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Paleoecological Conditions of Yuka Mammoth's Habitat and the Yano-Indigirka Lowland's Vegetation Patterns during the Late Pleistocene

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Abstract—The vegetation, widespread during the life of a young female mammoth "Yuka", about 34300 yr ago (GrA-53289) was reconstructed as a complex of phytocenoses confined to coastal water and floodplain habitats. The main pastures were herb-gramineous floodplain meadows. Here, floodplain shrub communities of birches and alder forests grew, the reservoir was of an lake or swamp, as indicated by the corresponding vegetation. In the presented work, a new method of reconstruction of specific paleophytocenoses is proposed, which makes it possible to take a fresh look at the nature of the vegetation cover of the Late Pleistocene of Yakutia.

Keywords: Yuka mammoth, vegetation reconstruction, paleophytocoenoses, Kargin Interstadial, Spore-pollen spectrum, paleophytocoenoses

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INTRODUCTION

Interpretation of results of paleobotanical studies (palynological and carpological) is rather subjective depending on investigator's experience, her knowledge and is mainly based on actualism.

The vegetation reconstruction starts from revealing floristic composition by means of spore-pollen spectra or plant macroremains analysis. The floristic composition is always incomplete, and the main goal at this step is to reveal as many taxa at species level as possible. The revealed list of taxa represents a paleofloristic list, and thus can be considered as an incomplete and arbitrarily selected local flora (Ukraintseva, 2013).

To reconstruct the vegetation of the period when the mammoth Yuka lived, an author's technique was developed. Therefore, the section of this article devoted to research methods is quite extensive. This is the first public presentation of the new methodology, and we tried to substantiate it in sufficient detail.

MATERIALS AND METHODS

The initial material for the reconstruction of vegetation of the period when the mammoth Yuka lived was taken from our article (Rudaya et al., 2014), where the results of palynological and carpological studies from the host sediments were presented. The samples were taken from the inner parts of the skull, which excludes their contamination with later pollen or seeds. Thus, the paleoflorocomplex of the place of death of the mammoth calf was revealed exactly corresponding to the Karginsky period.

Before presenting a technique for the reconstruction of plant communities, it is necessary to dwell on two approaches to the classification of modern phytocenoses. The first approach was asserted in phytocoenology in early 20th century. It was based on the concept of discretization, and vegetation was classified on the principle of dominancy. According to this approach, coenoses were concerned as discrete and determined plant communities being real and historically contingent population assemblages within a homogenous habitat (organismic paradigm). The second approach is based on the principle that phytocoenoses are determined conditionally, being more or less homogenous parts of plant continuum with blurred boundaries (continuum paradigm) (Ramensky, 1971).

One of the continuum paradigm founders L.G. Ramensky (1971) developed the indicator values for plant ordination along various ecological gradients (Ramensky et al., 1956). The moisture values contained 120 numbers ranging from very dry to wet habitat conditions.

Table 1. Correlation of moisture indicator values and ecological groups of plants for Yakutia (according to Korolyuk et al., 2005)

Moisture conditions (grades)	Ecological group	Indicator values
Dry steppe	Euxerophytes (EuX)	31–39
Steppe	Xerophytes (X)	40–46
Meadow steppe	Mesoxerophytes (MsX)	47–52
Dry meadow	Xeromesophytes (XMs)	53–63
Mesic meadow	Mesophytes (Ms)	64–76
Wet meadow	Hygromesophytes (HgMs)	77–88
Bog-meadow	Mesohygrophytes (MsHg)	89–93
Bog	Hygrophytes (Hg)	94–103
Semi-aquatic and aquatic	Hydatophytes (Hd)	104–109

As against Ramensky's interval scale, when each species was assigned a range of values reflecting its realized ecological niche, Korolyuk (2002) elaborated indicator point values, i.e. ecological optimums for Siberian plants. Modified after supplement with Yakutian geobotanical data, these values were used for ecological assessment of species and communities growing in Yakutia (Korolyuk et al., 2005). He correlated the grades of moisture conditions offered by Ramensky with plant ecomorphs (Table 1).

For reconstruction of paleophytocoenoses it was enough to use only four grades of moisture conditions: dry meadow (XMs, 53–63), mesic meadow (Ms, 64–76), wet meadow (HgMs, 77–88), and bog-meadow (MsHg, 89–93). Single species from meadow steppe (47–52) and bog grades (94–103) were inserted into the neighbouring grades of dry meadow and bog-meadow moisture conditions respectively. However, they were payed special attention during reconstruction as the reference marker species.

Another approach that we used for reconstruction was similar to that offered by R. Gittins (1965) and based on species contingency by two-dimensional ordination. The indicator values of moisture gradient were ranged along the X-axis, while the Y-axis represented coenomorphs, i.e. plant populations confined for certain phytocoenoses types (Fig. 1).

