Synopsis

Plant macrofossils together with other proxy data enable the reconstruction of Eurasian vegetation history during the Quaternary, indicating that the climatic impact on vegetation in high latitudes is not just restricted to global temperature fluctuations but also depends decisively on the oceanic influence on climate. It is shown that Arctic climate in Eurasia during both cold and warm stages was much more continental than today, resulting in tundra-steppe or forest-tundra vegetation. Increased oceanic influence during the Holocene in the major Beringian refugium of Arctic vegetation may have resulted from neotectonic subsidence and the transgression of the East Siberian Arctic shelves.

text

MS 219, Kienast, Arctic vegetation history Eurasia

Arctic Vegetation History – Eurasia

Even though the number of Quaternary plant macrofossil records in the Arctic has increased considerably in recent years, the lack of fossil sites is still problematic. We are consequently still far from gaining a complete understanding of the complex interactions between Quaternary climate fluctuations and vegetation responses. The Arctic, in all likelihood, is the region that will be affected first and most by the predicted anthropogenic global warming (ACIA 2004). Expected future vegetation changes, conversely, may affect global climates by their impact on albedo and permafrost. Arctic permafrost is climatically important because it forms a large and very susceptible sink for terrestrial carbon. The few macrofossil records already studied enable us, in conjunction with other disciplines like palynology, chorology, and molecular genetic analysis, to delineate the consequences of past climate changes on high latitude vegetation. Given the results already in hand, the response of arctic vegetation to global temperature fluctuations depends highly on the direction and extent of changes in humidity. In the following discussion, the climatic causes of vegetation development during the Quaternary are highlighted in particular.

The Arctic today

Recent Vegetation

The Arctic is regarded as the region north of the polar circle, which, in consequence of the Earth's axial precession, is characterized by extreme seasonal fluctuations of incoming solar radiation, culminating in the semi-annual alternation of polar day and polar night. Due to the low altitude of the sun in the sky, the radiant flux density is very low. Nevertheless, the radiation balance is positive in summer and, owing to the polar day, the radiation supply during the growing season is among the highest in Eurasia. In a geobotanical sense, the Arctic is the region of tundra beyond northern tree-line, which correlates approximately with the 10°C mean July-isotherm in West Eurasia or with the 12°C July isotherm in the more continental East. As apparent by ancient *in situ* wood remains beyond the tree line, the northernmost tree limit shifted, during the Quaternary, numerous times far to the south and to the north of its modern location in response to climate fluctuations and coast-line shifts (MacDonald *et al.* 2000, MS 216, 217, Fig1).

<(Fig.1)>

Boreal coniferous forests grade into tundra gradually via the forest-tundra region, where trees slowly diminish northwards. As in every vegetation zone, tundra is composed of a mosaic of various plant communities which are controlled by a variety of environmental factors. Due to the frozen ground, tundra soils are often saturated. Consequently, wetland vegetation, mainly composed of sedges, cotton grass, grasses, mosses, and dwarf shrubs, mostly on leached and acidic soils or on thick peat, dominates the landscape (CAVM Team 2003).

In today’s arctic tundra, low temperatures and a short growing season are assumed to be the causes of treelessness and the main factors limiting arctic life. Both factors are quite variable over the vast Eurasian Arctic because they are highly dependent on the degree of oceanic influence on climate.

The impact of the Sea on arctic climate

Proximity to the ocean results in small seasonal temperature amplitudes, thus relatively mild winters, cool summers, and increased humidity. Due to the proximity of the Arctic Ocean and the North Eurasian shelf seas respectively, the whole Eurasian arctic tundra region is more or less under oceanic climate influence today. Oceanic influence results in increased cloudiness, which hampers the warming of the Earth’s surface by direct solar radiation. Heightened precipitation brings thick snow cover in winter and saturated soils in summer. Because of the late snow melt, the growing season is very short and a high percentage of received solar energy lost to snow albedo or is transformed in latent, not sensible heat, because of waterlogged soils. Soil paludification is strengthened additionally by the damming effect of near-surface permafrost and low evaporation.

East Siberia is affected by maritime air masses, however, much less than Europe and West Siberia. In regions with continental climate, both the insolation during the summer and the energy emission during the winter can pass through the cloudless atmosphere much easier. This results in extreme seasonal temperature fluctuations. Despite low mean annual and winter temperatures, the timber line is shifted much farther northward in East Siberia (MS 217, Fig. 1), owing to relatively high summer mean temperature and lengthened growing season, and the floristic composition is more diverse than in more oceanic regions.

Permafrost impact on soils

Permafrost is another characteristic feature of polar latitudes during the Quaternary epoch (MS 103). Permafrost affects soils and thus vegetation by stabilization and damming groundwater. Under humid climate, permafrost highly amplifies soil paludification (MS 104). Today even in Northeast Siberia, where precipitation is less than 300 mm, the landscape is characterized by widespread wetlands because of the damming effect and the melting of ice-rich permafrost deposits (Thermoerosion). In contrast, under arid climate conditions, permafrost is accompanied by high seasonal fluctuations of soil moisture due to high evaporation and supports salt accumulation in the soil by damming groundwater and supplying moisture and solutes (Yelovskaya *et al.*, 1966, Fig. 2).

<Fig.2>

The arctic vegetation during the Quaternary

Refuges and centers of dispersal

Many arctic plants obtained circumpolar ranges early in the Quaternary. However, these ranges shrank several times during Pleistocene climate oscillations (MS 21). Most arctic plants had to withstand enormous range losses during interglacials, when they were eliminated by competition. During cold stages, however, they expanded far to the south and west and reached their maximum distribution (Fig.3). The Arctic flora was likewise heavily influenced by glaciations. It is now accepted, however, that large parts of the Eurasian arctic have never been glaciated (MS 121, 123, 124, 127, 132, Svendsen *et al*. 2004, Fig. 3).

<Fig.3>

Based on phytogeographical (Hulten 1937, Nimis *et al.* 1998), molecular genetic (Abott & Brochmann 2003), and fossil evidence (Goetcheus & Birks 2001, Kienast *et al.* 2005), we can state that Beringia, the northern landmass between the Lena and Mackenzie Rivers, was the major refugium for arctic plants throughout the Quaternary, even during the most warm-humid stages of former interglacials (Kienast *et al*. in prep.). The cause for this continuity in Beringia is its climatic continentality that partly still exists today, but was much stronger during most of the Pleistocene when the North Siberian Shelves were dry land and the Bering Land Bridge existed (MS 147, Fig. 4).

<Fig.4>

The composition of the Arctic Vegetation in the Past

From our current point of view, it is difficult to realize that the modern characteristics of climate and vegetation in Eurasia are the exception, when compared with most of the Quaternary. But even though the abrupt climate shifts between glacial and interglacial environments involved serious consequences for arctic Biota, we must keep in mind that these oscillations constituted less than 20% of Quaternary time. During the remaining 80%, a cold stage vegetation complex, the tundra-steppe, more diverse than modern Arctic vegetation, dominated northern Eurasia from the arctic coast south to the middle latitudes, (Fig. 3).

