



## The Bering Land Bridge: a moisture barrier to the dispersal of steppe–tundra biota?

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### ABSTRACT

The Bering Land Bridge (BLB) connected the two principal arctic biological refugia, Western and Eastern Beringia, during intervals of lowered sea level in the Pleistocene. Fossil evidence from lowland BLB organic deposits dating to the Last Glaciation indicates that this broad region was dominated by shrub tundra vegetation, and had a mesic climate. The dominant ecosystem in Western Beringia and the interior regions of Eastern Beringia was steppe–tundra, with herbaceous plant communities and arid climate. Although Western and Eastern Beringia shared many species in common during the Late Pleistocene, there were a number of species that were restricted to only one side of the BLB. Among the vertebrate fauna, the woolly rhinoceros was found only to the west of the BLB, North American camels, bonnet-horned musk-oxen and some horse species were found only to the east of the land bridge. These were all steppe–tundra inhabitants, adapted to grazing. The same phenomenon can be seen in the insect faunas of the Western and Eastern Beringia. The steppe–tundra beetle fauna of Western Beringia was dominated by weevils of the genus *Stephanocleonus*, a group that was virtually absent from Eastern Beringia. The dry-adapted weevils, *Lepidophorus lineaticollis* and *Vitavitus thulius* were important members of steppe–tundra communities in Eastern Beringia, but were either absent or rare in Western Beringia. The leaf beetles *Chrysolina arctica*, *C. brunnicornis bermani*, and *Galeruca interrupta circumdata* were typical members of the Pleistocene steppe–tundra communities of Western Beringia, but absent from Eastern Beringia. On the other hand, some steppe tundra-adapted leaf beetles managed to occupy both sides of the BLB, such as *Phaedon armoraciae*. Much of the BLB remains unstudied, but on biogeographic grounds, it appears that there was some kind of biological filter that blocked the movements of some steppe–tundra plants and animals across the BLB.

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### 1. Introduction

The concept of a land connection between northeast Asia and the Americas began more than 400 years ago (Hoffecker and Elias, 2007). The existence of a northern land connection between Asia and America was first proposed in AD 1590 by the Spanish missionary Fray Jose de Acosta. He suggested that a land bridge had allowed people to enter the New World (Wilmsen, 1965). Some naturalists, including Charles Darwin (1859, pp. 365–382), believed that the entire circumpolar region had been ice-covered during Pleistocene glaciations, but G.M. Dawson (1894) suggested that much of Alaska had been unglaciated and joined to Northeast Asia by a “wide terrestrial plain”. Dawson noted the shallow depths of the Bering and Chukchi seas, and was impressed by the discovery of mammoth remains on the Aleutian and Pribilof Islands (Dall and

Harris, 1892). The fact that the flora and fauna of the Eurasian and American Arctic zone were nearly identical prompted biogeographers such as Wallace (1876) to argue for a land bridge linking the two regions. The biogeographic evidence eventually formed the primary basis for the concept of Beringia.

The term ‘Beringia’ was first proposed by the Swedish botanist Eric Hultén in 1937. Since his pioneering work, scientists have continued to speculate on the role of the Bering Land Bridge as a biotic migration route between North America and Asia. In his monumental work describing the Alaskan flora, Hultén (1968, p. xiv) observed that “the present ranges of Alaskan plants seemed to demonstrate that Beringia had been a pathway for the interchange of biota and that its Asian and American remnants lie at the center of many present distributional patterns”. In these early writings, Hultén used the term ‘Beringia’ only to mean the Bering Land Bridge (BLB). Beringia has since taken on far broader geographic meaning, as Quaternary scientists discovered that the vast lowland regions of northeast Asia and northwest North America remained ice-free during Pleistocene glaciations. The eastern and western sectors

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were linked together by the BLB each time sea level dropped by more than about 70 m below the modern level.

Alaskan geologist David Hopkins (1967) broadened the geographic definition of Beringia to include unglaciated regions of Alaska and Northeast Asia, as far west as the Kolyma River. Hopkins et al. (1981) later expanded the eastern boundary to the lower Mackenzie River in the Northwest Territories of Canada, thus aligning the eastern edge of Beringia with the western margin of the Laurentide ice sheet. Russian palaeobotanist Boris Yurtsev (1984) also proposed extending the western boundary of Beringia to the Lena Basin, based on the distribution of relict flora. Archaeologists working in Beringia also argued for the extension of this boundary to the Verkhoyansk Mountains, along the eastern margin of the lower Lena Basin (Hoffecker et al., 1993) (Fig. 1).

Thus we see that from the beginning, Beringia has been of vital interest to biogeographers, palaeoecologists, glacial geologists, and archaeologists. The idea that the BLB may have served as the primary pathway for people to enter the New World has always added interest and vitality to Beringian research. As far as we can tell, humans did not enter the New World deliberately. They merely crossed the broad, low plains of the land bridge in search of game animals, eventually climbing up a bank to enter what we know as Alaska. If this otherwise unremarkable lowland region between the continents really was the conduit for the entry of humans and other arctic biota into the New World, then we want to know what it was like.

