

Juri P. Kozhevnikov & Valentina V. Ukraintseva
Komarov Botanical Institute, RAS, St. Petersburg

Pleistocene tundra-steppe: arguments *pro* and *con*

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The hypothesized existence of a Pleistocene ‘tundra-steppe’ must find support in three components: phytogeography, palynology, and paleozoology. However, in reality each component separately does not provide the evidence to uphold the interpreted existence of a tundra-steppe. We suggest the idea of tundra-steppe is a false scenario that prevents us from understanding the actual habitats that existed in the Pleistocene.

Argumenten voor en tegen de Pleistocene toendra-steppe – Het veronderstelde bestaan van een Pleistocene ‘toendra-steppe’ zou ondersteund worden vanuit drie vakgebieden: plantengeografie, palynologie en paleozoologie. In werkelijkheid echter is geen van deze drie vakgebieden op zichzelf bij machte de veronderstelde toendra-steppe te beargumenteren. Wij veronderstellen dat het idee van een toendra-steppe een onjuiste hypothese is die ons ervan weerhoudt om de werkelijke omstandigheden zoals die tijdens het Pleistoceen heersten, te begrijpen.

Correspondence: Juri P. Kozhevnikov & Valentina V. Ukraintseva, Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg 197376, Russia.

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INTRODUCTION

The tundra-steppe scenario for a long time has been debated, but the debate reached an impasse owing to unresolved contradictions or, more often, imprecise and erroneous thinking by researchers in different subfields. The continued existence of this scenario says more about the way scientists adhere to untested concepts, in order to be accepted in mainstream thinking, a social phenomenon, and little about scientific objectivity, historical awareness, and the need to test actual biogeographical hypotheses. Here we discuss ‘tundra-steppe’ and point to some stretches of logic and the continuing absence of a wide view of the problem, and to the lack of rigor in scientific interpretations. Science has its own way of using language, and this

language exists so that different investigators working in different subfields can precisely understand each other. Many concepts of scientific interpretations and explanations are by nature seemingly indistinct by virtue of the indistinction of the natural objects to be described and explained. When scientists construct an interpretive scenario based on the data from many different fields and subfields of study, very careful and exact definitions must be developed to reduce the indistinctness or potential confusion. If this is not done, progress in the general understanding of historical processes will not be possible. We argue here that the ‘tundra-steppe’ concept is poorly defined, full of contradictions, and should be scrapped.

'TUNDRA-STEPPE'

The idea that periglacial tundra-steppe existed in northern Eurasia originated at the end of the last century and the beginning of this one, specifically among phytogeographers who studied relict plant complexes. These extrazonal plant complexes include some species that are distributed in the Arctic and high mountains, and others that are more common in temperate-southern regions including the zonal steppes. The arcto-steppic periglacial flora was discussed by Litvinov (1891), Tanfiliev (1902), and Pohle (1903). An important role in developing the view of periglacial tundra-steppe belongs to the modern relations of steppe and alpine vegetation in the south Siberian mountains, where there are ecotones with mixed alpine and steppic plants. Later the idea of a mixed arcto-steppe flora was supported by some authors (Fedorow & Fedorow 1929), and rejected by others (Leskov 1938, Tolmat-shev 1938, Gorodkov 1939, Yudin 1963). In time it has been realized that modern relict plant complexes containing arcto-alpine and steppic species were not formed at one time.

PLANT GEOGRAPHY AND THE 'TUNDRA-STEPPE' CONCEPT

In the north of Europe many relatively southern, partly xeromorphic species occur but nowhere are there the analogies of steppe communities in which one can see the fragments of ancient steppe vegetation. But fragments of periglacial vegetation composed of arcto-alpine species (*Salix reticulata*, *Dryas octopetala*, *Arctous alpina*, etc.) are very common on high rocky slopes in river valleys. Also there are no paleobotanic and paleopalynologic data firmly interpreted as evidence of former steppes. But steppe vegetation is firmly proved for the more southern part of the Russian Plain where tundra species are absent (Hopkins *et al.* 1982). Since Szafer's time, steppe plants have not been found in the classic *Dryas* floras.

Another situation is in the north of Asia,

especially the Northeast. Steppes were described in the Jana and Indigirka river basins (Sheludyakova 1938, 1957; Yarovoy 1939) and later on the Kolyma River and its tributaries. Now the vegetational cover of the Asian Northeast is characterized, if not comprehensively, at least very carefully as to the geographic ranges of the vegetation types. Steppic and steppe like patterns of vegetation were always under great attention (Yurtsev 1981, Kozhevnikov 1981, Khokhrjakov 1983). Some regularities have been established in the distribution of this vegetation, which we discuss below. The real steppic vegetation on watersheds reaches its most northern position at the upper Jana and Indigirka. Here it is surrounded by taiga and is considered as relict vegetation (Yurtsev 1981). At the middle part of these rivers, and also on the Kolyma, the real steppic vegetation is absent on watersheds but is represented by small patches on the southern slopes. It includes the steppic species (*Arabis turchaninovii*, *Orostachys spinosa*, *Astragalus fruticosus*, *Clausia aprica*, etc.), which disappear in the more northern and eastern territories. In the steppic communities are common not only steppic plants, but also as many arcto-alpine ones. We can model a 'spectrum' of communities based on the degree of steppic appearance, i.e. the plant density, production, and its differences from real steppic species. On the Kolyma river basin the steppic patterns are often replaced by xeromorphic patches of sparse vegetation that lack a coenotic relation of the plants: these patches are called steppoids (Kozhevnikov 1981). In these patches are partly xeric, boreal, and plurizonal species, which are distributed further to the Northeast, and also the species of dry tundras. In the northeastern direction the steppic communities (with the solid cover) are met more and more rarely, giving place to steppoids. The real steppe communities are developed mainly in the northern taiga and forest-tundra zones. Steppe is very rare on continental Chukotka, namely in the southern