The principle of actualism

The Quaternary is characterized by enormous changes of plant distribution rather than by evolutionary processes (Lang 1994). Based on numerous palaeobotanical records, the distribution of plant communities within Eurasia, in consequence of Quaternary climate oscillations, changed dramatically (Frenzel 1968, Godwin 1975, Hibbert 1982, Lang 1994). The same is widely accepted concerning the composition of plant communities. It has been the general consensus that the vegetation composition of the Pleistocene, especially during cold-stages, is without modern analogue. Since Pleistocene vegetation was however composed of still existing plant species, this assumption contradicts the principle of actualism, which is a basic principle of geology (Lyell 1830) and the basis for the reconstruction of past ecological conditions. Accordingly, every phenomenon, including the occurrence of plant species, follows the same rules, now and in the geological past. Correspondingly, the palaeoecology of an existing plant species corresponds to its current ecology. This applies to both, the plant's environmental requirements for temperature, moisture, light, etc. and its grouping with ecologically similar plants. Thus, there exist analogues of the arctic cold-stage vegetation mosaic in extremely continental North Siberian refugia (Yurtsev 1982, 2001; Fig. 5). According to the rule of relative habitat constancy (Walter 1954), both individual plant species and plant communities compensate for climate shifts by relocation so that their habitat conditions remain relatively constant. It is only when constituent species of plant communities fail to persist in a given region during unfavourable climate phases that the communities can change by the occupation of the then-free niche by other species with broader tolerances. These changes of vegetation composition correspond to a decline in floristic diversity. Community modification is indeed a characteristic phenomenon of the Quaternary, but it was apparently restricted mainly to oceanic regions, which have been most affected by climate fluctuations.

<Fig. 5>

Conservative versus changing vegetation types

Depending on the availability of refuges for plant communities during climate-induced retreat phases and the amplitude of environmental fluctuations, the Eurasian Quaternary vegetation can be divided into two main types: (1) ancient vegetation that is relatively conservative in species composition; and (2) changeable, unstable vegetation.

- *Conservative vegetation types*

Since they are independent on the degree of climatic continentality, aquatic and wetland plant communities are ancient and very conservative (Mai 1985). Their modification towards modern composition already began 20 million years ago. Because of their floristic conservatism, a reconstruction even of Tertiary aquatic plant communities is possible and was suggested by Mai (1985).

Another group of relatively conservative vegetation that persisted throughout the Quaternary consists of steppes and coniferous forests (Frenzel 1968). Connected with cooling and increased continentality, the species-poor NE-Siberian coniferous forests (with *Larix, Picea, Pinus*) had already evolved from the late Miocene onwards. They decreased in diversity but remained conservative in species composition during the Quaternary. According to the sparse pollen and macrofossil records, all warm stages since the Middle Pleistocene have been alike in tree composition (Frenzel 1968). Only their distribution has changed in response to climate oscillations, which resulted in the expansion of steppe vegetation during cold stages. The Siberian cold steppes seem to have evolved as continuously as the taiga. Steppe dominated the plant cover throughout Eurasia during cold stages and even replaced taiga, which was restricted to moist refuges (Frenzel 1968). Both vegetation types are associated with continental climate, which, even during the warm stages with maximum humidity, continued to exist in the interior regions of the huge Eurasian continent. Within a glacial/interglacial cycle, the climate and consequently also the vegetation did not change as radically in eastern Siberia as it did in the more oceanic regions of western Europe. The transformation of the vegetation in response to colder and more continental conditions occurred in Northeast Siberia on a greater scale and much earlier than elsewhere in the Northern Hemisphere. Northeast Siberian steppe and taiga are therefore relatively stable in their floristic composition.

- *Changeable vegetation types*

In contrast to these relatively stable plant communities, western arctic communities typically experienced oceanic climate, and consequently they were not tolerant of continental climate conditions. During Quaternary climate oscillations, they therefore were highly unstable, floristically. The changes of vegetation towards a cold stage were much more distinctive in the oceanic climate areas of the continent than in the continental regions and the character of the vegetation conformed to the latter. Tundra species with amphi-atlantic and west arctic distributions suffered frequent and heavy range losses during cold stages in response to glaciations that ushered in continental climate conditions and associated competitors (dry-resistant east arctic species and steppe plants). Likewise, during warm stages, forests expanded, and the west arctic flora had to retreat to refuges in the remaining cold regions. A great amount of phytogeographical evidence supports the survival of west arctic plants in highly disjunctive ranges along the coast and in ice-free refugia within glaciated areas (nunataks). Allopolyploidy is a viable strategy against gene pool impoverishment in consequence of the founder effect in such very small populations. Genetically differing haploid chromosome sets of formerly isolated taxa are fused and the resulted hybrid genome thereafter becomes multiplied and thus stabilized. As a consequence of this, every individual in a small population contains a broader genetic variability in its genome and is thus able to successfully exploit a broader range of habitats. The high percentage of polyploid species among arctic plants in oceanic West Eurasia contrasts with the flora of the Beringian refuge areas. This phenomenon is a distinct indicator of frequent isolation and subsequent fusion of very small populations (Murray 1995). Many allopolyploid arctic plants originated no earlier than during Holocene (Abott & Brochmann 2003). Summarizing, the changeability of the west-arctic vegetation is not based on floristic impoverishment alone but also on intense recent genotype modification of its constituent species.

The vegetation complex of cold stages

Progressive cooling and increasing continentality resulted in the formation of treeless grassland and open parkland vegetation in high latitudes, at first in NE-Siberia (Beringia), during the Early Pleistocene (Sher 1997). Steppes had already spread out over large portions of Eurasia during the first cold stage, connected with a diverse fauna of grazing mammals (MS 262). The early

Pleistocene cold stages were probably not as harsh as the later Saalian and the Weichselian glaciations. This is indicated by the diversity of thermophilous, extralimital plants and steppe mammals during early Pleistocene warm stages and in the absence of extremely cold resistant taxa during the first cold stages. During the middle Pleistocene, environments in Beringia resembled those of the Late Pleistocene. Tundra steppe was the dominant vegetation, closely connected with the Mammoth faunal complex (MS 262). As apparent from pollen records, the vegetation was much more uniform across broad regions than it is today, due to smaller latitudinal and longitudinal climate gradients in Eurasia. This seems to have been true not only during glacials but even during interglacials, except during the current one. The kind of latitudinal zonation of vegetation known today from West Eurasia did not exist in the Pleistocene (Sher 1997).

Within this “tundra-steppe”, zonal biome there co-existed, of course, a great range of plant communities reflecting a wide variety of habitat conditions. The basic character of arctic vegetation during cold stages, however, differed substantially from modern tundra. At first, the set of plant communities and habitat conditions was much more diverse, mainly depending on the availability of warmth and moisture. During the Pleistocene these factors limited arctic plant growth and fluctuated considerably, both seasonally and spatially. Due to the scarcity of plant macrofossil records in the Eurasian Arctic, the set of reconstructed plant communities, described below and mainly basing on Godwin (1975) for northwestern Europe and Kienast (2005, in prep.) for NE-Siberia, is still small and will be, without doubt, enhanced in the future, but it reflects a much greater spatial environmental gradient than modern tundra, which has been shaped by consistently cool and wet conditions.

- *Aquatics*

Frequent finds of aquatic plant remains in high latitude Pleistocene cold stage assemblages (Fig. 6) may surprise most readers, since most of these plants do not occur so far north today. The occurrence of boreal or even temperate aquatics in the Arctic during cold stages is the most striking evidence of warm summers that were a part of greatly increased continentality. The inland occurrence of species indicating brackish water (e.g. *Potamogeton vaginatus*) can be traced back to fluctuating salt contents in freshwater due to high evaporation under arid conditions inland. These species have very restricted modern ranges, but were widespread in the Pleistocene. According to Mai (1985), warmth-indicating southern aquatic plants had already expanded rapidly during the initial subarctic-boreal stages of Interglacials or during tree-less interstadials in Central Europe, even exceeding their spread in earlier warm stages. These phenomena can be ascribed to the extremely rapid dispersal of aquatics by birds after the re-establishment of favourable conditions. Apparently, summer temperatures rose abruptly during the onset of warm stages. Freshwater aquatics are pioneers and can occupy suitable habitats very quickly, whereas most tree species disperse slowly and can only become established following sufficient soil formation.