## 2. Palaeoenvironments of the Bering Land Bridge

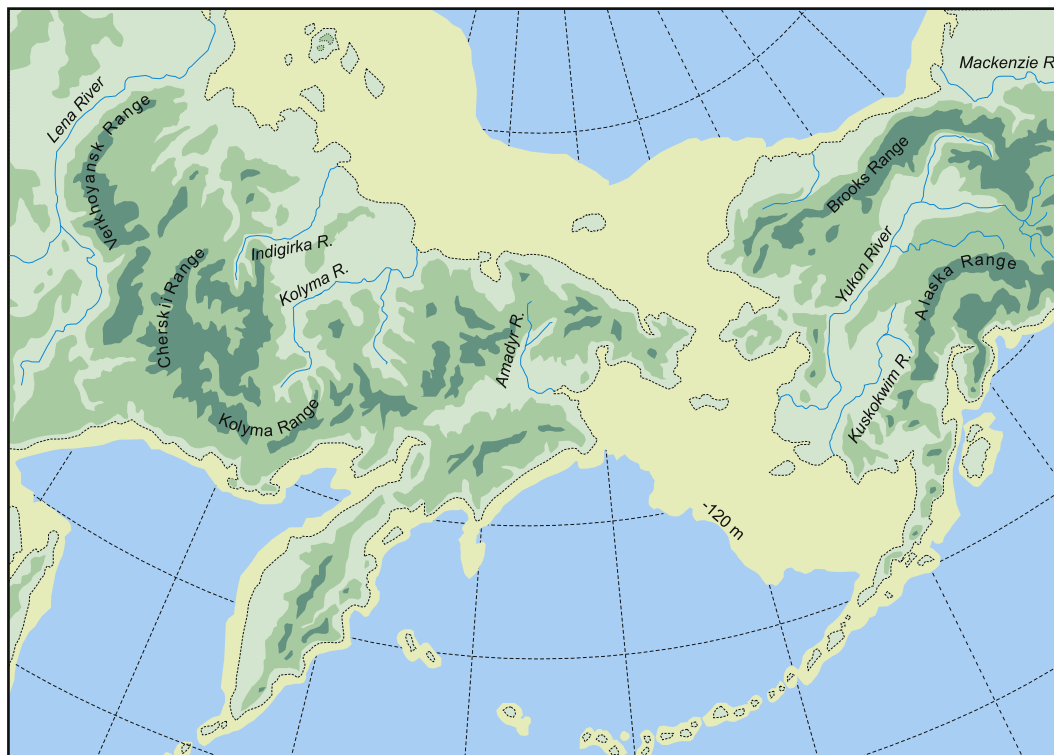
In this review, we focus mainly on the environments of the Last Glacial Maximum (LGM). LGM ice in Western Beringian highlands reached its maximum extent between 27,000 and 20,000 cal yr BP (Brigham-Grette et al., 2003). The vegetation cover of the land bridge was undoubtedly some mixtures of various kinds of tundra. Brief definitions of Alaskan tundra types are provided in Table 1. The timing of the LGM in Eastern Beringia (the unglaciated regions of

Alaska and the Yukon Territory) is not as well defined, but climatic cooling towards the LGM began by 32,000 cal yr BP (Elias and Brigham-Grette, 2007). Late Wisconsin ice began to advance in the mountains of southwestern Yukon by 31,000 cal yr BP (Tom Hamilton, personal communication, October, 2008), and mountain glaciers expanded in the Alaska Range by about 29,000 cal yr BP. Deglaciation was likewise time-transgressive. Hughes (1983) suggested that the western limit of the Cordilleran ice sheet began retreating in the Yukon Territory by about 19,000 yr BP. Mann and Hamilton (1995) suggested that the retreat of ice in southern Alaska began about 16,000 cal yr BP. The LGM is generally thought to have been the coldest, possibly driest interval of the last 100,000 years in many parts of Beringia. During this interval the regions of the Chukchi and Bering Seas above about 120 m below modern sea level were exposed, forming a BLB of considerable size. This land bridge effectively blocked moisture from entering much of interior Alaska and the Yukon. Given this moisture barrier, the LGM should have been the last interval of time in which steppe–tundra vegetation was able to flourish at the expense of mesic tundra in Eastern Beringia.

Various lines of evidence have been used to reconstruct the environments of the BLB. Palaeoecological reconstructions have largely been based on fossil pollen studies, but a considerable body of evidence has been developed from plant macrofossil and insect fossil analyses. Another approach to the reconstruction of BLB environments, indeed the approach taken by Hultén when he coined the term *Beringia*, was to examine the modern distributional patterns of species across the regions that were formerly part of Beringia. This biogeographic approach can also shed light on the role of the BLB in either facilitating or limiting the spread of flora and fauna from one side of the land bridge to the other.

### 2.1. Fossil evidence

Starting in the 1960s, palaeobotanists began attempting to reconstruct the vegetation cover of the BLB, based on pollen spectra



**Fig. 1.** Relief map of northeast Asia and northwest North America, showing proposed boundaries of Beringia (from the Lena River in the west to the Mackenzie River in the east) and the maximum extent of the Bering Land Bridge during the Last Glaciation (after Hoffecker and Elias, 2007).