We proceeded from the coenomorph system elaborated by A.L. Belgard (1950) and based on the statement that plant species get adapted to a whole phytocoenosis. This approach works within the organismic paradigm of phytocoenology. We used it in our reconstruction since the continuum paradigm assumes stochastic boundaries of phytocoenoses (Mirkin et al., 1989) making impossible determining certain plant communities without complete floristic lists. And plant species that were conditionally assigned to certain phytocoenoses types may help to distinguish the ecological-coenomorphic complexes and, subsequently, to identify certain types of paleophytocoenoses.

Presently, there is no generally accepted coenomorph system though many of its types are actively used in various floristic studies to emphasize species confinement to certain ecotopes. For instance, such terms as "petrophyte", "psammophyte", or "halophyte" are often used in botanical literature. E.P. Gnatyuk and A.M. Kryshen (2005) used 12 coenomorphs in their study of forest cuttings in Karelia. O.V. Bezrodnova (Bezrodnova et al., 2014) used 10 coenomorphs to

Pal				
Tu				
Mon				
Syl				
Pr				
Alv				
StMon				
St				
Ru				
Coenomorphs/ Hygromorphs	53–63 XMs	64–76 Ms	77–88 HgMs	89–93 MsHg

Fig. 1. Ordination of coenomorphs and hygromorphs.

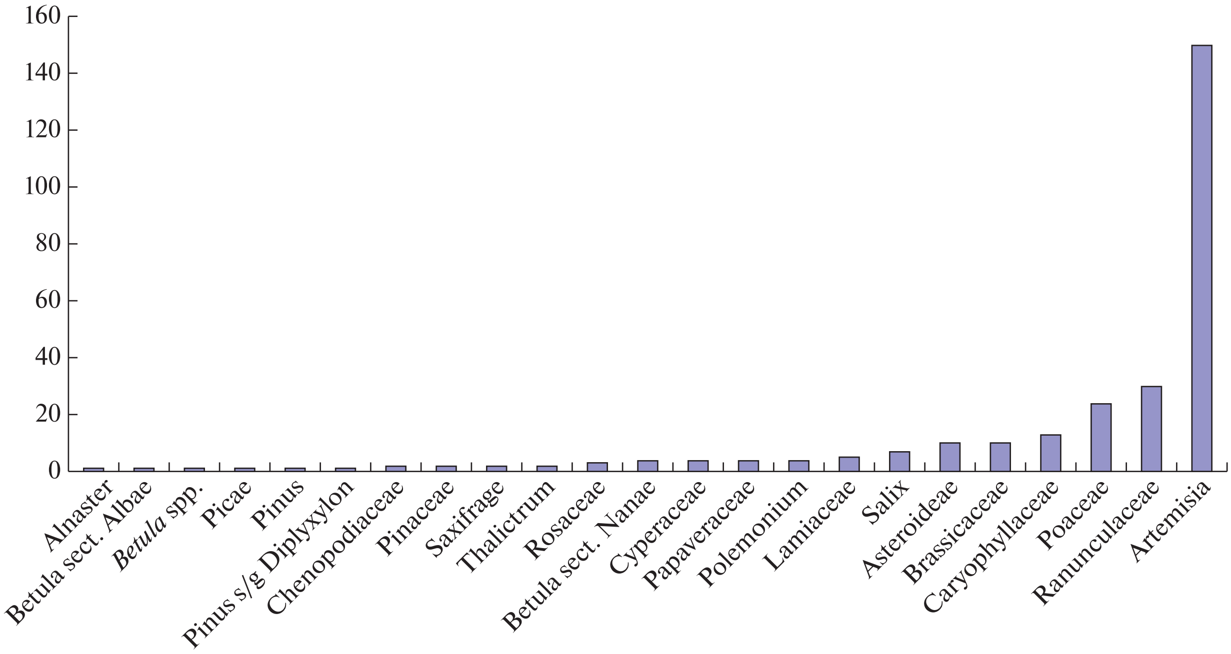

Fig. 2. Spore-pollen spectrum of Yuka mammoth enclosing sediments (Rudaya et al., 2014).

study vegetation of the national parks of Kharkov. E.G. Nikolin (2011) used 7 basic coenomorph types and 15 variations while analyzing the flora of Verkhoyansk Range. Thus, coenomorphs are not postulatory and have no generally accepted uniform classification, however they are rather useful. For instance, in our study we use such coenomorphs as “tundrant” (Tu), “alluviophyte” (Alv), and “montane” (Mon) along with rather widespread “paludant” (swampy) (Pal), “sylvant” (forest) (Syl), “ruderal” (weedy) (Ru), “pratant” (grass) (Pr), “stepant” (St) or mountain steppe species (StMon) (Fig. 1).

