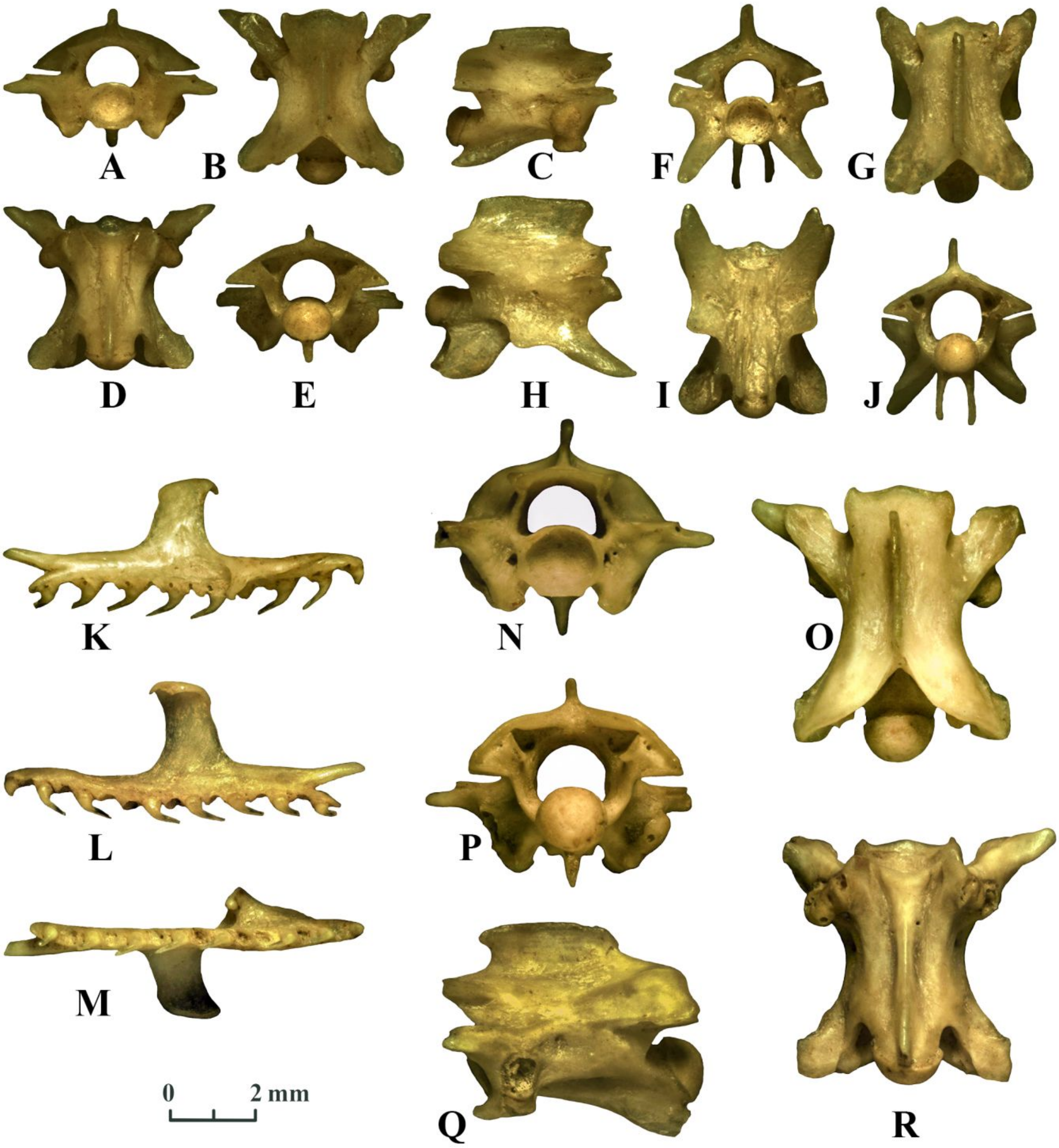

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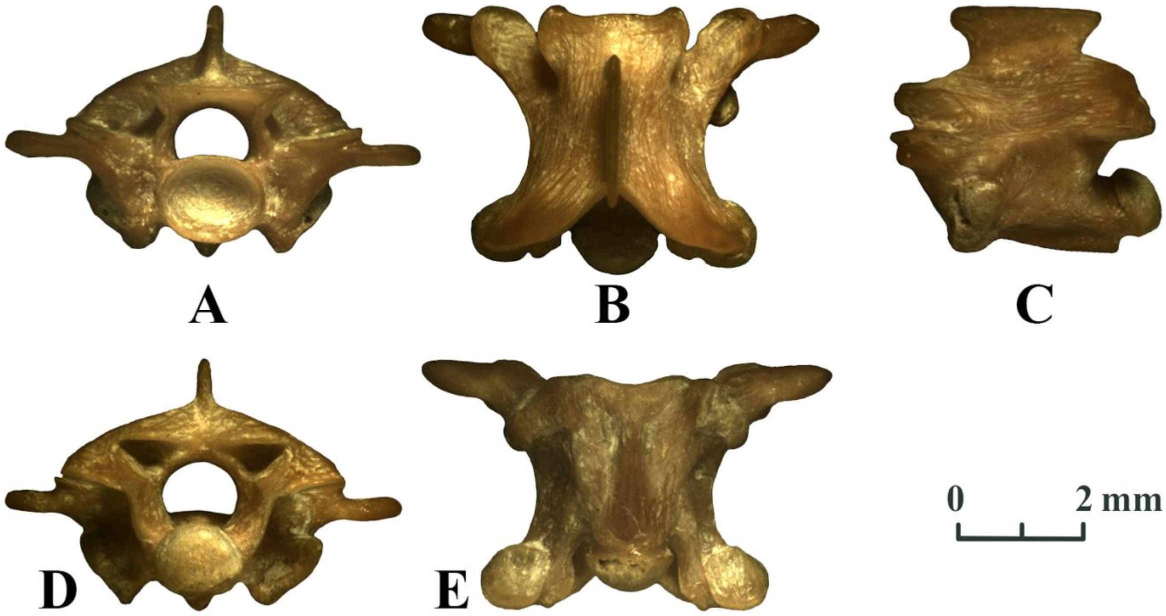

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