**Table 1**  
Alaskan tundra vegetation communities (after Hoffecker and Elias, 2007)

| Tundra type           | Brief definition   |
|-----------------------|--|
| Alpine tundra         | Tundra vegetation growing above the elevational limit of trees on mountains. In the Alaska Range, for instance, dwarf scrub communities grow on well-drained, windswept sites. More protected slopes provide moist to mesic sites that support low or tall scrub communities.  |
| Dry herbaceous tundra | Tundra vegetation dominated by herbs (grasses, sedges, and other non-woody tundra plants), growing in relatively dry soils, such as uplands with sandy substrates.   |
| Lichen tundra         | Tundra vegetation dominated by lichens, including <i>Cladina</i> and <i>Stereocaulon</i> , with dwarf shrubs and mosses.   |
| Mesic tundra          | Tundra vegetation growing in mesic (medium moisture) conditions.   |
| Shrub tundra          | Tundra dominated by dwarf shrubs, such as dwarf birch, dwarf willow, narrow-leaf Labrador-tea, mountain-cranberry, and crowberry. This type of vegetation requires mesic (medium moisture) to moist conditions.  |
| Steppe-tundra         | A mixture of plant species found today in steppe regions (mid- to high-latitude grasslands) and in Arctic tundra regions. This once-widespread vegetation type is now restricted to relict patches on south-facing slopes of mountains in both Eastern and Western Beringia. The vegetation included a wide variety of herbs and dwarf shrubs. The herbs included tufted grasses, sedges, and tufted sedges. The tufted grasses included several species of fescue ( <i>Festuca</i> ), grasses, including <i>Poa botryoides</i> , <i>P. stepposa</i> , <i>P. arctosteporum</i> , <i>P. glauca</i> , <i>Calamagrostis purpurascens</i> , and <i>Helictotrichon krylovii</i> , <i>Koeleria cristata</i> and <i>K. asiatica</i> , and wheatgrasses ( <i>Elytrigia</i> ). The sedges included true steppe species, such as <i>Carex duriuscula</i> , meadow-steppe species such as <i>C. obtusata</i> and <i>C. rupestris</i> , and tufted sedges, such as <i>Carex pediformis</i> , <i>C. filifolia</i> , <i>C. rossii</i> , and <i>C. aenea</i> (Yurtsev, 2001). |
| Tussock tundra        | Tundra vegetation growing in the form of tussocks, compact mounds of grasses or sedges, held together by root masses, growing in mesic to moist environments.  |
| Wet herbaceous tundra | Tundra dominated by moisture-tolerant sedges and grasses, often with standing pools of shallow water. On the Alaskan North Slope, wet herbaceous tundra is dominated by sedge communities with <i>Carex aquatilis</i> and <i>Eriophorum angustifolium</i> . Grass communities are generally dominated by <i>Dupontia fischeri</i> and <i>Alopecurus alpinus</i> , but <i>Arctophila fulva</i> dominates where surface water is 15–200 cm deep (Gallant et al., 1995).  |

from sediment cores and exposures in western Alaska. The first of these efforts was by Paul Colinvaux (1964), who cored sediments from Imuruk Lake on Seward Peninsula (Fig. 2, No. 1). He concluded that the BLB must have been covered in 'cold Arctic tundra' during glacial intervals. The Imuruk lake site is more than 300 m above sea level, and Colinvaux conceded that even though his full glacial-age pollen spectra were dominated by grasses, the BLB itself might have had a slightly less severe climate, and therefore might have supported tussock tundra vegetation.

In 1967 Colinvaux cored a lake on St Lawrence Island, a former highland region in the middle of the BLB. He reckoned that the study site, Flora Lake (Fig. 2, No. 2), would have been about 100 m above the surrounding plains of the BLB during the Last Glaciation. He interpreted the pollen spectra from last-glacial sediments as representing cold arctic tundra, dominated by grasses and sedges. He went on to say that "there was probably much bare ground, and dwarf birches (*Betula nana*) were scarce".