tundra zone. A cline can be seen towards oceanic Chukotka (the peninsula) together with other continental vegetation: forest-islets, alder groves, high *Betula nana* ssp. *exilis* patches and also many species of plants and birds (Kozhevnikov 1989a,b). On Chukotka, steppoids are dispersed to the East up to the Amguema River, a till region with an oceanic climate and a low hypsometric level. In the more eastern region (Vancarem River) steppoids are unique and occupy a small area. Steppoids in many cases have negligible plant cover that may be unseen from a even few meters distance on the stony substrata. Steppoids are composed of the relatively thermoxerophitic plants. Only in Chukotka do some of them grow exclusively in steppoids, whereas in the Anadyr basin they are found in diverse environments (*Silene repens*, *Dianthus repens*, *Lychnis sibirica*, etc.). Other taxa are not restricted only to steppoids on Chukotka itself, but also grow elsewhere on rocks, bare stony slopes, and gravels along rivers (*Dracocephalum palmatum*, *Oxytropis middendorffii*, *O. campestris*, *Helictotrichon krylovii*, etc.).

In the modern vegetational cover of the Asiatic Northeast, it is clear that there are strictly defined relationships in which the degree of climatic continentality shapes the distribution and presence of actual steppic vegetation, as well as other boreal vegetational types. Recently it has been made clear that the steppoid floral complex, earlier considered as formed at one time, actually formed at different periods. Some of its species (no more than 10) are conserved from the last glaciation, when Beringia functioned as a bridge for transcontinental migrations. Other steppoid inhabitants (a smaller part) appeared on Chukotka during the Holocene Optimum together with the different southern species of various other ecological groups. However, the greatest part of the steppoid plants migrated to Chukotka later (during the Subatlantic period of the Holocene) and now are actively dispersing (*Thymus serpyllum*,

Oxytropis middendorffii, *Carex pediformis*, *Astragalus inopinatus*, *Dracocephalum palmatum*, etc.). During the last two decades (1972 to 1989) some steppoid species changed their relative spatial proportions from 'rare' to 'common'. In this process the most important factor was time, not climate, needed for the migration of plants from more southern regions. That is why we believe the above species are absent in Alaska, where they would be found if they had migrated there during a period of preferred climatic conditions in the past. This is confirmed by the fact that some species (*Thymus serpyllum*, *Potentilla arenosa*, *Eritrichium sericeum*, *Galium verum*) have migrated to Taimyr at times up to the Byrranga mountains, whereas now the two latter species are only beginning to penetrate Chukotka, and others (*Veronica incana*, *Leontopodium ochroleuca*, *Scorzonera radiata*) have reached only the Anadyr forest-tundra.

The geography of the Chukotkan steppoid species is very different. Among them there are eastern-Siberian, Siberian, East-European-Siberian and also Siberian-American species. In it are many species that inhabit environments far from a steppic one. In the Taimyr tundra some species (common with Chukotkan steppoids) inhabit the moist meadows, bare stony slopes, and sand. So, the migrations of species that are often considered on Chukotka as steppic ones could have taken place under different ecologic conditions, but mainly in a continental climate (more continental than on the Chukotkan peninsula now). This is supported by the distribution of some plants on the Northeast of Asia and Northwest of America with disjunctions in the oceanic areas. Such species may reflect migrations via Beringia when it had a continental regime in its middle parts during the migrations. Because in modern landscapes of Chukotka these species are restricted to steppoids (which have been termed tundra-steppes) it is considered that some similar kind of tundra-steppes was more widely

distributed in Beringia. This viewpoint is very popular in botanical and paleogeographical literature, but its foundation does not seem to be based on palynologic and paleobotanic support.

At the end of the 1960's, the most northern steppic vegetation was shown in Southern Siberia, where different kinds of tundra were proclaimed, as in the north of Siberia (Giterman *et al.* 1968). After an International conference devoted to research on Beringian problems (Boulder, U.S.A., in 1965) the classification of vegetation changed. As a result of converging thinking by Canadian and Soviet (former USSR) palynologists, the concept of Beringian tundra-steppe was recognized, applied also for northern Siberia. The new idea about vegetation superseded the old ones in publications, and the floral interpretations were offered as a solution to problems in the paleozoologic data about Beringian mammals, to explain their feeding needs. All arguments seemed logically complementary. Thus the tundra-steppe concept seemed to have overflowed most investigators' consciousness and literally flooded the paleogeographic literature, in spite of the fact that supporting arguments were at best equivocal.