<Fig. 6>

- *Littoral pioneers and riparian ruderals*

The unstable moisture conditions that were so characteristic of Pleistocene cold stage environments in the Arctic are especially well indicated by littoral pioneer plants, which occur on wet, bare, erosive soils along the shores of shallow lakes and ponds with highly fluctuating water levels. This vegetation type, including *Ranunculus reptans*, clearly shows that pools, filled with water after snow melt, decreased in size or even dried up in the course of summer owing to high aridity. Similar to aquatics, some littoral plants are facultative halophytes. Their tolerance of high salt content in soils further strengthens the indication of high evaporation given by their pioneer character. Some representatives, such as *Puccinellia* sp., *Rumex maritimus*, *Chenopodium* sp., and *Stellaria crassifolia*, found in Arctic East Siberian cold stage deposits (Kienast et al. 2005) occur today primarily on the coast, and otherwise are only found in extremely continental areas of Asia. Of particular interest is that during the last cold stage, even in the westernmost, more oceanic Europe, the right conditions existed for the inland occurrence of salt-tolerant littoral pioneers like *Atriplex* spp., *Chenopodium album*, *Potentilla anserina*, and *Tripleurospermum maritimum* as well as even obligate halophytes including *Glaux maritima*, *Sueda maritima* and *Triglochin maritimum* (Godwin 1975). Littoral ruderals cannot endure competition and disappear after the establishment of stable wet conditions fostering vegetational succession. In contrast, frequent disturbances by animals; e.g. at watering places; promote this type of vegetation (Fig.7).

<Fig. 7>

- *Meadows*

Intense seasonal moisture fluctuations are also shown by the presence of meadows, which were, in Northeast Siberia, composed of grasses including *Puccinellia* sp. and *Hordeum brevisubulatum* as well as *Carex duriuscula* (Kienast et al. 2005), characteristic of floodplains along streams and around lakes outside the range of seasonal inundation under arid conditions (Fig. 8). This halotolerant vegetation type is productive due to its proximity to seasonally fluctuating groundwater. Also in the Northwest European Weichselian Periglacial, meadows with *Festuca* spp. and Poa spp. occurred in Great Britain (Godwin, 1975) and with *Puccinellia* in Norway (Alm & Birks 1991).

<Fig.8>

- *Steppes*

Beginning with Nehring (1890), the discovery of the fossil remains of grazing, steppe-characteristic mammals like bison, horse, saiga-antelope together with high arctic species such as reindeer and musk ox, as well as the extinct grazers mammoth and woolly rhinoceros, have shown that grasslands have been an important component of cold stage environments in the Eurasian mid-latitudes during the Pleistocene. Steppe plant occurrences in periglacial environments of Western Europe were demonstrated later by macrofossils (Godwin 1975). But the low pollen influx rates in cold stage records from the Arctic led some researchers to believe that glacial conditions would make the high latitudes uninhabitable.

<Fig 9>

These arguments were, however, rebutted by the discovery of the remains of grazing mammals in high latitude cold stage deposits in North America (Guthrie 1990) and Eurasia (Sher et al. 2005). They were also rebutted by disjunctive relict occurrences of steppe vegetation in northern Siberia (Yurtsev 1982) (Fig. 5, 9, 10), and finally by the discovery of Weichselian macrofossils of southern steppe plants in arctic permafrost records (Kienast et al. 2005) (Fig. 11). The spectrum of steppe plant macrofossils in Arctic Siberia is illustrated on Figure 11.

<Fig. 10>

In the western European periglacial zone that existed in glacial times, macrofossils of *Linum perenne*, *Corispermum* sp., *Onobrychis viccifolia*, *Poa* sp., *Festuca* sp., *Rumex acetosella*, and *Centaurea scabiosa* were found (Godwin 1975). These steppe plants clearly indicate aridity and high summer temperatures.

<Fig. 11>

- *Arctic and Subarctic upland vegetation*

The other temperature related climate feature of continentality - extremely cold winters - is indicated by arctic upland vegetation mainly composed of arctic pioneer plants forming the northernmost plant life in arctic deserts as well as *Kobresia* meadows and *Dryas* heaths (Fig. 12). They all indicate little or no snow cover and today occur at sites most exposed and frequently disturbed by deflation in winter.

<Fig.12>

The vegetation Complex of warm stages

As discussed above, the arctic cold stage vegetation differed considerably from modern tundra. Plant communities that require constant moisture were therefore largely absent during cold stages but became abundant during warm stages, not only because of increasing humidity but also due to thermal erosion of ice-rich permafrost, which resulted in extensive wetland formation. Due to less harsh winter temperatures and the protective effect of a thick snow cover, less hardy boreal and maritime-adapted plants could spread into the arctic. Steppe plants in contrast shrunk in distribution. Some of the vegetation types detailed below also occurred during cold stages, especially in the more oceanic western Europe (Godwin 1975). They were, however, more typical of warm stages.

- *Woodlands and Forest Tundra*

During warm stages, woodlands with *Larix*, *Betula*, and *Alnus* extended considerably northward and forest tundra constituted the northernmost vegetation belt in central and eastern Siberia, as evidenced by macrofossils in interglacial deposits on Kotelny Island, Wrangel Island, (Frenzel 1968) and on Bolschoy Lyakhovskiy Island (Fig.13, Kienast et al. in prep.). Woodlands, mainly composed of tree birches and pine, occurred in the periglacial regions of Western Europe during the Weichselian cold stage (Godwin 1975); they were restricted to favorable sites however.

<Fig 13>

- *Shrub and Heath*

Shrubs, especially willow shrubs, are important and diverse constituents of arctic vegetation during both cold and warm stages. Willow species composition of cold stage floras, and their ecological significance, differs from those of warm stages. We are unable, however, to give environmental implications since most arctic willows are impossible to identify by macrofossils. Contrary to this, shrubs of *Empetrum nigrum* s.l., dwarf birches and Ericaceae such as *Vaccinium* spp., *Ledum palustre,* and *Arctostaphylos uva-ursi* in Siberia give clear implications of a thick, protective snow cover and acidic soils, both characteristic of interglacials. In the more oceanic Western Europe, these plants, together with *Calluna vulgaris* and *Erica tetralix,* form regular heaths. Such heathlands were also present during cold stages and acted as precursors of forest succession (Godwin, 1975).

- *Snow-bed Vegetation*

Due to reduced precipitation and thin snow cover during cold stages, plant communities that are typical of late snow beds occur almost exclusively during warm stages in continental Northeast Siberia, (Kienast et al. 2005). Based on their appearance in Eurasia, there is a spatial humidity gradient detectable during cold stages because this vegetation was also found in the Weichselian British flora (Godwin 1975). It indicates thick snow cover, late snow melt, soils permanently soaked and cooled by melting water, and a short growing season.