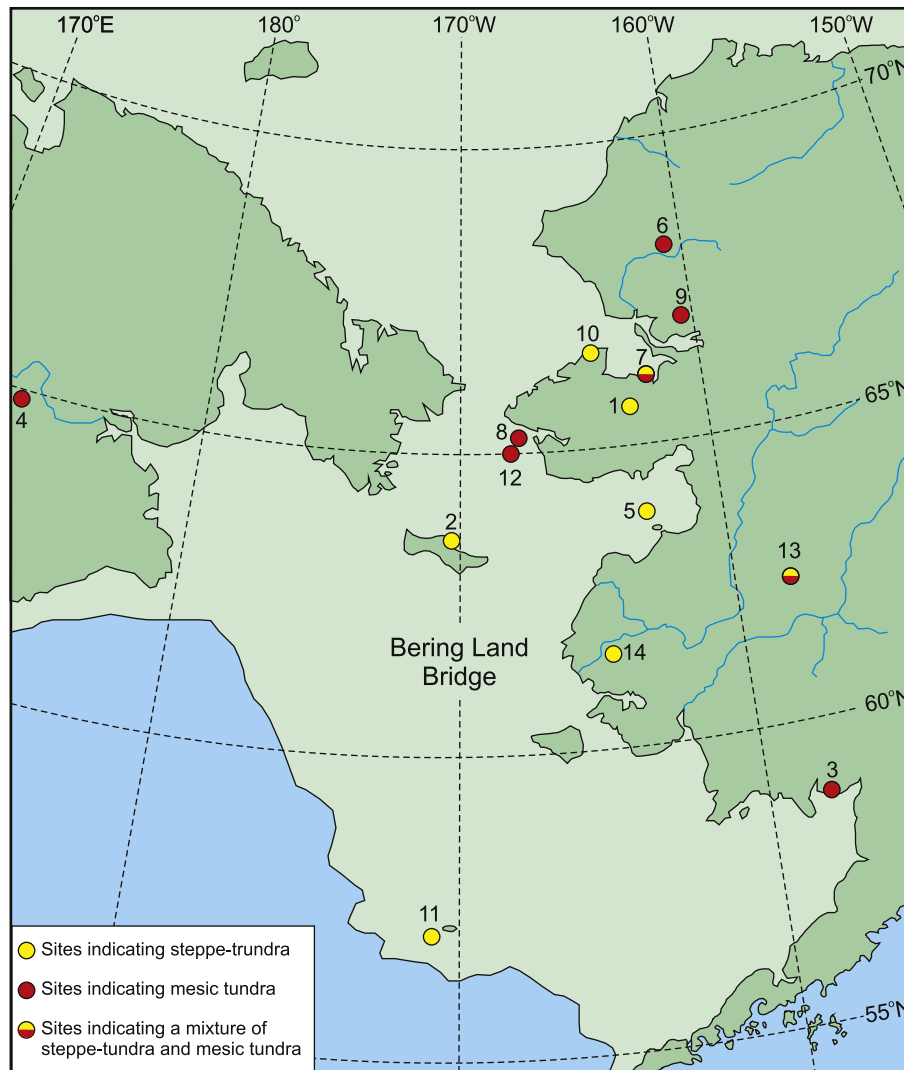
In 1974 Matthews published an extensive study of pollen, plant macrofossils and insect fossils from a suite of organic deposits exposed at Cape Deceit on the northeast coast of the Seward Peninsula (Fig. 2, No. 7). One sample, S-1, dates to the LGM interval (ca 21,500 cal yr BP). This sample is an intriguing mixture of mesic tundra beetles and steppe-tundra plant remains. The beetle assemblage contains five species in the *Cryobius* group of *Pterostichus*. All of these species are associated with mesic tundra today. The other abundantly preserved species in this assemblage include two highly cold-tolerant species: the ground beetle *Amara alpina*

(MNI = 37) and the rove beetle *Micralymma brevilingue* (MNI = 89). *Amara alpina* is the most northerly distributed ground beetle today, ranging north to the Canadian Arctic archipelago and Greenland. Lindroth (1968) describes it as an insect of "open, rather dry country, notably on the true tundra". While this generalization is accurate, Elias has certainly collected numerous specimens of *A. alpina* in mesic tundra habitats, both in Arctic Alaska and in the alpine tundra of the Rocky Mountains. *Micralymma brevilingue* is a rove beetle most often associated with coastal habitats. It is often found today under stones on beaches, close to the high water mark. However, it has also been found well away from the shore, for instance under moss-covered rocks, in snow beds, and shaded gorges in Greenland. Böcher (1988) described its habitat as "both the upper tidal zone and in damp situations in different plant communities further inland". It has been found as a fossil in numerous sites well away from ancient shorelines in Eastern Beringia. However, it can survive in extreme environments, such as the polar desert regions of Severnaya Zemlya in arctic Siberia. Here it has been collected throughout the archipelago of islands. Makarova et al. (2007) concluded that this tiny rove beetle "should be considered as the most cold-tolerant beetle species of the Northern Hemisphere". Another highly cold-adapted beetle was identified from this assemblage, the leaf beetle *Chrysolina sub-sulcata*. This is an Arctic species that ranges north to the polar desert regions of Siberia today. It was a common member of Siberian steppe-tundra faunas in the Pleistocene (Kuzmina et al., 2008).

Interestingly, no specimens of the typical steppe-tundra pill beetles *Byrrhus* or *Morychus* were found in sample S-1 from Cape Deceit. Only four specimens of the characteristic steppe-tundra weevil *Lepidophorus lineaticollis* were recovered. Although the steppe-tundra 'signal' is relatively weak in the Cape Deceit LGM beetle fauna, the palaeobotanical record from this sample gives clear indications of herbaceous vegetation. Matthews (1974) noted the abundance of macrofossils of *Potentilla* and Cruciferae. Based on various lines of evidence, Matthews considered that the LGM soils at Cape Deceit were not acidic, as are found in most tundra regions today. Rather, they had the higher pH levels associated with modern grassland and steppe soils. He reconstructed the LGM vegetation cover at the site as "grassy tundra with shrub birches".

In 1981 Colinvaux published the results of another study attempting to reconstruct the vegetation cover of the BLB during the Last Glaciation. This time he took a sediment core from a lake on St Paul Island, near the southern edge of the BLB region (Fig. 2, No. 11). His interpretation of the pollen spectra from the last glacial interval was that the southern sector of the BLB was covered by herb tundra without trees or shrubs. Dwarf birch was "at best a rare plant and may have been completely absent". Likewise Colinvaux considered that tussock vegetation was lacking from this region. Colinvaux does not provide the elevation of the lake from which the sediment core was taken, but he mentions that the modern island would have been a hill that was 150–300 m above the BLB plain during intervals of lowered sea level.