POLLEN STUDIES

One of the arguments in support of periglacial tundra-steppe was the abundance of *Artemisia* pollen along with the absence of tree and bush pollen in appropriate layers. However, this argument in support of the proposed tundra-steppe habitat is not convincing: in the modern landscapes of Chukotka there are a few *Artemisia* species, such as *A. tilesii*, *A. arctica*, *A. glomerata*, and *A. borealis*, which may be locally plentiful and produce much pollen. Their distribution in Chukotka and Alaska must mean they also had a past presence in Beringia, but it is not proof of the existence of 'tundra-steppe' there. Spores of *Selaginella rupestris* (*S. sibirica*) in many papers are interpreted as a tundra-steppe indicator, but this species has a rather wide ecolo-

gical range, growing in steppoids, on rocks, in stony sites within plain tundras, on river terraces, and on mountain slopes in the highest elevations where there are only lone plants. Sometimes the normal taxa of tundras, meadow-like vegetation, and even bogs are interpreted as the indicators of steppe, as seen, for example, in Giterman (1985). In another case, a find of fossil pollen of Chenopodiaceae and a seed 'most probably *Sium cicutaformis*' was thought to indicate the existence of a periglacial tundra-steppe in the Main River Basin of the Anadyr System; the argument was that Chenopodiaceae are absent from the modern flora of the region. But *Chenopodium album* in the modern flora there is the common species on unweathered loam. Because *Sium* is a semi-aquatic plant (and we think it is probable that the authors misidentified the seed as *Sium*, when it actually was *Cicuta*, which is present in the modern flora, and which also is a semi-aquatic plant) the joint finds of Chenopodiaceae pollen and the seed indicate clearly a ground on which existed hydrophilous vegetation, ecologically opposed to any sort of 'tundra-steppe'.

We can summarize the faulty palynological support for a Beringian tundra-steppe here. First of all the taxonomic identification of pollen has been made only to the genus or family rank when interpretations are offered that attempt to prove that certain plants never grow in certain areas today. The assumption that in Beringia *Artemisia frigida* grew but not *A. tilesii*, *A. glomerata*, or other wormwood species has no basis because pollen determination has been done only to the genus rank. In the erroneous view of many palynologists the modern vegetation has been well reflected by published spore and pollen spectra. But special investigations show that such a reflection is not as simple as in the boreal zone (in Kolyma River basin), or in the tundra zone (in Chukotka; Votzhilko & Kozhevnikov 1982, Kozhevnikov 1995). The problem is that under steppic-like vegetation there is a poor correspondence of spore-pollen spectra

with the spore- and pollen-producing vegetation. Another equally important problem is that in some palynologic papers the ecological relationships of plants are misunderstood, and some plants are thought to be steppic species though in fact they have other preferences.

CLIMATE, PLANT MIGRATIONS, AND THE CONDITIONS UNDER WHICH TRUE STEPPE EXISTS

As mentioned above, in Chukotka the so-called 'relic tundra-steppes' are inhabited mainly by Asiatic species that are unknown in Alaska. A parallel conclusion can be made for Alaska where the steppic complex consists mainly of American species (Murray *et al.* 1983). Some Alaskan steppic species are known in Chukotka where they do not inhabit steppoids (*Erigeron compositus*, *Lesquerella arctica*). These species are adapted to very severe environmental conditions; the latter species migrated west to Taimyr where it grows in polar deserts of the Byrranga Mountain, especially on carbonate rocks. The fact that in the Alaskan steppic complex only American species predominate corresponds to the predominance of Asiatic species in Chukotkan steppoids. It means that most plant migrations were to the north on both sides of the Bering Strait, and during the Holocene, when central Beringia was already inundated. This conclusion is confirmed by the presence of many hydrophilous and mesophilous plants in the neighbourhood of hot springs. It needs to be emphasized that specific thermophilous complexes near Chukotkan and Alaskan hot springs are quite different from each other, with only *Agrostis scabra* in common. This indicates that these complexes were created without relation to each other, in the time when the Bering Strait existed as a separating body of water, not at the time of the Beringian land connection. Also indicated is the warming climate that occurred when the migrations took place. Now many species of the hot springs' neighbourhoods are separated by hundreds of kilo-

meters. So, the migration story of the thermophilous and steppic species was mainly the same, depending on climate warming after the flooding of central Beringia. The true steppic plant complex in Alaska and Yukon is found in inner regions where it associates with the northern taiga vegetation. For arctic Alaska, any data about steppic vegetation are absent (Britton 1966, Hulten 1968, Murray 1978, 1981, Howenstein *et al.* 1985). There are some parallels with the Asian Northwest, although the land outlines are distinct, and consequently the isolines of climate continentality are located otherwise than in Alaska, resulting in a different ratio of continental and oceanic types of vegetation.

The external similarity of steppic vegetation in the Northeast of Asia and Northwest of America, as well as in other regions that have various sets of species, is in fact only a biomorphic similarity. The vegetation is composed mainly of grasses, which grow where the moisture quickly dries up so that in the second half of summer the sites are covered only by whisps; these sites are sharply distinguished from the background of green heath or bare substrata (gravel, rock, sand). The majority of well developed steppoids resemble in structure the ruderal vegetation, having a wispy appearance and unpatterned combinations of species, characteristic of vegetation that is not in a long-term and widepread synchrony, distinct from true steppe where the plant associations reach an equilibrium. In true steppes there are coenotic relations, meaning that species dispersion depends on the associations of vegetation, which also affects soil formation. Steppoids are made up of pioneer vegetation that is fully determined by the abiotic component of the environment; as well, no soil forms under steppoids. In forest regions steppe-like vegetation is formed as a rule on slopes where the trees have burned off. In the Kolyma river basin a well-developed steppe-like vegetation, including a set of variants

that are rich with species, exists in the places where strong fires burned about 50 years ago. Nearby these sites, in similar relief conditions where the woods were not burned, there are no steppic signs. When the trees regrow or thickets of *Pinus pumila* develop, the steppe-like vegetation disappears. In the tundra zone steppoids are formed on steep slopes that have a continual recycling of substrata to surfaces as a result of slope movements. In this region if the substrata are immobile and fixed, the major factor in steppoid development and its stabilization is the wind action on the open ground during winter, keeping it snowless. On such open and cleared surfaces heath cannot exist and steppoid taxa temporarily establish themselves. A combination of summer warmth and winter snowlessness is a necessary condition for the existence of steppoids. In tundras the heath in many cases literally props up steppoids and gradually supersedes them because it keeps the snow in winter; the number and extent of snowless sites gradually decreases very slowly.