- *Wetland Vegetation*

Modern tundra is the treeless, boggy area characterised by a stable wet environment north of timberline (Frenzel 1968). Due to humid conditions and frozen ground, soils are saturated with water and, consequently, wetlands dominate the landscape. Sedges and cotton grass (*Eriophorum scheuchzeri)* are characteristic of permanently wet mineral soils with circumneutral substrates (Fig. 14). Dwarf birches and *Vaccinium* spp., *Saxifraga hirculus* and *Eriophorum vaginatum* occur at rather acidic mires with fluctuating wetness.

<Fig. 14>

The Holocene tundra as an exception within the Quaternary

As discussed above, tundra is mainly an interglacial vegetation type. As tundra became the prevailing vegetation in northern latitudes during the Holocene, the Pleistocene grazing mammals became extinct (MS 266). Due to marine transgressions in northern Europe and western Siberia, and the northward expansion of taiga, tundra was more constricted in earlier warm stages (Frenzel 1968). During thermal optima, forests expanded north to the coastline. Tundra existed only within the context of forest tundra, and came into being as a consequence of paludification, rather than of climate cooling during warm and moist intervals (Frenzel 1968). This is confirmed by Eemian macrofossil records from the Bolschoy Lyakhovskiy Island, clearly showing that forest tundra with an admixture of steppe and meadow communities, combined with warmth-requiring aquatics, prevailed on the Laptev Shelf during the last warm stage (Kienast et al. in prep.). The Eemian palaeovegetation indicates a greater seasonal temperature gradient, with summers at least 8°C warmer than today, and more variable moisture conditions. All the climatic implications point to more continental conditions persisting beyond the Saalian cold stage and giving rise to the assumption that the study site was inland during the Eemian interglacial and that consequently the marine transgression was less advanced than in the Holocene. It seems that the regional Holocene transgression exceeded all previous ones. This was probably caused by neotectonical subsidence of the shelf due to spreading of the Laptev region. The development of the Asian anticyclone depends decisively on the extension of the continent above which it forms. Thus, it could be easily influenced by the large-scale transgression that took place through the Holocene. The extreme increase of maritime influence greatly affected Beringia. Of all arctic regions, this was the major refugium for arctic vegetation, so the increased maritime influence resulted in the transformation of vegetation towards modern tundra and in the loss of the mammoth faunal complex (MS 266). It seems that proximity to the sea exerts more influence on regional climate in high latitudes than do global temperature trends. Summer temperature and length is crucial for life in the arctic. Both depend on the degree of continentality.

References,

MS 219, Kienast, Arctic vegetation history Eurasia

ACIA 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

MacDonald G.M., Cwynar L.C., Riding R.T., Forman S.L., Edwards T.W.D., Aravena, R., Hammarlund D., Szeicz J.M., Gattaulin V.N. 2000. Holocene treeline history and climate change across Northern Eurasia. Quaternary Research 53, 302-311.

CAVM Team 2003. Circumpolar arctic vegetation map. Scale 1:7,5000,000. Conservation of arctic Flora and Fauna (CAFF). Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Svendsen J.I., Alexanderson H., Astakhov V.I., Demidov I., Dowdeswell J.A., Funder S., Gataullin V., Henriksen M., Hjort C., Houmark-Nielsen M., Hubberten H.-W., Ingólfsson Ó., Jakobsson M., Kjær K.H., Larsen E., Lokrantz H., Lunkka J.P., Lyså A., Mangerud J., Matiouchkov A., Murray A., Möller P., Niessen F., Nikolskaya O., Polyak L., Saarnisto M., Siegert C., Siegert M.J., Spielhagen R.F., Stein R. 2004. Late Quaternary ice sheet history of northern Eurasia. Quaternary Science Reviews 23, 1229-1271.

Yelovskaya L.G., Konorovsky A.K., Savinov D.D. 1966. Salt-rich soils above permafrost (kryosols) in Central Yakutia. Nauka, Moscow. In Russian.

Hulten E. 1937. Outline of the history of Arctic and Boreal Biota during the Quaternary period. Bokförlags Aktiebolaget Thule, Stockholm.

Nimis P.L., Malyshev L.I., Bolognini G., Friesen N. 1998. A multivariate phytogeographic analysis of plant diversity in the Putorana Plateau (N Siberia). Opera Botanica 136, 5-72.

Abott R.J., Brochmann C. 2003. History and evolution of the arctic flora: in the footsteps of Eric Hultén. Molecular Ecology 12, 299-313.

Goetcheus V.G., Birks H.H. 2001. Full-glacial upland tundra vegetation preserved under tephra in the Beringia National Park, Seward Peninsula, Alaska. Quaternary Science Reviews 20, 135-147.

Kienast F., Schirrmeister L., Siegert C., Tarasov P. 2005. Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage. Quaternary Research 63, 283-300.

Kienast F., Grosse G., Siegert Ch., Schirrmeister L., Tarasov P., Hubberten H.-W. in prep. Continental climate on the Laptev Sea Shelf during the last interglacial: evidence of lacking marine transgression by terrestrial plant macrofossils. Journal of Quaternary Science.

Lang G. 1994. Quartäre Vegetationsgeschichte Europas (Quaternary vegetation history of Europe). Gustav Fischer Verlag, Jena. (in German).

Frenzel B. 1968. Grundzüge der pleistozänen Vegetationsgeschichte Nord-Eurasiens (Basic principles of the Pleistocene vegetation history of North Eurasia). Franz Steiner Verlag, Wiesbaden.

Godwin H. 1975. The history of the British Flora. Cambridge University Press, Cambridge.

Hibbert, D., 1982. History of the Steppe-Tundra Concept. In: Paleoecology of Beringia (*eds.* D.M. Hopkins, J.V. Matthews Jr., C.E. Schweger, S.B. Young) Academic Press, New York.

Lyell C. 1830. The principles of Geology. John Murray, London.

Yurtsev B.A. 1982. Relics of the xerophyte vegetation of Beringia in Northeastern Asia. In: Paleoecology of Beringia (*eds.* D.M. Hopkins, J.V. Matthews Jr., C.E. Schweger, S.B. Young) Academic Press, New York.

Yurtsev B.A. 2001. The Pleistocene "Tundra-Steppe" and the productivity paradox: the landscape approach. Quaternary Science Reviews 20. 165-174.

Walter, H. 1954. Grundlagen der Pflanzenverbreitung; Volume 2, Arealkunde (floristisch-historische Geobotanik). Gustav Fischer Verlag, Stuttgart. (in German)

Mai D.H. 1985. Entwicklung der Wasser- und Sumpfpflanzen-Gesellschaften Europas von der Kreide bis ins Quartär Development of the waterplant- and swamp associations of Europe from the Cretaceous to the Quaternary. Flora 176, 449-511.

Murray D.F. 1995. Causes of Arctic plant diversity; origin and evolution. In: Arctic and Alpine biodiversity (*eds.* F.S. Chapin III and C. Körner). Springer, Berlin.

Sher, A.V. 1997. A brief overview of the Late-Cenozoic history of the Western Beringian lowlands. In: Terrestrial palaeoenvironmental studies in Beringia (*eds.* M.E. Edwards, A.V. Sher, R.D. Guthrie). Alaska Quaternary Center, Fairbanks.

Alm, T. & Birks, H.H. 1991. Late Weichselian flora and vegetation of Andøya, northern Norway – macrofossil (seed and fruit) evidence from Nedre Æråsvatn. Nordic Journal of Botany 11, 465-476.

Nehring A. 1890. Über Tundren und Steppen der Jetzt- und Vorzeit unter besonderer Berücksichtigung ihrer Fauna (On tundras and steppes in former and present times with special consideration of their fauna). F. Dummer, Berlin. In German.