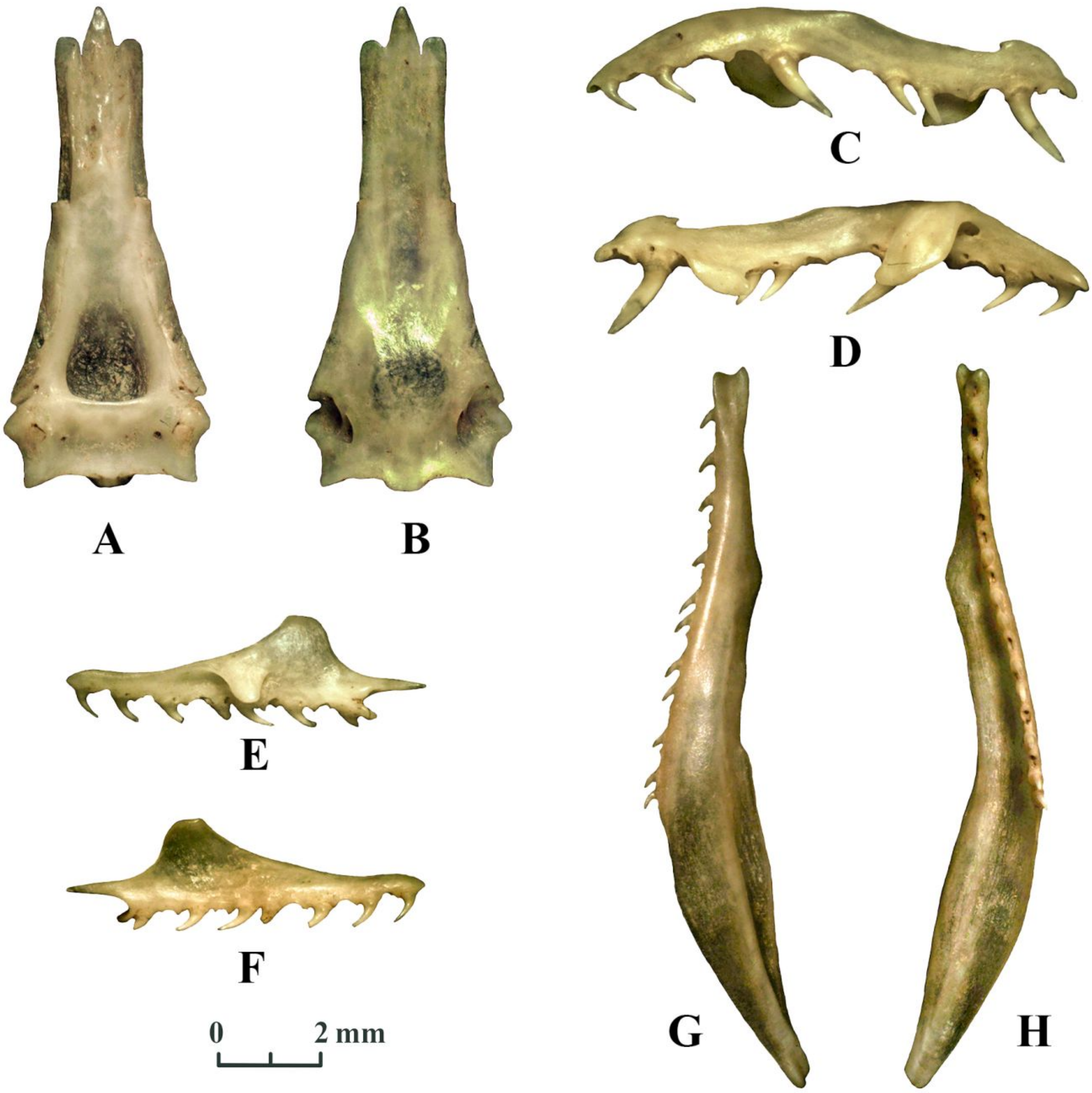


Figure 5

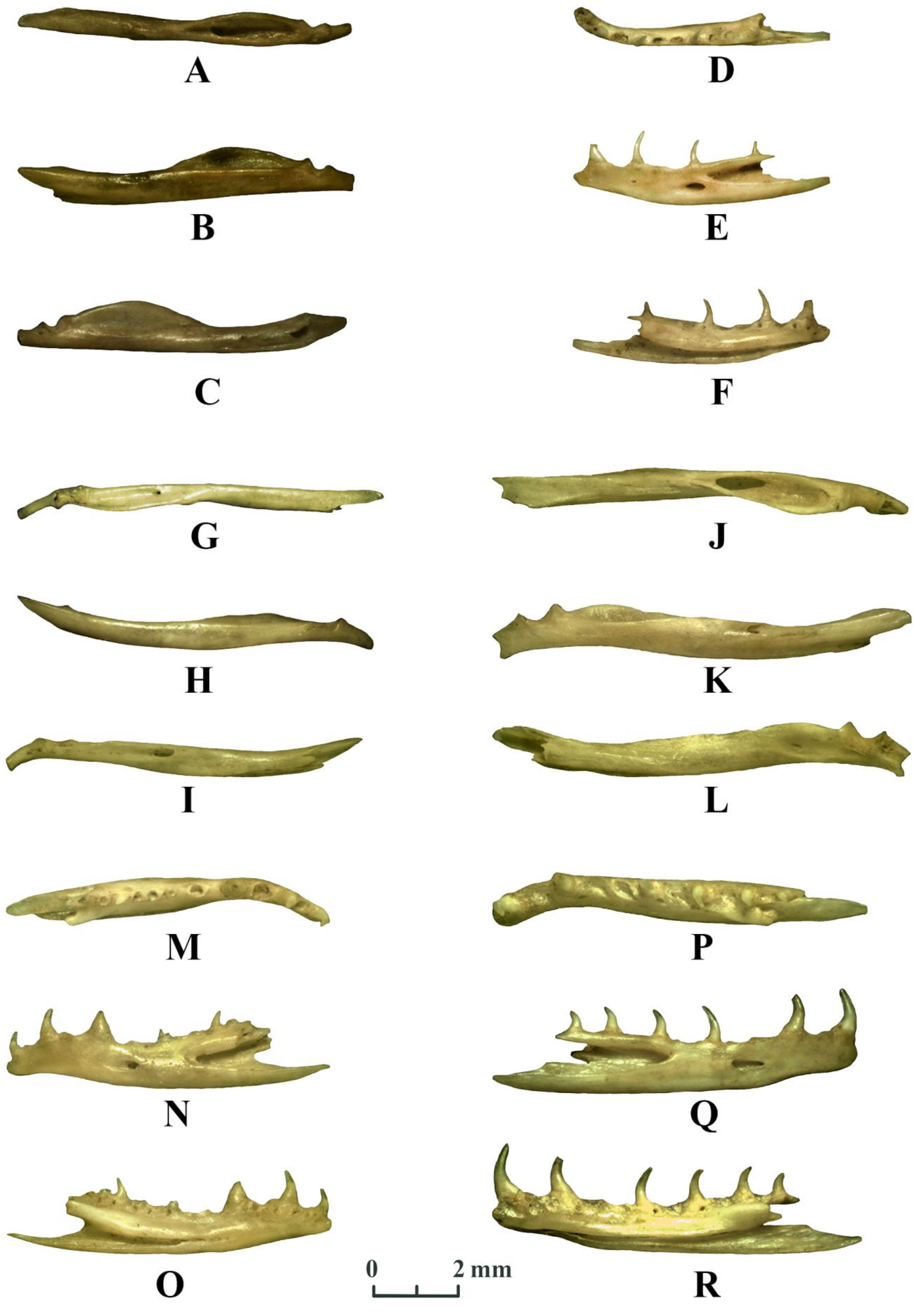


Figure 6

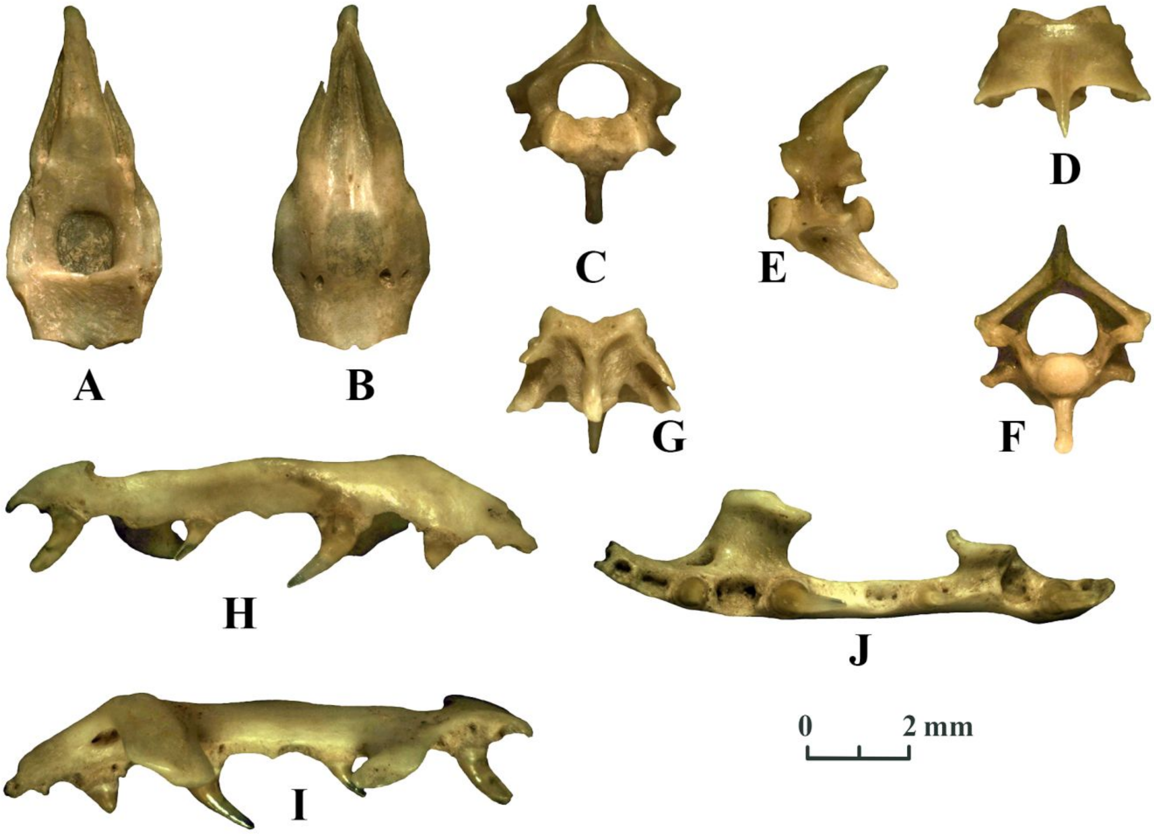
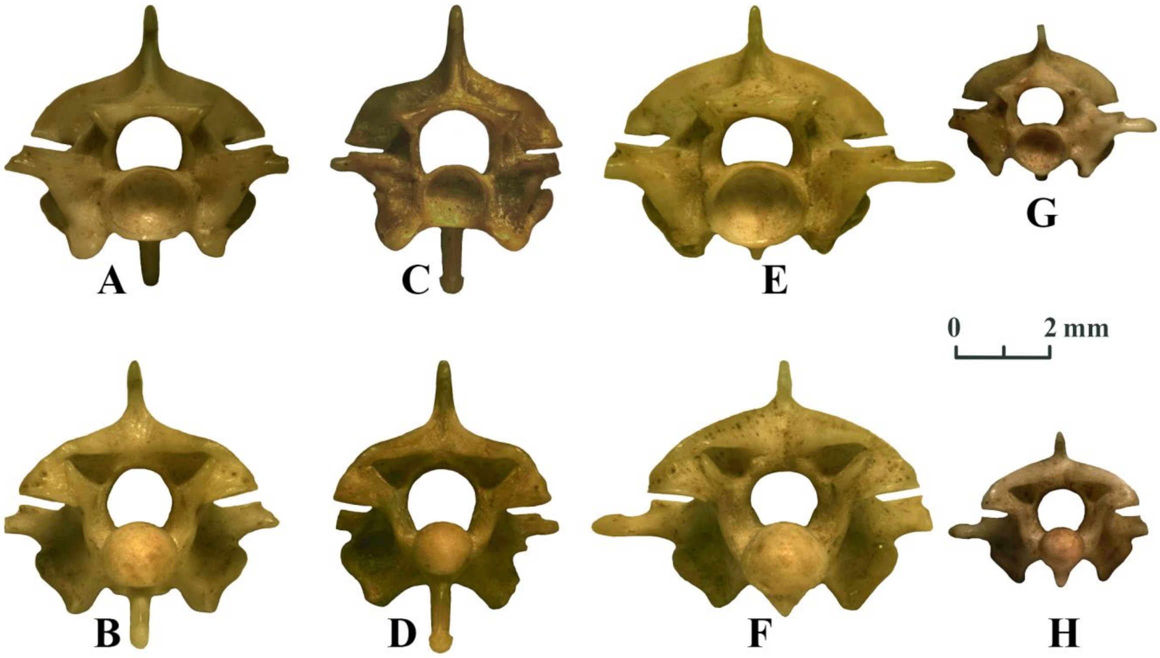


Figure 7