In order to reconstruct Beringian vegetation the modern ecological connections of the steppoid species naturally should be taken into account. However, the concern can only be for those species that are distributed in the Northeast of Asia and the Northwest of America, namely: *Carex obtusata*, *C. supina* ssp. *spaniocarpa*, *C. duriuscula*, *Silene repens*, *Dianthus repens*, *Pulsatilla nuttalliana* ssp. *multifida*, *Chamaerhodos erecta*, *Artemisia frigida*, *A. laciniatiformis*, and *Oxytropis campestris* s.l., *Smelowskia calycina* ssp. *intergifolia*. Perhaps also we can consider *Calamogrostis purpurascens*, *Rosa acicularis*, *Draba cinerea*, *Potentilla nivea* ssp. *hookerana*, as they live in not only steppoids but also other places that are dry. Other amphi-Beringian species of steppoids have a rather wide ecological range and cannot be useful for reconstructing paleobiogeographic conditions in Beringia. However, some obligate taxa of steppoids on Chukotka do grow

outside it in different environments.

Proceeding from the modern situation we propose that steppoids in Beringia existed on the tops of hills which in winter were snowless, but there is no basis for considering steppoids a zonal vegetation, as proposed by Hopkins (1967, 1972) and after him others (Sher 1971; Shilo *et al.* 1983; Guthrie 1985).

THE ROLE OF 'TUNDRA-STEPPE' IN SUPPORTING LARGE MAMMALS

The oft-cited 'paradox of high productivity of Pleistocene tundra-steppe' is an imaginary representation which developed out of the 1976 Vienna meeting devoted to Beringian problems (Hopkins *et al.* 1982). The 'paradox' arose when the question was hastily answered about where Beringia's large herbivores got their food. The postulated 'tundra-steppe' was accepted as a vegetation type that must have had high productivity. Yet the botanical data behind this assumption are contradictory. True steppe (the zonal type) does have high productivity, but botanical and geographical analyses show that in the Pleistocene nearly no steppes existed in Beringia; there were steppoids but these have a very low phytomass and could not have been important as forage for mammals. In Beringia, as a part of the Arctic, the high productivity must have been in hydrophyllous vegetation, a type that existed at period of low sea level and whose existence then is proved by species distribution now on both sides of the Bering Strait. That hydrophyllous vegetation existed is suggested by numerous different kinds of evidence. For example, it is known that the mammoth had an aserial type of foot (Garutt 1951). But the largest part of Beringia did not (and does not now) have wet ground but firm ground covered with a vegetation of the polar desert type. The generality of arcto-alpine species in Chukotka and arctic Alaska indicates this, namely those prevalent clumped and cushion species that developed in very severe conditions (*Draba stenopetala*, *Saxifraga eschscholtzii*, *Artemisia senjavinensis*, *Stellaria*

dicranoides, among others). Among the step-poid inhabitants only *Smelowskia calycina* ssp. *integrifolia*, which migrated to Chukotka from Alaska, has a similar life form.

However, in the modern landscapes of Chukotka this species is maximally distributed on the sand gravel of the Amguema river.

This domination by desert, high Arctic landscapes in Beringia also has been established by palynologists (Cwynar & Ritchie 1980, Cwynar 1982, Colinvaux & West 1982), who show that pollen production in the relevant stratigraphic units was of a lower order than it is in real steppe. The pollen horizons also correlate with the general organic contents of the levels: organics are low in samples of Beringia tundra-steppe. We may imagine that in relief hollows there existed a rather advanced vegetation of the arcto-alpine type. Colinvaux & West (1982) likewise concluded that the arguments were ambiguous on behalf of tundra-steppe, a conclusion they reached even without considering the phytogeographic aspect of the problem, which is all the more ambiguous. Their main conclusion is that Beringia was dominated by polar deserts. Guthrie (1985) deemed their arguments 'woolly', but it seems premature for a zoologist to dispute the palynologists' results simply because they can not explain how so many large herbivores could find forage in polar deserts. The arguments of Guthrie (1985) do not effectively negate the interpretation that polar desert existed. In Beringia most of the ground was firm and snow cover over a large part of the region was negligible. The character of the large mammals' grazing possibly was the same as in modern Tibet, where vast sections of ground lack much vegetation but in the valleys are 'oases' (Yusov 1958). In search of forage the animals are compelled to travel from one oasis to another.