Guthrie R.D. 1990. Frozen Fauna of the Mammoth Steppe. University of Chicago Press, Chicago.

Sher A.V., Kuzmina S.A., Kuznetsova T.V., Sulerzhitsky L.D. 2005. New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals. Quaternary Science Reviews 24, 533-569.

Figure captions,

MS 219, Kienast, Arctic vegetation history Eurasia

Figure 1. Polar tree line in northern Eurasia and its northward shift in the Early Holocene. The tree line is formed by birch, pine, and spruce in the oceanic West and by larch in the more continental East Siberia. From MacDonald *et al.* (2000).

Figure 2. Shore of a shrinking thermokarst lake in the extremely continental Central Yakutia with a seasonally fluctuating water level (A) and salt crust formation in the range that becomes dry in summer (B). Photos: C. Siegert.

Figure 3. Maximum distribution of arctic vegetation in Eurasia during the last glacial maximum. Adapted from Frenzel (1992), modified according to ice-sheet limits reconstructed in Svendsen *et al*. 2004. 1- arctic and periglacial vegetation, 2- Mountain glaciers, 3- Sea-ice cover. 4- inland ice sheets, 5- Sea and large freshwater lakes

Figure 4. Exposed shelves in Northeast Siberia (Beringia, according to Hulten 1937) and expansion of the mainland during the Weichselian cold stage. Adapted from Kienast et al. (2005) with permission.

Figure 5. A: Cold-arid “Goltsy” region in the alpine belt of the Momsky Mountains (Northeast Siberia). The precipitation is too low to support a perennial snow cover or even a glacier. B: Steppe and alpine plants occur there side by side (here: Festuca kolymensis and Dryas punctata). Photos: F. Kienast.

Figure 6. Late Pleistocene aquatic plant macrofossils preserved in permafrost deposits from the Laptev Sea coast (Arctic Northeast Siberia). From Kienast et al. (in prep.)

Figure 7. Littoral ruderals at the shore of a shrinking thermokarst lake, used as cattle watering place, in Central Yakutia, with *Rumex maritimus, Stellaria crassifolia, Puccinellia tenuiflora, Senecio congestus, Peucedanum salinum, Chenopodium rubrum*, among others. A salt crust formed at the surface of the hardly disturbed soil. Photo: F. Kienast.

Figure 8. *Puccinellia tenuiflora* (loose panicles) and *Hordeum brevisubulatum* (large spikes) as constituents of a floodplain meadow around a thermokarst lake in Central Yakutia. The productive meadow is intensely used as pasture. Photo: F. Kienast.

Figure 9. Distribution of steppe and tundra-steppe relicts in Northeast Siberia. The occurrences are disjunctive, so they are too far away from their main range in Mongolia and southern Siberia to enable genetic exchange. Thus they clearly indicate a formerly closed range. Stlanik: extensive scrublands with stone pine, birch, and poplar. From Yurtsev 1982.

Figure 10. Relict steppe with *Koeleria cristata* and *Artemisia commutata* in Central Yakutia. Photo: F. Kienast.

Figure 11. Weichselian steppe plant macrofossils preserved in permafrost deposits of arctic Siberia.

Figure 12. Weichselian macrofossils from arctic and subarctic upland vegetation preserved in Siberian permafrost.

Figure 13. Macrofossils of forest tundra shrubs and dwarf shrubs preserved in Eemian interglacial deposits at the Bolshoy Lyakhovsky Island, arctic Siberia in the zone of today’s northern arctic tundra. Adapted from Kienast et al. (in prep.).

Figure 14. Sedge-cotton grass wetland in the Lena River Delta. Photo: H.Meyer.