Anderson (1985) described herb tundra from LGM lake sediments in northwest Alaska. The Squirrel Lake site is in the Kallarichuk Hills region, northeast of the Baldwin Peninsula (Fig. 2, No. 9). Kaiyak Lake is in the Kugoruk River valley of the Baird Mountains (Fig. 2, No. 6). While neither of these sites is near enough to the BLB to shed much light on land bridge environments, they do provide evidence concerning LGM environments in western Alaska. Both sites yielded pollen spectra from the LGM interval (Table 1); these pollen assemblages are dominated by grasses and sedges. Poaceae pollen percentage values range from about 20–50% through the LGM at Kaiyak Lake; Cyperaceae pollen percentages range from about 10–35%; there is also about 20% sage, and 10% birch and willow pollen in most LGM spectra. Anderson (1985) interpreted



**Fig. 2.** Map showing fossil sites discussed in text, and the approximate margin of the Bering Land Bridge during the Last Glacial Maximum. 1, Imuruk Lake; 2, Flora Lake, St Lawrence Island; 3, Flounder Flat; 4, Chukotka site ChM-B21; 5, Zagoskin Lake, St Michael Island; 6, Kaiyak Lake; 7, Cape Deceit; 8, Bering Sea shelf core 78-15; 9, Squirrel Lake; 10, Cape Espenberg; 11, Cagaloq Lake, St Paul Island; 12, Bering Sea shelf core 76-101; 13, Colorado Creek; 14, Tungak Lake.

the LGM vegetation cover of this valley as meadow-like tundra with dwarf birch forming a local shrub component in the vegetation.

Elias led a research team that analysed pollen, plant macrofossils, and insect fossils from a series of sediment cores taken from the Bering and Chukchi shelves by the U.S. Geologic Survey in the 1970s. The cores contained sediments associated with the lowland surfaces of the BLB, and our team focussed on sampling organic-rich sediments, in order to maximize the recovery of plant macrofossils and insects. We obtained organic sediments from 20 cores, but only a few sampling horizons yielded  $^{14}\text{C}$  ages associated with the LGM. These included samples from the Bering shelf region off the coast of the Seward Peninsula, near Port Clarence (Fig. 2, Nos. 8 and 12). The team's LGM-age samples were dated  $20,725 \pm 165$  yr BP and  $16,540 \pm 200$  yr BP. It could be argued that the latter of these post-dated the full glacial interval, but most studies in Alaska have shown that regional climates did not begin to warm significantly until about 13,000 yr BP (Elias, 2001). Ager (2003) drew the boundary between LGM and Lateglacial pollen zones at about 14,500  $^{14}\text{C}$  yr BP for the BLB region.

This study of Bering shelf sediments yielded different results than what Colinvaux and others predicted would be found on the lowland surfaces of the land bridge. Instead of evidence for dry, herb-dominated tundra, we found evidence for mesic shrub tundra,

such as is found today in Arctic Alaska. All three lines of evidence (pollen, plant macrofossils and insects) indicate shrub tundra. It might be possible to explain away the plant macrofossil and insect evidence for mesic habitats, as our samples undoubtedly represent local wetland localities, where organic detritus accumulated. However, the pollen spectra from our samples also indicate mesic tundra, and the pollen rain certainly represents regional vegetation, not just local environments. These pollen samples contain about 20% birch pollen, 10% Ericales, 15% willow, and 40% grasses (Poaceae) (Elias et al., 1997). There is only about 1% *Artemisia* pollen in these samples. This is the signature of mesic shrub tundra, not of steppe-tundra.

In 2001, Goetcheus and Birks published the results of their study of plant macrofossils from the LGM at a site on Cape Espenberg, on the north coast of the Seward Peninsula (Fig. 2, No. 10). This region was buried by tephra from a volcanic eruption that has been radiocarbon dated at 18,000 yr BP (Table 1). The site is a geological Pompeii, with plant and invertebrate life extinguished by the tephra, then frozen and preserved *in situ* by the permafrost until its discovery by David Hopkins in 1968 (discussed in Hopkins, 1988). Goetcheus and Birks were able to recover patches of vegetation from the former land surface, thereby documenting the regional vegetation cover in a way that is essentially unique to this region.

They found that the vegetation cover was dominated by *Kobresia myosuroides*, a dry-adapted sedge that grows today on dry mountain slopes and lichen tundra in Alaska (Hultén, 1968). There were a few remains of dwarf willow, but no other dwarf shrub remains were found. The mosses and herbs that made up most of the flora are all dry-adapted species that do best on calcareous soils. There was a second set of plant species identified from their samples: plants with high moisture requirements that most likely represent snow-bank communities or wet hollows. These included arctic willow (*Salix arctica*), mock wallflower (*Eutrema edwardsii*), and alpine mountain sorrel (*Oxyria digyna*). Under glacial-stage climates, the regular deposition of calcareous loess is interpreted by the authors to have been an important source of calcium in regional soils. The calcium-enriched soils played an important role in determining the composition of plant species in the regional vegetation (Goetcheus and Birks, 2001).