In Beringia the members of the mammoth faunal complex must have had enough space to travel widely and to feed in the rich

patches. It is worth considering how many of these large mammals must have lived at any one time (Murray 1981). We have few or no reasons for considering that the large animals were ever especially abundant. More than likely in Beringia, which was a huge and continuous intercontinental connection during the cold climatic intervals, relatively small herds, families, or populations of animals crossed from Asia into Alaska at any time. A larger population existed in the more southern regions where a periglacial zone transitioned into extraglacial ones and more solid vegetation was available, including the forest islets in valleys. During the warm climate intervals the mammoth complex of animals advanced to the north at the same time as the shift of zone borders marked by vegetation. The preserved contents of mammal stomachs and intestines from most of the frozen large-mammal carcasses included pollen and plant macroremains indicative of interglacial rather than periglacial type (Ukrainitseva 1986, 1993). The larger part of the dated bones, according to Hopkins *et al.* (1982) also belong to the Karginisk Interglacial, when the forest border in the near-Beringian regions was much shifted to the North. We see the meaning of these facts as that not only in warm periods were there more favorable conditions for preserving animal carcasses, but also that in the cold periods in the more northern regions the conditions for preserving carcasses were worsened. The number and densities of large mammals were much reduced at the same time.

Murray (1981) thinks that the existence of steppe vegetation in the Pliocene does not support Repenning's (1967) postulation that the greatest variety of open-country mammals in Beringia developed only in the Middle and Late Pleistocene. However, first we would counter this argument by stating that the maximum variety is not obligately connected with higher numbers of individual animals. We do not dispute that in the Pliocene many ancestral taxa of a future

mammoth faunal complex lived in the more southern regions of Asia and America. Time was required for them to reach Beringia. Second, we would argue that at the beginning of the second half of the Pliocene there existed quite another climatic situation in comparison with the Pleistocene. Increasing climate deterioration in Beringia led to specific biozonation: taiga with *Tsuga* and broad-leaved elements appeared along the southern coast, savanna-like or steppe-forest landscapes developed in the inner part, and forest-tundra appeared along the northern coast north of Wrangel island. At this time there was significant general establishment of coniferous tree stands in Northeast Asia and Northwest America, and a two-way movement of *Taxus*. It was only in this time interval that migrations across Beringia occurred by *Stipa* and other true steppic plants, because during the Pleistocene, as shown by the different kinds of data, the conditions for making their migration possible simply were not present (Kozhevnikov 1996).

That the maximum development of steppe took place in Beringia at a different time from the maximum migrations by mammalian taxa is not impossible. Plant species such as *Stipa* are clearly known to be steppic, but the mammoths, horses, bison, and other large mammals of the Beringian ecosystem need not have been obligate steppic taxa. Modern musk oxen in the Canadian Arctic Archipelago and on Piri Land, as well as yaks and kiangs in Tibet, survive very well without steppe vegetation and the larger Pleistocene species may have done so too.

According to Iversen (1973), in Europe during the Late Würm a widely distributed periglacial tundra-steppe was marked by pollen spectra similar to spectra of the 'subarctic steppe' of Greenland described by Bocher (1954, among others). However, we note that Bocher's description of Greenland pollen pertains only to steppoids, which are in fact less productive than on Chukotka. Thus, as

we have argued, the apparent congruence of phytogeographic, palynologic, and paleozoologic data and interpretations in withholding a tundra-steppe scenario for Beringia is the result of poorly understood ideas about a type of vegetation mis-represented as 'periglacial tundra-steppe'. This vegetation does not at all represent any kind of swaying sea of grasses, and frequently it is hardly appreciable and has very low productivity. Even hares prefer more clearly tundra-like vegetation.

CONTRADICTIONS AND MISPERCEPTIONS

Despite of a strong refutation of the popular tundra-steppe scenario (Cwynar & Ritchie 1980, Ager 1982, Cwynar 1982, Kozhevnikov 1977, 1989a,b, 1996) as an artificial creation without reality in the past, it continues to be prominent in the literature about Pleistocene communities. For example, Roland (1994), who compared data from soil samples and vegetation in the upper Kolyma river of Asia and in the Yukon of Canada, concluded there had been similar ecological control in both regions. But he overlooked the possibility that the degree of their floristic similarity can be interpreted with reference to Beringian migrations, rather than to climate controlled tundra-steppe development. It is clear that now scholars such as Roland and others (e.g., Wesser *et al.* 1994) *a priori* seem to proceed accepting the tundra-steppe existence in Beringia, and no longer question the validity of this construct. Yurtsev (1994), referring to the remains of Wrangel Island dwarf mammoths radiocarbon-dated 7000-4000 years ago (Vartanyan *et al.* 1993), writes that mammoth survived on the island up to middle Holocene time because of a unique grassy vegetation, including steppe, meadow-steppe, and grassland with *Arctagrostis*. For zoologists the probable existence of steppes on Wrangel Island 7000-4000 y ago appears to be supported by testimony from respected botanists, and therefore it is seen to have a rather reliable

basis. Yet the existence of steppe on Wrangel Island in Recent times is not at all proved by the available paleobotanic data. The island's modern vegetation was described by Petrovsky (1967) who did see a few steppic features in the fragments of cryoxerotic vegetation. But sometime later this vegetation was unjustifiably re-named as tundra-steppe (Yurtsev 1974, 1981, 1982). Even if cryoxerotic vegetation is called tundra-steppe, its importance as forage for large animals remains negligible. The low productivity of specific communities from Wrangel Island can be seen in an example of one study of phytomass stock and fodder, made by Polozova (Yurtsev 1981: 153-154):