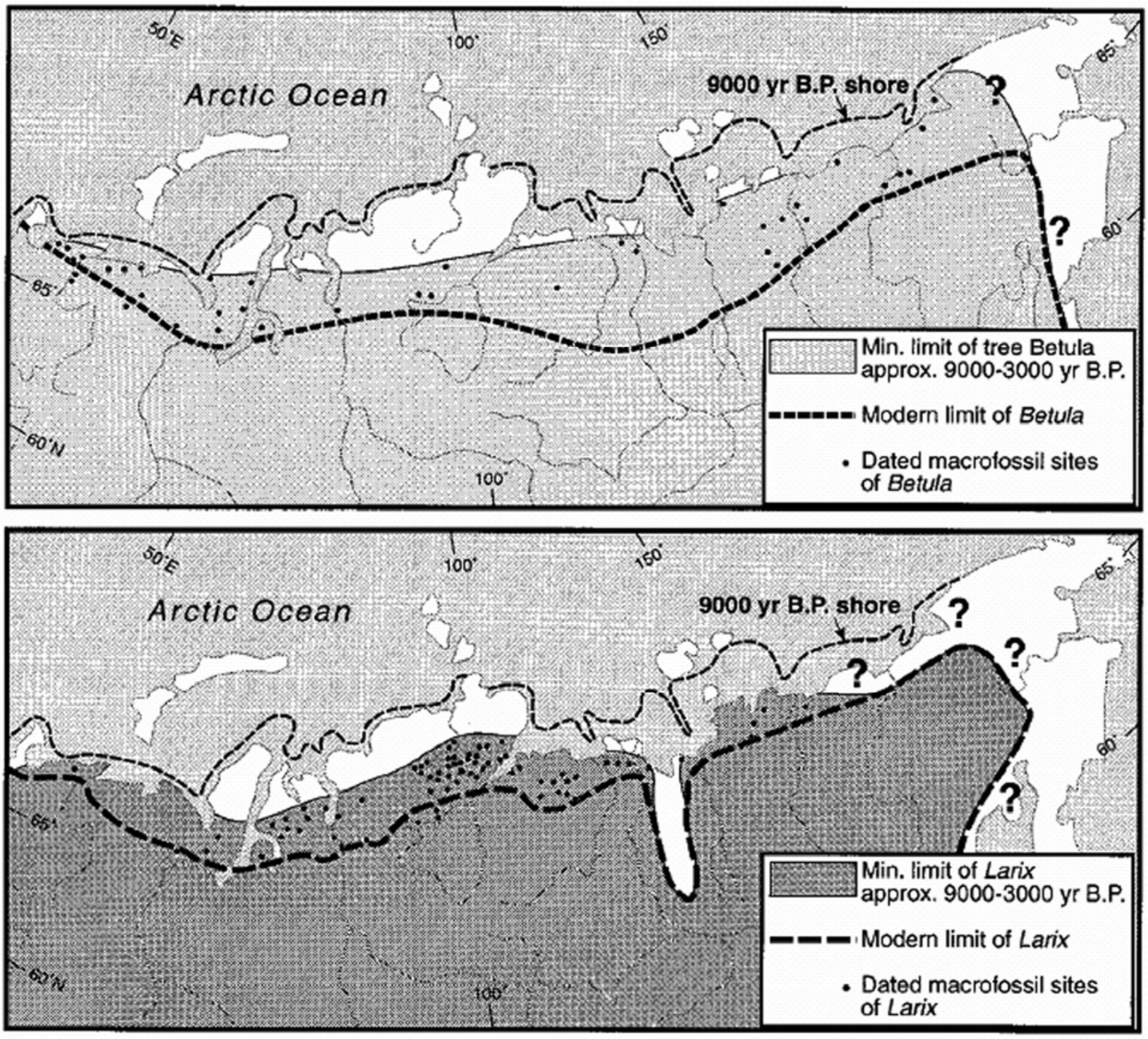
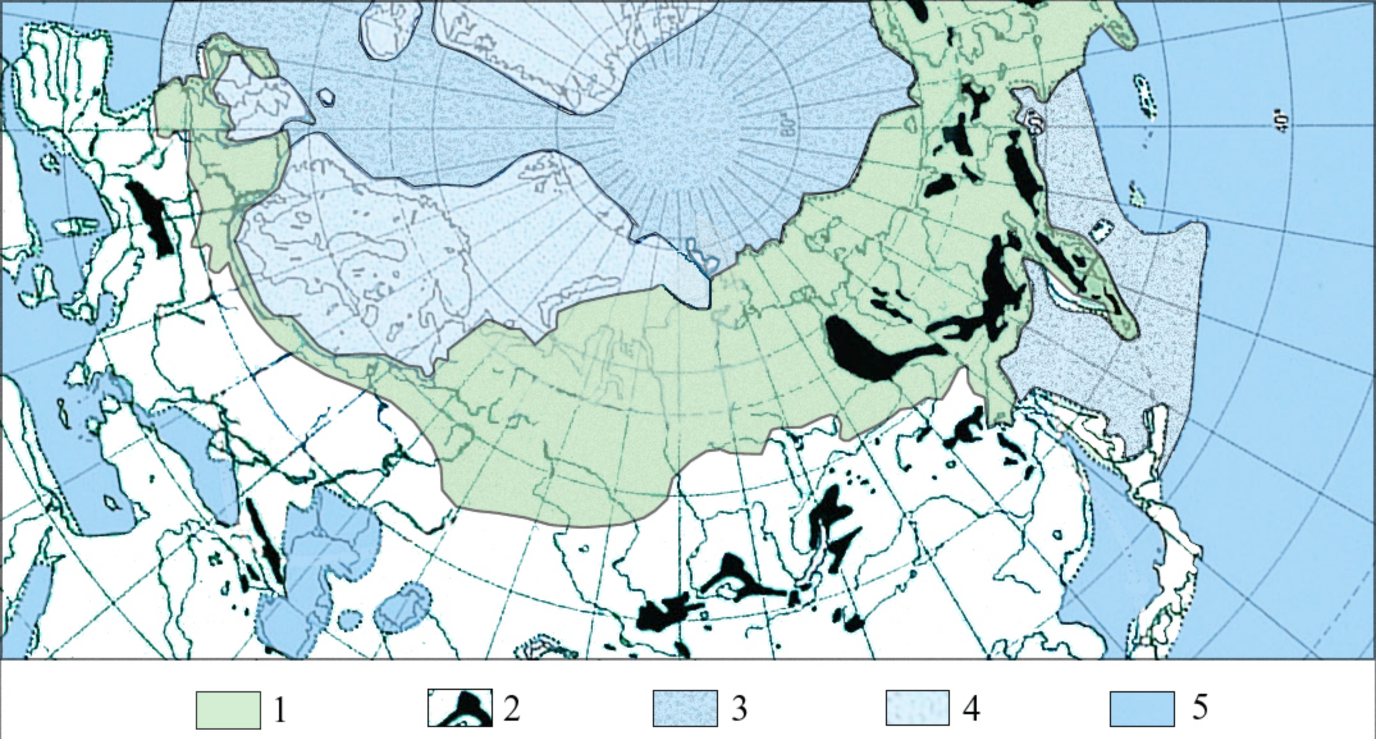
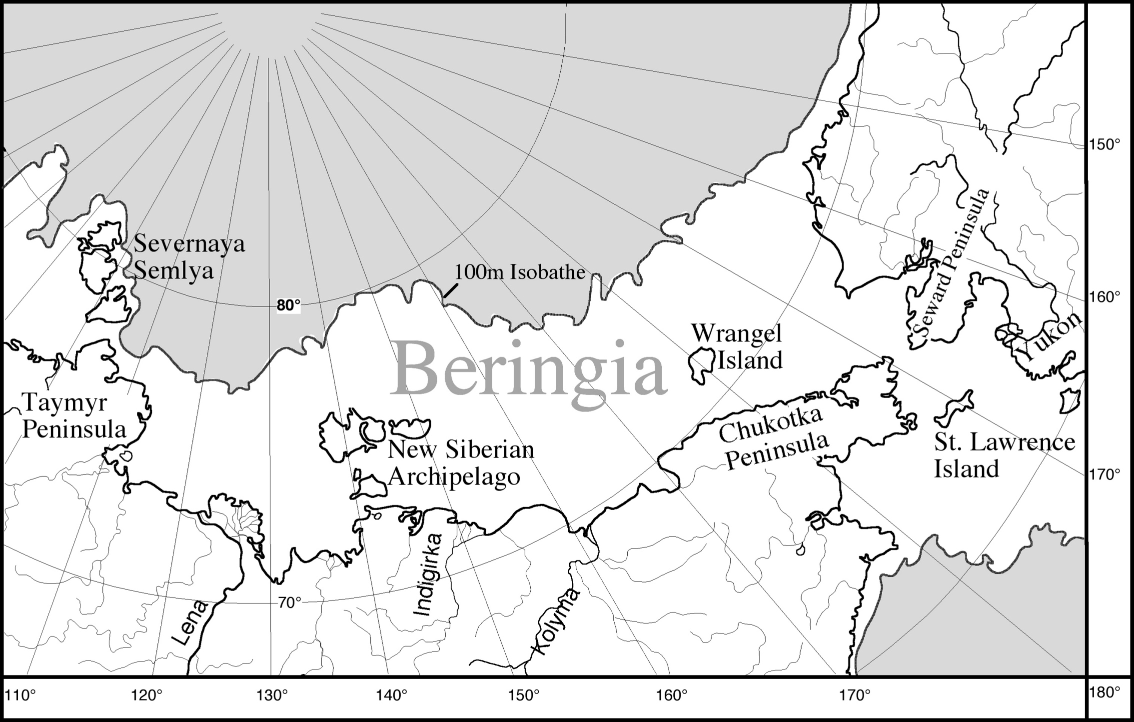