Kuzmina et al. (2008) have described fossil insect assemblages collected from the 18k buried surface at Cape Espenberg. The insect fossil assemblages from these samples are dominated by beetle species associated with steppe–tundra environments, such as the weevils *Lepidophorus lineaticollis* and *Coniocleonus*, and the pill beetle *Morychus*. The palaeoenvironmental reconstruction from these fossil assemblages is in close agreement with the plant macrofossil interpretation: steppe–tundra vegetation growing in cold, dry environments.

While the reconstruction of cold, dry environments at Cape Espenberg matches the evidence from the LGM sample at Cape Deceit (Matthews, 1974), the two beetle faunas are very different. The Cape Deceit (S-1) fauna is dominated by mesic tundra species and contains very few steppe–tundra indicators. The Cape

Espenberg faunas are just the opposite: dominated by steppe–tundra species with a much small mesic tundra component. Yet both sites are at essentially the same latitude on the modern north coast of the Seward Peninsula. While the Cape Espenberg flora is dominated by *Kobresia*, Matthews (1974) did not find any *Kobresia* plant remains in his LGM sample.

Ager (2003) set out to test the reconstructions of BLB vegetation of Elias et al. (1996, 1997) by analysing the pollen from a sediment core taken from St Michael Island, in the southern Norton Sound region of the Bering Sea (Fig. 2, No. 5). The core was taken from Zagoskin Lake, situated 7 m above modern sea level. St Michael Island, like St Paul Island and St Lawrence Island in the Bering Sea, would have constituted a highland region, perched above the plains of the BLB. The core yielded fossil pollen spanning the LGM interval, with radiocarbon dates from about 26,000–15,000 yr BP (Table 2). The LGM pollen assemblages were dominated by grasses and sage (*Artemisia*). Ager (2003) interpreted the LGM vegetation as “grassy herbaceous tundra”. He went on to conclude that this kind of vegetation probably dominated the BLB, and that mesic shrub tundra was “largely restricted to stream banks, ponds, lakeshores, and sites that trapped windblown snow”. He rejected the arguments made by Dale Guthrie (2001) that the BLB contained a broad belt of mesic tundra vegetation that served as an ecological filter, preventing some megafaunal species from crossing the land bridge.

Additional evidence for herbaceous tundra comes from LGM pollen assemblages from Tungak Lake, near the Yukon River delta in southwestern Alaska (Fig. 2, No. 14). Ager (1982) described an herb zone in the basal section of a lake core. The upper boundary of this zone was radiocarbon dated at  $14,230 \pm 350$  yr BP. The pollen spectra in this zone are dominated by Gramineae (15–30%) and

**Table 2**

Summary of radiocarbon ages and palaeoenvironmental reconstructions for fossil sites discussed in text

| Site                                    | <sup>14</sup> C age (yr BP)  | Fossil evidence   | Vegetation reconstruction  | Reference                               |
|---|------------------------------|---|--|---|
| 1 Imuruk Lake, central Seward Peninsula | LGM—undated                  | Pollen dominated by grasses and sedges, with sage and birch   | Herb tundra vegetation with minor birch shrub component  | Colinvaux, 1964                         |
| 2 Flora Lake, St Lawrence Island        | LGM—undated                  | Pollen dominated by grasses and sedges  | Cold arctic tundra dominated by grasses and sedges   | Colinvaux, 1967                         |
| 3 Flounder Flat, Bristol Bay            | LGM—undated                  | Mesic tundra beetles, no steppe–tundra species present  | Cold mesic tundra environments   | Elias, 1992b                            |
| 4 Chukotka ChM-B21                      | LGM—undated                  | Arctic tundra beetles, aquatic and riparian beetles, no steppe–tundra species   | Cold, mesic tundra   | Kuzmina et al., 2008                    |
| 5 St Michael Island                     | 25,690 ± 420 to 14,970 ± 170 | Pollen dominated by grasses and sage; mesic plant pollen only a minor component   | Herb tundra  | Ager, 2003                              |
| 6 Kaiyak Lake, Baird Mountains          | 21,690 ± 330 to 14,300 ± 140 | Pollen dominated by grasses and sedges with sage, birch and willow  | Meadow-like tundra   | Anderson, 1985                          |
| 7 Cape Deceit Sample S-1                | ca 21,500                    | Mesic tundra beetles; steppe–tundra beetles a minor component; plant macrofossils indicate calcareous soils             | Grassy tundra with shrub birches   | Matthews, 1974                          |
| 8 Bering Sea shelf off Port Clarence    | 20,725 ± 165                 | Mesic tundra beetles; pollen dominated by grasses, birch, sedge, <i>Sphagnum</i> spores                                 | Birch–graminoid tundra with small ponds choked with aquatic plants; no evidence of steppe–tundra vegetation or insects | Elias et al., 1996, 1997                |
| 9 Squirrel Lake, north of Kotzebue      | 20,300 ± 380 to 17,360 ± 200 | Pollen dominated by grasses and sedges with sage, birch and willow  | Meadow-like tundra   | Anderson, 1985                          |
| 10 Cape Espenberg                       | 18,070 ± 60                  | Plant macrofossils dominated by <i>Kobresia</i> , other sedges, and occasional dwarf willow; steppe–tundra beetle fauna | Herb-rich tundra grassland with a continuous moss layer  | Goetcheus and Birks, 2001               |
| 11 Cagaloq Lake, St Paul Island         | 17,800 ± 700                 | Pollen dominated by grasses, sedges, and sage   | Herb tundra  | Colinvaux, 1981                         |
| 12 Bering Sea shelf off Port Clarence   | 16,540 ± 200                 | Pollen dominated by grasses, birch, sedge, <i>Sphagnum</i> spores   | Birch–graminoid tundra with small ponds choked with aquatic plants; no evidence of steppe–tundra                       | Elias et al., 1996a,b                   |
| 13 Colorado Creek                       | 16,150 ± 230                 | Mixture of mesic tundra and steppe–tundra beetles   | Mosaic of steppe–tundra and mesic tundra habitats  | Elias, 1992a; Thorson and Guthrie, 1992 |
| 14 Tungak Lake                          | >14,230 ± 350                | Pollen dominated by Cyperaceae and Poaceae, willow and sage, smaller amounts of Ericaceae and birch pollen              | Herb tundra with some mesic to wet habitats locally  | Ager, 1982                              |