'Description 8A. Grass - (*Festuca auriculata*, *Poa glauca*, *Hierochloe alpina*) - herbs-sedge (*Carex obtusata*, *C. rupestris*) cryophytic-steppic community. Coast of Somnitelnaya Bay, an edged low mountain 6 km to north-west from Uschakovsky settlement on right side of Somnitelnaya River about its entrance to south coastal plain. Middle part of southern slope 20-25 degrees. Community looks like a wide straw-yellow strip on background gray schist talus. General covering of vegetation 85 % , of which grasses 20 %, sedges (mainly *Carex obtusata* and *C. rupestris*) 30 %, herbs 25 %, green mosses 5 %, lichens 5%. Overground part of community consists of 3 layers: 1 (mosses- lichens) interrupted, the height of it 1-2 cm; 2 (sedges: *C. obtusata*, *C. rupestris*), the height of it 3-5 cm; 3 (grasses: *Poa glauca*, *Festuca lenensis*, *F. auriculata*, *Hierochloe alpina*), the height of it 15-20 cm'.

Similar vegetation was described from Greenland by Bocher (1954). The phytomass of the vegetation can be appreciated when we examine the ground cover and height of the layers, and also after taking into account the very small patches of it and its rarity. Communities like the one described (and many others from the same book) can account for the survival of mammoths (even small ones) only up to the Subboreal period of the Holocene. Not mentioned in the Wrangel study is the fact that there are *Salix* thickets present as well, which in the earlier Subboreal period (when the sharp climate

cooling had began) were more extensive in size and distribution. It needs to be explained why tundra-steppe did not exist on Kotelny Island during the last 12,500 y (Makeev & Ponomareva 1988) or on Bolshoy Lyachovsky Island during the last 10,500 y (Ukrainitseva *et al.*, 1989), both of which are the nearest islands to Wrangel Island in the high Arctic.

CRYOLITHIC EVIDENCE TO REFUTE 'TUNDRA-STEPPE'

It is well known that in northern Yakutia and Alaska a thick cryogenic stratum of 30-80 m thickness (called edoma or yedomas) developed from alluvia containing a lattice of syngenetic ice enclosing animal remains from the mammoth faunal complex. The edoma has been determined to have formed by the middle- and late Pleistocene (Popov 1982). According to Popov (1982) the edoma complex has two main facies: (1) gray, layered icy alevrite with turf and large ice veins, found in the inner valley zone; (2) brown, weak-layered, less icy alevrite without peat, with fewer ice blocks, a facies called 'sor'. Both are associated with higher humidity and more intensive ice-forming conditions than found in modern floodplains of the region. Hence cryogenetic-lithologic data do not confirm the existence of vast steppic landscapes when the edoma formed in the middle and later Pleistocene. In cold aridic regions (Yakutia, Mongolia, Canadian Arctic Archipelago, Northern Greenland, Antarctica), ice veins do not form today, which indicates that such veins would not have formed under hypothesized periglacial 'tundra-steppes' and that therefore such steppes could never have existed. An analysis of palynological data from the edoma strata shows that it is an indicator of tundra that has normal or above-normal moisture input, and few or very subordinate xerophytes (Popov 1982). The contradictory representations of landscapes in the edoma-forming period are confused: from one side there is a view about dry landscapes at the period, and

from the other (based on analysed cryolithic data) there is a reconstruction of high humidity. Popov (1982) provides a reasonable point of view about this apparent contradiction, and we completely agree with his arguments. He concluded that Eurasia and North America, including the exposed continental shelves, were undergoing alluvial deposition during the period of edoma-formation (the Middle and Late Pleistocene). The increase in land area caused by the exposure of the shelves and a corresponding strengthening of climate continentality allowed for a wider distribution of xerophytes in the expanded favorable places on flooded alluvial plains, such as on natural levees, terrace edges, etc., with the best conditions being on pediment slopes and intermountain hollows. The spatial differences between the wet and the xeric landscapes were greater during the periods of strengthening continentality, and lesser at its easing. The dominance of wet landscapes over xeric ones occurred in the edoma epoch

when the extremes of humidification and xerification during increasing continentality depended on site characteristics that were more sharply differentiated than they are today. But from this observation, some authors mistakenly consider the reversing dominance of xeric landscapes over wet ones to be more important than it ever was; the wet landscapes have been ignored at the expense of the drier ones in paleoecological studies (see Popov 1982: 259).

CONCLUSIONS

A number of Beringian research problems need solutions. Very different researchers will go to work over them and it is important that beginners do not proceed from the outset using insupportable assumptions and models, but instead acquaint themselves with opposing points of views and by so doing try to objectively determine what models better explain the data.