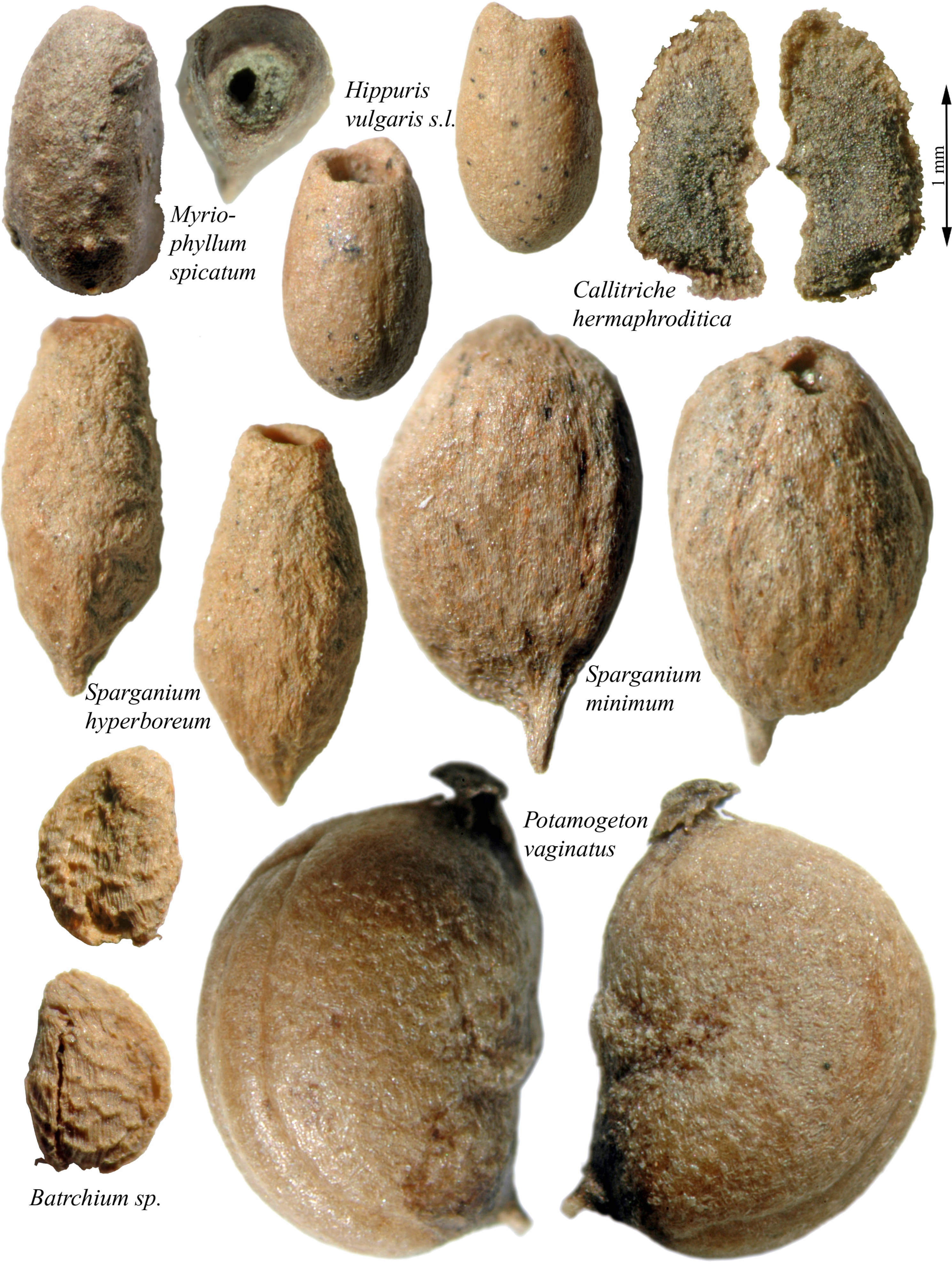
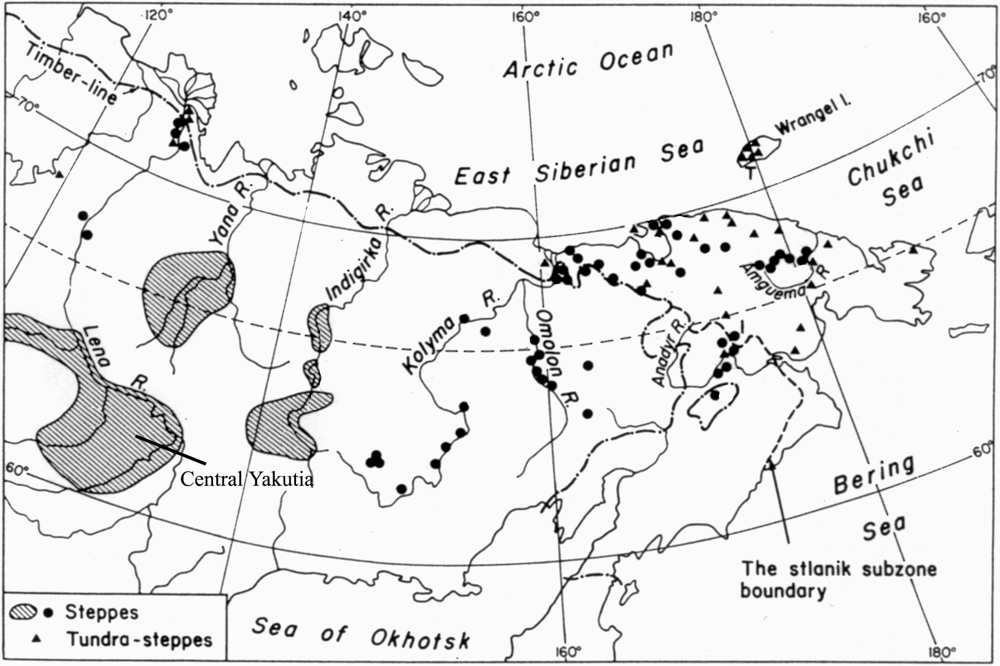