Coenomorphs ranging along the Y-axis is determined by the latest dates of spring growth starting point. A.I. Tolmachev (1986) emphasized the importance of snow melt and vegetation growth start dates for the plants of high latitudes. In all climatic zones the earliest growth is observed in ruderal communities and these dates are concerned as reference dates. In tundra and northern taiga, vegetation development in bogs, which are situated in depressions, starts usually later than in upland zonal associations. So, the paludants are arranged at the end of the coenomorphic scale.

Grouping of plant species is made according to coenomorphs and moisture conditions. And if the moisture indicator values are constant, at least at regional level, then coenomorphs are variable. There are plant species, like *Larix dahurica*, that always refer to sylvants. However, the species of wide ecological range grow in different types of plant communities. *Polemonium boreale* is widespread in tundra zone and seemingly should be concerned as a tundrant. However, it is usually assigned to alluviophytes, the species growing on floodplain sand-and-shingle deposits. Thus, affiliation of plant species to a certain coenomorph depends primarily on local biotopes, and not on climatic zones. However, in some cases *Polemonium* can be concerned among tundrants depending on the reference marker species and the level of interspecific conjunctions forming groups of species.

The purpose of the reference marker species is not only indication of some ecological character. First of all, they are stenotopes or species with edge values of moisture grades, like *Lemna* sp. or *Myriophyllum* sp. indicating aquatic or semi-aquatic coenoses. The interspecific conjugations which are analogous to graphs (Galanin, 1973) or correlation pleiades (Vasilevich, 1969) form clusters of species representing ecological-coenomorphic complexes. These complexes are, in turn, key for distinguishing concrete paleophytocoenoses.

The level of interspecific conjugation which, as it was mentioned above, served for species grouping into ecological-coenomorphic complexes in 2-dimensional space of ordinates, was taken from various published sources concerning both interspecific correlations and overviews of Yakutian plant communities, as well as from personal observations.

Distinguished paleophytocenoses reflect a typological diversity of plant communities which directly surrounded the site of death of the fossil animal. They are the last grazing grounds of an animal, defined phytocoenoses and plant groupings that partly reflect the vegetation pattern of the studied period.

Pal			*Batrachium* sp., *Eleocharis* sp.	*Scirpus* sp., *Potamogeton* sp.
Tu				
Mon				
Syl		*Betula alba*, *Betula nana*		
Pr		*Hordeum* sp., *Thalictrum* sp.		
Alv		*Duschekia fruticosa*, *Polemonium* sp., *Deschampsia* sp., *Tephroseris atropurpurea*		
StMon				
St				
Ru				
Coenomorphs/ Hygromorphs	53–63 Ms	64–76 HgMs I	77–88 HgMs II	89–93 MsHgr

Fig. 3. Ecological-coenomorphic complexes of “Yuka mammoth” object

DISCUSSION

The palynological analysis of enclosing sediments taken from the skull base of Yuka mammoth showed predomination of herb pollen (91%), the portion of pollen of arboreous plants was 7%. The largest amount of pollen among herbs accounted for *Artemisia* sp. (46%) (Fig. 2). The spores of *Polypodiophyta* and *Lycopodiophyta* made up 2% (Rudaya et al., 2014).

The carpological analysis allowed to identify the following higher vascular plants up to species-genus level: *Salix* sp., *Betula nana, Duschekia fruticosa, Batrachium* sp., *Eleocharis* sp. *Scirpus* sp., *Potamogeton* sp. *Betula alba, Hordeum* sp., *Thalictrum* sp., *Polemonium* sp., *Deschampsia* sp., *Tephroseris atropurpurea* (Rudaya et al., 2014).

As a whole, three ecological-coenomorphic complexes were revealed. The reference marker species of complex 1: *Scirpus* sp., *Potamogeton* sp., *Batrachium* sp.; of complex 2: *Tephroseris athropurpurea, Deschampsia* sp., *Polemonium* sp.; of complex 3: *Betula alba, Hordeum* sp., *Thalictrum* sp. (Fig. 3).

The modern distribution and ecological confinement of the taxa identified in the course of palynological and carpological analyses are given in Table 2.

The revealed ecological-coenomorphic complex *Scirpus–Potamogeton–Batrachium* is in no doubt and indicates the presence of hygrophilous vegetation. The identified taxa *Eleocharis* sp., *Scirpus* sp., *Potamogeton* sp. and *Batrachium* sp. unambiguously confirm that aquatic and semi-aquatic communities existed in the studied area during the Kargin thermochrone. They most likely grew alongside an oxbow lake rim since the riverine *Duschekia fruticosa* shrubberies, birch forests with *Betula nana* undergrowth and forb-grass mesic meadows were admittedly present there as well which is supported by the distinguished ecological-coenomorphic complex *Betula–Hordeum–Thalictrum*.