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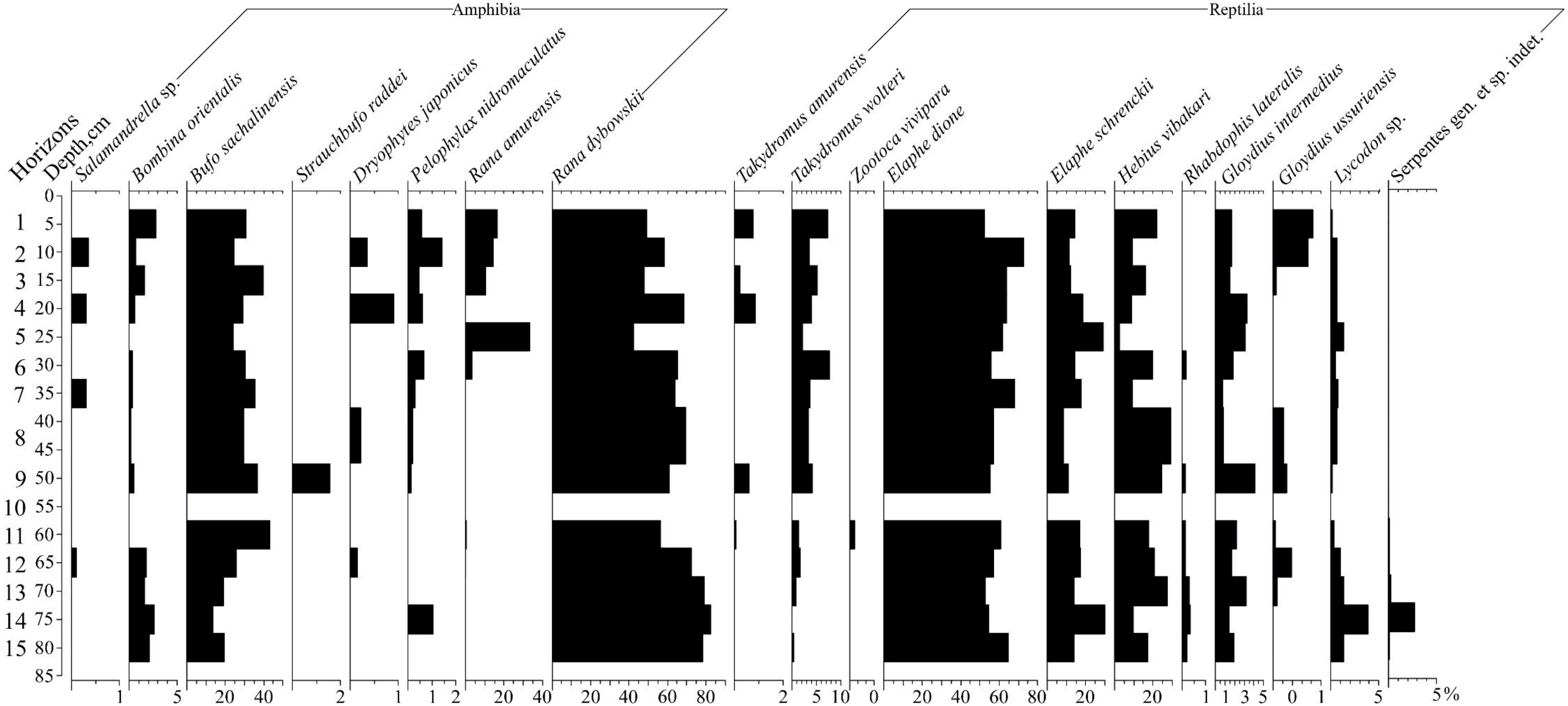
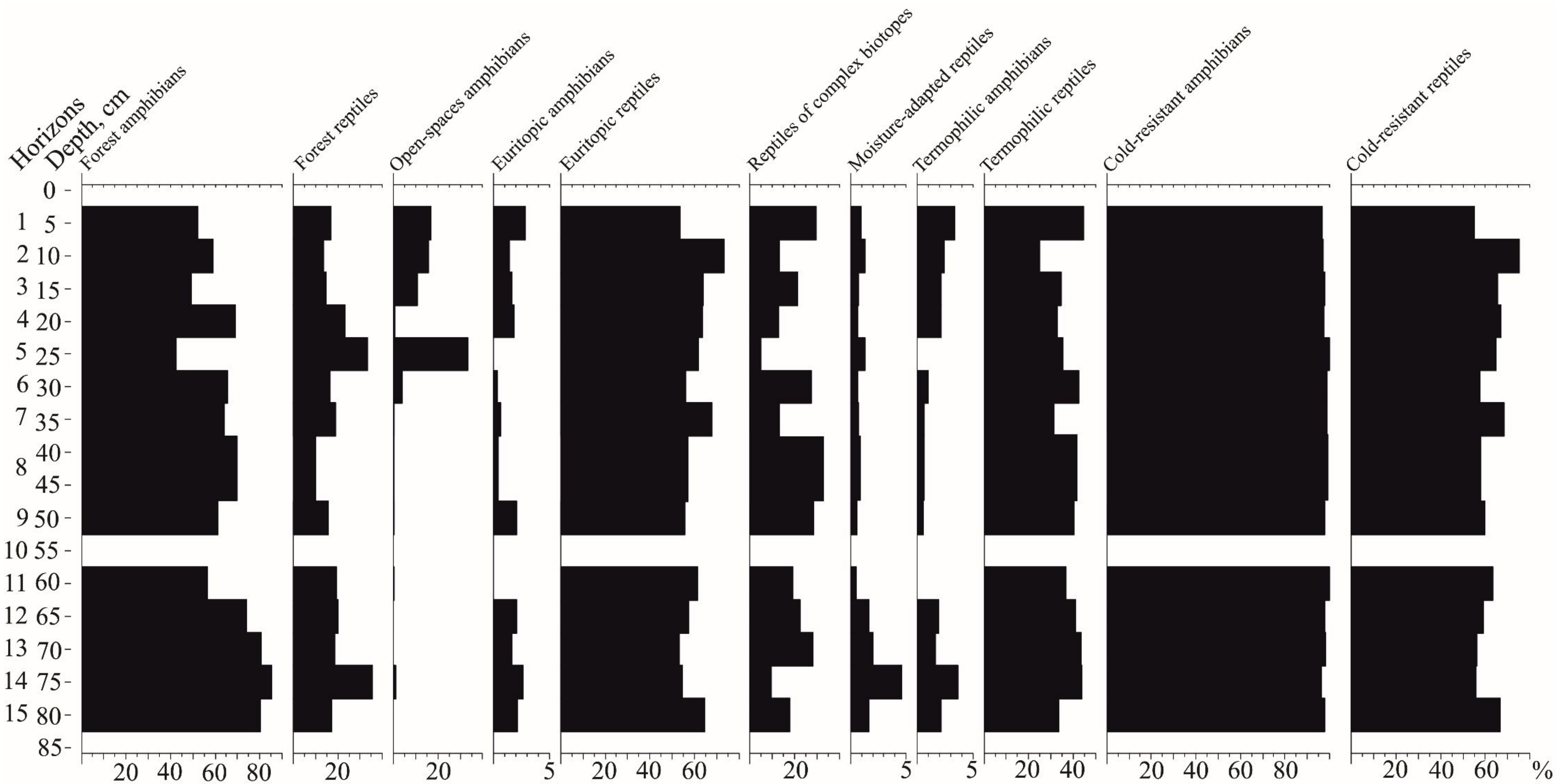

Amphibia
Reptilia
Horizons
Depth,cm
Salamandrella sp.
Bombina orientalis
Bufo sachalinensis
Strauchbufo raddei
Dryophytes japonicus
Pelophylax nidromaculatus
Rana amurensis
Rana dybowskii
Takydromus amurensis
Takydromus wolteri
Zootoca vivipara
Elaphe dione
Elaphe schrenckii
Hebius vibakari
Rhabdophis lateralis
Gloydius intermedius
Gloydius ussuriensis
Lycodon sp.
Serpentes gen. et sp. indet.
5%

Figure 9


Horizons
Depth, cm
Forest amphibians
Forest reptiles
Open-spaces amphibians
Euritopic amphibians
Euritopic reptiles
Reptiles of complex biotopes
Moisture-adapted reptiles
Termophilic amphibians
Termophilic reptiles
Cold-resistant amphibians
Cold-resistant reptiles
0
1 5
2 10
3 15
4 20
5 25
6 30
7 35
40
8
45
9 50
10 55
11 60
12 65
13 70
14 75
15 80
85
20 40 60 80
20
20
5
20 40 60
20
5
5
20 40
20 40 60 80
20 40 60
%
Figure 10