50°E
100°
150°
65°
Arctic Ocean
9000 yr B.P. shore
?
?
60°
65°
60°N
100°
Min. limit of tree Betula approx. 9000-3000 yr B.P.
Modern limit of *Betula*
Dated macrofossil sites of *Betula*
50°E
100°
150°
65°
Arctic Ocean
9000 yr B.P. shore
?
?
?
?
60°
65°
60°N
100°
Min. limit of *Larix* approx. 9000-3000 yr B.P.
Modern limit of *Larix*
Dated macrofossil sites of *Larix*

Figure 1

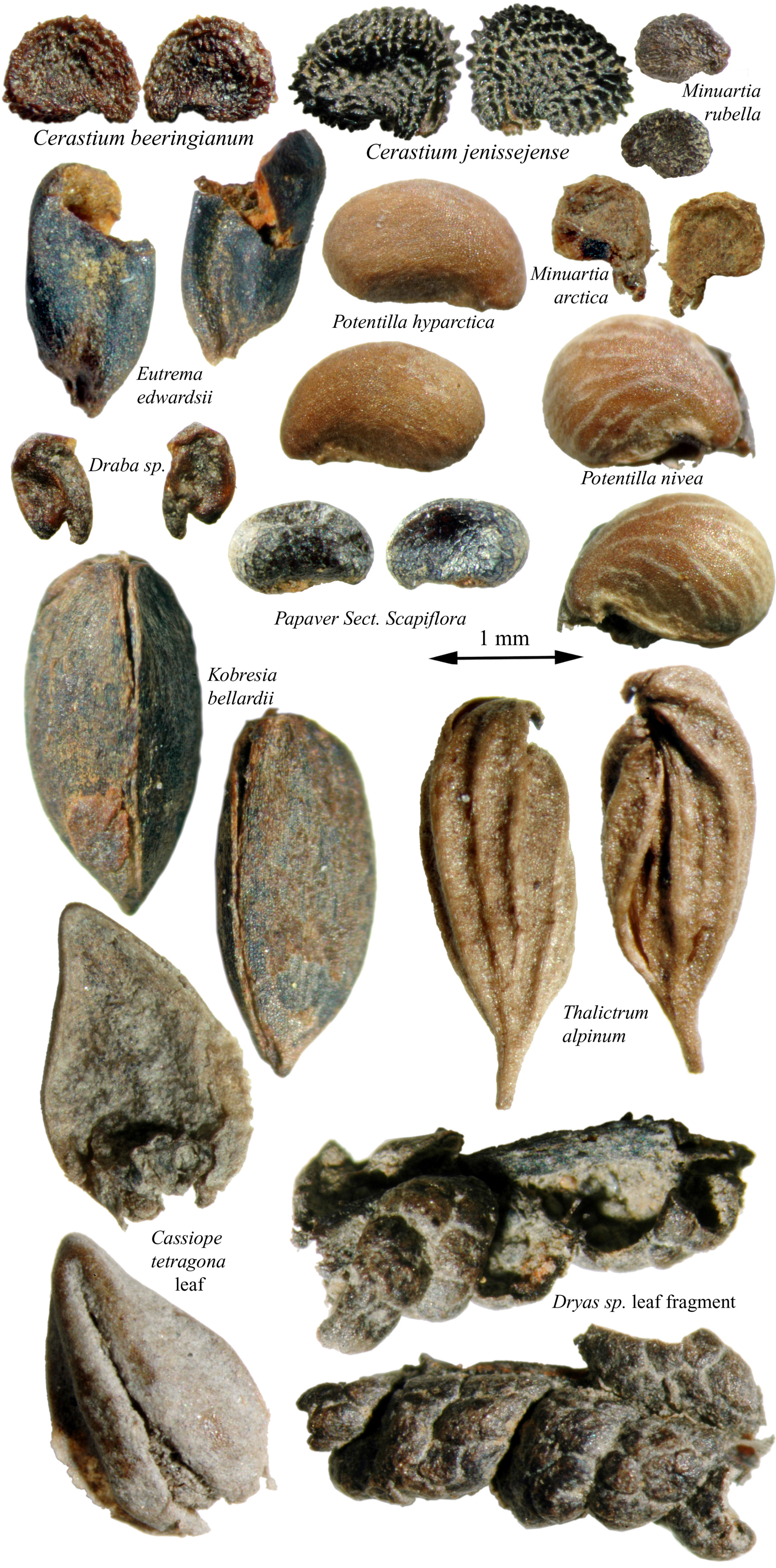

80°
40°
1
2
3
4
5

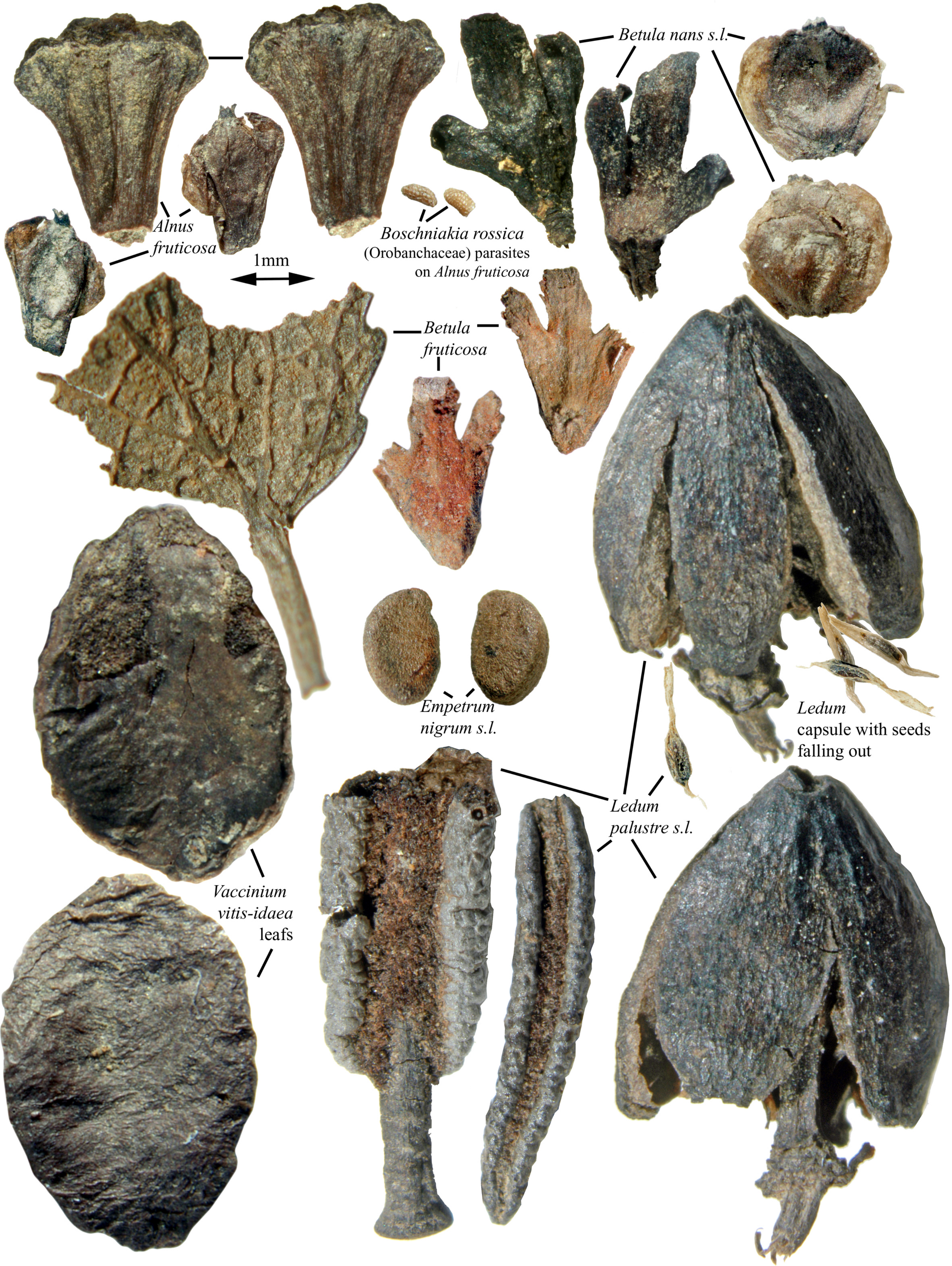

Severnaya
Semlya
100m Isobathe
80°
Beringia
Wrangel
Island
Seward Peninsula
Yukon
Taymyr
Peninsula
New Siberian
Archipelago
Chukotka
Peninsula
St. Lawrence
Island
Indigirka
Lena
Kolyma
70°
150°
160°
170°
110°
120°
130°
140°
150°
160°
170°
180°


Myrio-
phyllum
spicatum
Hippuris
vulgaris s.l.
Callitriche
hermaphroditica
1 mm
Sparganium
hyperboreum
Sparganium
minimum
Potamogeton
vaginatus
Batrchium sp.


120°
140°
160°
180°
160°
70°
70°
60°
60°
160°
180°
Timber-line
Arctic Ocean
East Siberian Sea
Wrangel I.
Chukchi Sea
Yana R.
Indigirka R.
Kolyma R.
Omolon R.
Anadyr R.
Amguema R.
Lena R.
Central Yakutia
Bering Sea
The stlanik subzone boundary
Sea of Okhotsk
▨ ● Steppes
▲ Tundra-steppes


Koeleria cristata
Poa sp.
Thesium sp.
Artemisia sp.
Linum perenne
Potentilla arenosa
Potentilla stipularis
Festuca sp.
Carex duriuscula
Silene repens
Androsace septentrionalis
Alyssum obovatum


Cerastium beeringianum
Cerastium jenissejense
Minuartia rubella
Eutrema edwardsii
Potentilla hyparctica
Minuartia arctica
Draba sp.
Potentilla nivea
Papaver Sect. Scapiflora
1 mm
Kobresia bellardii
Thalictrum alpinum
Cassiope tetragona leaf
Dryas sp. leaf fragment


Alnus fruticosa
1mm
Boschniakia rossica (Orobanchaceae) parasites on *Alnus fruticosa*
Betula nans s.l.
Betula fruticosa
Empetrum nigrum s.l.
Ledum capsule with seeds falling out
Ledum palustre s.l.
Vaccinium vitis-idaea leafs