REFERENCES

- Ager, Th.A., 1982 - Vegetation history of western Alaska during the Wisconsin glacial interval and the Holocene - in: Hopkins, D.M., Matthews, Jr., J.V., Schweger, C.E. & Young, B. (eds.) - *Paleoecology of Beringia* - pp. 221-224. Academic Press, New York
- Bocher, T.W., 1954 - Oceanic and continental vegetation complexes in Southwest Greenland - *Meddr Grønland* 147 (9): 1-85
- Britton, M.E., 1966 - *Vegetation of the arctic tundra* - Oregon State University Press, Oregon
- Colinvaux, P.A. & West, F.H., 1982 - The Beringian ecosystem - in: Hopkins, D.M., Matthews, Jr., J.V., Schweger, C.E. & Young, B. (eds.) - *Paleoecology of Beringia* - pp. 10-16. Academic Press, New York
- Cwynar, L.C., 1982 - A Late-Quaternary vegetation history from Hanging Lake, Northern Yukon - *Ecological Monographs* 52 (1): 1-24
- Cwynar, L.C. & Ritchie, J.C., 1980 - Arctic steppe-tundra: a Yukon Perspective - *Science* 208: 1375-1377
- Fedorow Al. & Fedorow, A., 1929 - The relic character of arctoalpine and steppic plants of Pinega flora (in Russian) - *Leningrad Society of Naturalists* 59: 55-102
- Garutt, V.E., 1951 - Change in the structure of foot of Proboscidea, related to habitat (in Russian) - *Dokladi Akademii Nauk USSR* 77 (3): 513-515
- Giterman, R.E., 1985 - History of vegetation of the Northeast of the USSR in the Pliocene and Pleistocene (in Russian) - Nauka, Moscow
- Giterman, R.E., Golubeva, L.V., Zaklinskaya, E.D., Koreneva, E.V., Matveeva, O.V. & Skiba, L.A., 1968 - Main Stages of Development of Vegetation of North Asia in the Anthropogene (in Russian) - Nauka, Moscow
- Gorodkov, B.N., 1939 - Is there a resemblance between the tundra and the steppe? (In Russian) - *Sovetskaya Botanika* 6-7: 41-66
- Guthrie, R.D., 1985 - Woolly arguments against the Mammoth Steppe - a new look at the palynological data - *Quaternary Review of Archaeology* 6 (3): 1351-1361
- Hopkins, D., 1967 - The cenozoic history Beringia - a synthesis - in: Hopkins, D. (ed.) - *Bering Land*

- Bridge - pp. 451-484. Stanford University Press, Stanford
- Hopkins, D., 1972 - The paleogeography and climate history of Beringia during late Cenozoic time - *Inter-Nord* 12: 121-150
- Hopkins, D.M., Matthews, Jr., J.V., Schweger, C.E. & Young, B. (eds.), 1982 - *Paleoecology of Beringia*. Academic Press, New York
- Howenstein, R.E., Murray, D.F. & Ambruster, W.S., 1985 - Vegetation ecology of south-facing bluffs in subarctic interior Alaska - *Technique and Science, Proceedings of the Arctic Science Conference*, Fairbanks: 168-176
- Hulten, E.A., 1968 - *Flora of Alaska and neighbouring territories* - Stanford University Press, Stanford
- Iversen, J., 1973 - The development of Denmark's nature since the Last Glacial - C.A. Reitzels Forlag, Copenhagen
- Khokhryakov, A.P., 1983 - Steppe flora in the Kolyma River basin (in Russian) - *Ecologo-coenotic and geographic peculiarities of vegetation* - Nauka, Moscow: 218-231
- Kozhevnikov, Yu.P., 1977 - A critical review of the data concerning the history of the Chukotsk flora - *Botanical Journal* 62 (3): 445-460
- Kozhevnikov, Yu.P., 1981 - *Ecologo-floristical studies on the Indigirka, Kolyma rivers and in the North-East of the Putorana Plateau, Part 1 (in Russian)* - All-Union Institute of Scientific and Technical Information, Moscow
- Kozhevnikov, Yu.P., 1989a - *Geography of the Chukotka vegetation (in Russian)* - Nauka, Leningrad
- Kozhevnikov, Yu.P., 1989b - *Geosystems aspects of the Chukotka vegetation cover (in Russian)* - Academy of Sciences of USSR, Far-Eastern Scientific Centre, Vladivostok
- Kozhevnikov, Yu.P., 1995 - On the connection of the extant vegetation and surface spore-pollen spectra on Chukotka (Basin of Chantalveergyn River) - *Botanical Journal* 80 (5):74-88
- Kozhevnikov, Yu.P., 1996 - *Vegetational cover of Northern Asia in historical perspective (in Russian)* - World and Family, St-Petersburg
- Leskov, A.I., 1938 - Relic elements in the flora of the forested north-east of the European part of the USSR (in Russian) - *Problems of relics in the flora of USSR* 1: 41-48
- Litvinov, D.I., 1891 - *Geobotanical notes about flora of the European Russia (in Russian)* - Moscow University Printing House, Moscow
- Makeev, V.M. & Ponomareva, D.P., 1988 - *Paleogeography of the Kotelný island in the Holocene* - in: Gogichishvili, L. (ed.) - *Abstracts of the International Conference on the Problems of the Holocene, 17-23 October, Tbilisi, USSR* - p. 64. N.N. Ketskhoveli Institute of Botany, Academy of Sciences of the Georgian SSR, Tbilisi
- Murray, D.F., 1978 - *Vegetation, floristic and phytogeography of Northern Alaska* - in: Tieszen, L.T. (ed.) - *Vegetation and Ecology of an Alaskan Arctic Tundra, Ecological Studies* 29: 19-36. Springer-Verlag, New York
- Murray, D.F., 1981 - The role of arctic refugia in the evolution of the arctic vascular flora: A Beringian Perspective - in: Scudder, G.C. & Reveal, J.V. (eds.) - *Evolution today, Proceedings of the second International Congress of Systematic and Evolutionary Biology* - pp. 11-20. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh
- Murray, D.F., Murray, B.M., Yurtsev, B.A. & Howenstein, R.F., 1983 - *Biogeographic significance of steppe vegetation in subarctic Alaska* - in: Gerasimov, I.P. & Velichko, A.A. (eds.) - *Permafrost: Fourth International Conference, Proceedings* - pp. 883-888. Washington
- Petrovsky, V.V., 1967 - *An outline of the plant communities in the central part of Wrangel Island (in Russian)* - *Botanical Journal* 52 (3): 212-224
- Pohle, R., 1903 - *Pflanzengeographische Studien über die Halbinsel Kanin und das angrenzende Waldgebiet* - *Acta Horti Petropol.* 21 (1): 12-24
- Popov, A.I., 1982 - On the genesis and conditions of formation of the sedimentary-cryogenic (Edoma) complex on the Primorsky Plains of the subarctic (in Russian) - *Bulletin of the Moscow State University, Geographical Series* 6: 60-65
- Repenning, C.A., 1967 - *Palaearctic-Nearctic mammalian dispersal in the Late Cenozoic* - in: Hopkins, D. (ed.) - *Bering Land Bridge* - pp. 232-244. Stanford University Press, Stanford
- Roland, C.A., 1994 - *A comparison of topographic controls of steppe vegetation in the upper Yukon and Kolyma river basins* - in: *Bridges of science between North America and the Russian Far East, 45th Arctic Scientific Conference, Book 2*: 29. Dalnauka,