Cyperaceae (10–40%), *Salix* (2–10%) and *Artemisia* (5–20%). While Ager interpreted the dominant vegetation cover of the site as “herb-dominated tundra”, he noted that the presence of Ericaceae and birch (probably dwarf-birch) pollen in the samples meant that mesic to wet habitats persisted there during the LGM.

At Colorado Creek in west-central Alaska (Fig. 2, No. 13), fossil insect assemblages associated with woolly mammoth remains have been dated at  $16,150 \pm 230$  yr BP (Elias, 1992a; Thorson and Guthrie, 1992). Because of its interior continental locality, this fossil locality bears no relation to BLB environments, but it sheds light on LGM environments in western Alaska. The small fossil insect fauna identified from this site (Table 3) is an intriguing mixture of steppe-tundra and mesic tundra beetle taxa. The steppe-tundra elements include the pill beetle *Morychus* and the weevil *Lepidophorus lineaticollis*. However, there is a strong mesic-tundra component in this fauna, including the ground beetles *Pterostichus brevicornis* and *P. caribou*, and the rove beetles *Holoboreaphilus nordenskiöldi*, *Micralymma brevilingue*, and *Tachinus brevipennis*. All of these ground beetle and rove beetle species are found today in mesic tundra habitats on the Alaskan North Slope. The dung beetle *Aphodius congregatus* was found in association with a mammoth dung bolus. This species is found today in the highlands of the Pacific Northwest, and at lower elevations farther north in Alaska (R. Gordon, personal communication cited in Bain et al., 1997). The carrion beetle *Thanatophilus coloradensis* is known today from alpine tundra regions in the Rocky Mountains, northern British Columbia, and central Alaska (Anderson and Peck, 1985). This beetle was probably feeding on mammoth remains at Colorado Creek. Elias has collected modern specimens that were feeding on

carrion in *Kobresia* meadows in the alpine tundra of northern Colorado.

The Colorado Creek fauna thus presents almost an equally balanced combination of steppe-tundra and mesic tundra insects—a mixture unique among Beringian fossil insect assemblages. The steppe-tundra beetles may well have lived on upland surfaces surrounding the gully containing the mammoth carcasses. The mesic tundra beetles may have lived along a moist stream bank or adjacent to perennial snow banks in the gully. The mixed palaeoenvironmental signal from Colorado Creek is in some ways similar to the ‘mixed’ signal obtained from the LGM sample from Cape Deceit (Matthews, 1974). The former site has a mixture of steppe-tundra and mesic tundra beetles, while the latter site has predominantly mesic tundra beetles, combined with botanical indicators for grass-dominated vegetation. The ‘mixed signal’ quality of these two sites is indicated in Fig. 2 by showing them with circles filled half with black and half with white.

At Flounder Flat in the Nushagak Lowland region (Fig. 2, No. 3) of southwestern Alaska, LGM beetle assemblages contained only mesic tundra taxa. No steppe-tundra beetles were found at this site during the LGM (Elias, 1992b). Faunal diversity declined in this region during the LGM, but the species that persisted through the glacial interval, such as the rove beetle *Tachinus brevipennis* and several species of ground beetles in the *Cryobius* group of the genus *Pterostichus*, are associated with cold mesic tundra habitats today. Elias (1992b) went as far as proposing that southwest Alaska had served as a refugium for mesic and hygrophilous insects during the Late Pleistocene.