The ecological-coenomorphic complex *Tephroseris–Deschampsia–Polemonium* points at the

Table 2. Distribution area and habitats of the studied higher vascular plants

Taxon	Distribution
Salix sp.	The genus represents widely distributed arboreous plants, trees and shrubs. There are 56 *Salix* species growing in Yakutia and featuring wide distribution area and ecological range. They grow in tundra, forests, on riversides, in mountains. In our study, the pollen most likely belongs to willows growing by water bodies, like *Salix viminalis* L. Affiliation with tundra willows is less probable.
Betula nana L.	The hypoarctic shrub growing in tundra, woodlands and forests, sphagnum bogs, in mountains in fell-field and mountain tundra belts; often grows in the understory of the northern taiga forests.
Betula alba L.	The Eurasian boreal species growing in dark and light coniferous forests, often on bogs. Life form tree. Sylvant. *Betula pendula* grows in forests, burned areas, on floodplains.
Duschekia fruticosa Rupr.	Shrub, less commonly tree up to 6 m high. It grows in the understory of coniferous and deciduous forests, by river banks and bog sides, in mountains, on petrophytic slopes; also occurs in tundra zone.
Batrachium sp.	Herbaceous plant. There are 6 species of this genus growing in Yakutia by river and lake sides.
Eleocharis sp.	Herbaceous plant. Most likely, *Eleocharis palustris* (L.) Roem. et Schult. Aquatic-bog plant growing by lake and small pond sides, bogs and wet meadows.
Scirpus sp.	Herbaceous plant. Most likely *Scirpus lacustris* L. Presently widespread in the upper streams of the Lena River growing on river and channel banks, lowland meadows.
Potamogeton sp.	Perennial aquatic and semi-aquatic plants growing in rivers, lakes and bogs. There are 9 species of this genus occurring in all floristic regions of Yakutia.
Hordeum sp.	Herbaceous plant. There are seven species of this bunch grass genus in Siberia, 4 of them growing in Yakutia. They all favour saline soils being common on alkaline meadows and meadow steppes.
Thalictrum sp.	Herbaceous plant. There are nine species of this genus growing in Yakutia. They are mostly meadow plants though occur in forests, steppes, on rocks and near bogs.
Polemonium sp.	Five species grow in Yakutia. They prefer sparse forests, moist tundra, bogs, meadows, petrophytic slopes. In the tundra zone, the grow on alluvial deposits and water body sides.
Deschampsia sp.	Herbaceous plant. There are 7 species of the genus growing presently in Yakutia. The portion of arctic plants is rather high. They are characteristic for littoral sand deposits, beach gravel, tundra, fell-field and mountain tundra belts.
Tephroseris atropurpurea (Ledeb.) Holub	Herbaceous plant. In tundra zone, it grows in meadows, sandy slopes, *Betula nana* shrubberies. It is a common species for moss, *Carex*-lichen and polygonal tundra.

presence of bywater shingle and sand deposits vegetation that conforms with floodplain phytocoenoses of the Arctic. The presence of such typical tundra plants as *Tephroseris atropurpurea, Polemonium* sp. and *Deschampsia* sp. in the studied paleoflorocomplex might indicate the distribution of tundra communities. However, the stated presence of birch forests and *Duschekia* shrubberies contradicts this assumption. Even more, the larch forest limit during the mentioned period of time was 500 km further north than present one (Geel et al, 2016).

A large portion of *Artemisia* pollen (46%) can be explained by the fact that it often inhabits sandy banks which represent rather xeric local biotopes under arid climatic conditions. This also contradicts the tundra scenario of vegetation cover.

Thus, during Kargin Interstadial, Yuka mammoth find site featured aquatic and semiaquatic plant communities with relatively thermophilous species. The floodplain shrub and meadow phytocoenoses as well as the vegetation of sand-and-shingle alluvial habitats were widespread there. This all consistently conforms with the fact that the mammoth calf died from an attack of cave lions because it fell into a floating mat and lost its mobility.

Thus, at the place of death of the mammoth, in the Karginsky interglacial, coastal aquatic communities with relatively thermophilic plant species were widespread. Floodplain shrub and meadow phytocenoses, as well as vegetation of alluvial-coastal, sandy-pebble habitats, are widespread. All this quite logically correlates with the fact that the baby mammoth died from the attack of cave lions, due to the fact that it got stuck in a swamp and lost its mobility. Our conclusions are quite consistent with the results of the reconstruction of the vegetation of this region in the Karginsky interglacial, carried out by F. Kienast (Kienast et al., 2011), which indicates the distribution of floodplain meadows and steppe communities here, which served as pastures for mammoths and other representatives of the mammoth megafauna. In earlier studies in the north of Yakutia in the Karginsky interglacial, tundra-steppe communities were reconstructed (Giterman, 1985), with which we disagree.

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