- Vladivostok
- Sheludyakova, V.A., 1938 - Vegetation of the Indigirka River Drainage (in Russian) - *Sovetskaya Botanika* 4-5: 49-79
- Sheludyakova, V.A., 1957 - Steppe vegetation beyond the Arctic Circle in Yakut regions (in Russian) - *Proceedings of Yakutsk branch of the Academy of Sciences of the USSR* 3: 68-82
- Sher, A.V., 1971 - Mammals and stratigraphy of the Pleistocene in the Far East of the USSR and North America (in Russian) - Nauka, Moscow
- Shilo, N.A., Lozhkin, A.V., Titov, E.E. & Shumilov, Yu.V., 1983 - *Khirgilyakh Mammoth* (in Russian) - Nauka, Moscow
- Tanfiliev, G.I., 1902 - The principal features of the vegetation of Russia – mentioned in: Varming, E., 1980 - Distribution of plants depending on environment St. Petersburg (in Russian) – in: Kaplin, P.A. (ed.), 1980 - The latest deposits and paleogeography from the Pleistocene of Chukotka (in Russian) – pp. 315-474. Nauka, Moscow
- Tolmatschov, A.I., 1938 - About characters of arcto-alpine floristic elements and some locally related with its elements in Pinega and Sotka rivers regions (in Russian) - in: Tolmatchev, A.I. (ed.) - Materials of floristic history on European north of USSR – pp. 5-42. Ogiz-Arkhobliz, Archangelsk
- Ukrainitseva, V.V., 1986 - Flora, Vegetation and Environment in Siberia in Late Antropogene (in Russian) - Unpublished professional biological and paleogeographic dissertation. Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia
- Ukrainitseva, V.V., 1993 - Vegetation Cover and Environment of the 'Mammoth Epoch' in Siberia – in: Agenbroad, L.D., Mead, J.D. & Hevly, R.H. (eds.). *The Mammoth Site of Hot Springs, South Dakota*
- Ukrainitseva, V.V., Arslanov, Kh.A., Belorusova, J.M. & Ustinov, V.N., 1989 - The first data on the Early Holocene flora and vegetation of the Big Lyakhovsky Island (The Novosibirsk Archipelago) (in Russian) - *Botanical Journal* 74 (6): 782-793
- Vartanyan, S.L., Garutt, V.E. & Sher, A.V., 1993 - Holocene dwarfish mammoths from Wrangel Island in the Siberian Arctic - *Nature* 362: 337-340
- Votzhilko, M.E. & Kozhevnikov, Yu.P., 1982 - The reflection of the modern vegetation by the surface spores-pollen spectra in the middle reaches of the Berezovka River (Kolyma River Basin) (in Russian) - *Botanical Journal* 67 (8): 1100-1111
- Wesser, S., Armbruster, W.S., Edwards, M. & Debevec, E., 1994 - Modelling arctic-steppe distribution using terrain variables as microclimate surrogates with a geographic information - in: *Bridges of the science between North America and the Russian Far East, 45th Arctic Scientific Conference, Book 1: 80-81. Vladivostok*
- Yarovoy, M.I., 1939 - Vegetation of the Jana river basin and Verkhoyansk Range (in Russian) - *Sovetskaya Botanika* 1: 21-40
- Yudin, Yu.P., 1963 - Relic flora of the limestones of the Northeast of the European part of the USSR (in Russian) - *Materiali po istorii flori i rastitelnosti USSR* 4: 493-571
- Yurtsev, B.A., 1974 - On the floristic relations between Steppes and Prairies - *Botanical notiser* 116 (3): 396-408
- Yurtsev, B.A., 1981 - The relic steppe complexes of Northeastern Asia (in Russian) – Nauka, Novosibirsk
- Yurtsev, B.A., 1982 - Relicts of the Tundra-Steppe Beringia in the vegetation cover of Northeast Asia (in Russian) - in: Grichuk, V.P. (ed.) - *Palynological methods in stratigraphy and paleogeography* – pp. 3-14. Northeastern Integrated Research Institute, Magadan
- Yurtsev, B.A., 1994 - Some new botanical data to the history of Beringia - in: *Bridges of the science between North America and the Russian Far East, 45th Arctic Scientific Conference, Book 1: 268. Vladivostok*
- Yusov, B.V., 1958 - Tibet (in Russian) - *Geographiz, Moscow*