The study of LGM environments near the eastern edge of Western Beringia (i.e., on Chukotka and further south along the Siberian coast of the Bering Sea) has only recently begun. Kuzmina et al. (2008) reported briefly on an LGM beetle fauna from a site on the Main River (Fig. 2, No. 4). The sediments sampled from this site are ice-rich sandy silts called ‘Yedoma’ by Russian researchers. The exact origins of Yedoma deposits remain unknown, but in this case the organic silts are thought to represent a flood plain deposit (Svetlana Kuzmina, written communication, August 2008). The fauna is dominated by beetle taxa found today in arctic tundra regions of northeast Asia. There are also substantial numbers of aquatic and riparian species. The fauna contains few species associated with dry tundra environments, and no steppe indicators, in spite of the fact that steppe-tundra taxa are dominant in assemblages from other time intervals at this site. The authors interpreted the LGM environment of the site to be cold mesic tundra. Ironically, it may have been too cold in this region during the LGM to support the Western Beringian steppe-tundra insect fauna. As discussed below, during warmer intervals of the Pleistocene, steppe-associated beetle species from southern Siberia were able to invade northeastern Siberia. Many of these relatively warm-adapted steppe species must have died out during glacial intervals. Alfimov and Berman (2001) examined the thermal requirements of the species that composed the Pleistocene steppe beetle fauna in northeastern Asia, and determined that these species require mean summer temperature (TMAX) values of at least 10–11 °C, even when they live in extremely continental climate where winter temperatures are very low. If TMAX values in some regions of Beringia were only 7–9 °C during the Late Wisconsin interval (Elias, 2001), this may have favoured the development of mesic tundra insect communities at the expense of steppe-adapted species (Elias et al., 2000).

## 2.2. Biogeographic evidence

The modern distribution patterns of plants, insects, and vertebrates have all been used by biogeographers to reconstruct environmental conditions on the BLB during the Late Pleistocene.

**Table 3**  
Fossil insects identified from the Colorado Creek site, Alaska

| Taxon                                      | Sample                        | Habitat |
|--|-------------------------------|---------|
| <b>DIPTERA</b>                             |                               |         |
| CALLIPHORIDAE (Blow flies)                 |                               |         |
| Genus indet.                               | Mammoth bone (nasal cavities) | N/A     |
| <b>HOMOPTERA</b>                           |                               |         |
| CICADELLIDAE (Leaf hoppers)                |                               |         |
| Genus indet.                               | Hair horizon                  | S-T     |
| <b>HYMENOPTERA</b>                         |                               |         |
| CHALCIDOIDEA (Chalcid Wasps)               |                               |         |
| Genera indet.                              | Hair horizon                  | N/A     |
| <b>COLEOPTERA</b>                          |                               |         |
| CARABIDAE (Ground beetles)                 |                               |         |
| <i>Carabus</i> sp.                         | Hair horizon                  | N/A     |
| <i>Pterostichus brevicornis</i> Kby.       | Hair horizon                  | MT      |
| <i>Pterostichus caribou</i> Ball           | ‘Mammoth Site’                | MT      |
| <i>Pterostichus (Cryobius)</i> sp.         | Hair horizon                  | MT      |
| STAPHYLINIDAE (Rove beetles)               |                               |         |
| <i>Holoboreaphilus nordenskiöldi</i> Mäkl. | Hair horizon                  | MT      |
| <i>Micralymma brevilingue</i> Schiodt      | Hair horizon                  | MT      |
| <i>Lathrobium</i> sp.                      | Hair horizon                  | MT      |
| <i>Tachinus brevipennis</i> Sahlb.         | Hair horizon                  | MT      |
| <i>Aleocharinae</i> gen. et sp. indet.     | Hair horizon                  | MT      |
| SILPHIDAE (Carrion beetles)                |                               |         |
| <i>Thanatophilus coloradensis</i> (Wickh.) | Hair horizon, ‘Mammoth Site’  | AT      |
| SCARABAEIDAE (Dung beetles, chafers)       |                               |         |
| <i>Aphodius congregatus</i> Mannh.         | Dung bolus, Hair horizon      | MT      |
| BYRRHIDAE (Pill beetles)                   |                               |         |
| <i>Morychus</i> sp.                        | Hair horizon                  | S-T     |
| CHRYSOMELIDAE (Leaf beetles)               |                               |         |
| <i>Chrysolina</i> sp.                      | Hair horizon, ‘Mammoth Site’  | S-T?    |
| Chrysomelidae gen. et sp. indet.           | ‘Mammoth Site’                |         |
| CURCULIONIDAE (Weevils)                    |                               |         |
| <i>Lepidophorus lineaticollis</i> Kby.     | Hair horizon, ‘Mammoth Site’  | S-T     |

Habitat abbreviations: AT, alpine tundra; MT, mesic tundra; S-T, steppe-tundra; N/A, habitat not defined at the generic level.

Yurtsev (2001) noted that even though the BLB may have functioned as a filter for the migrations of cold- and dry-adapted steppe and montane plants, more than 40 dry-adapted plant species that presently occur on both sides of the Bering Strait managed to cross over the BLB during the Pleistocene. Among these are the dry-adapted sedges, *Kobresia myosuroides* and *Carex rupestris*. Yurtsev (2001) considers these to have been of Central-Asian origin. Today, the vegetation cover of the alpine tundra zones in both northern Mongolia (Miehe, 1996) and the easternmost Rocky Mountains is dominated by *Kobresia myosuroides* (Cooper and Sanderson, 1997). It also occurs on dry, calcareous slopes up to 1800 m elevation in Alaska (Hultén, 1968).

If the BLB served as a mesic 'filter' that slowed or stopped the migration of dry-adapted insect species, it was a leaky filter, at best. It apparently prevented some species from spreading between the continents, but not others. Several groups of steppe–tundra beetles have distributional patterns limited to either the western or eastern side of Bering Strait. Among these are some cold-adapted leaf beetles (Chrysomelidae), including *Chrysolina arctica* and *C. brunnicornis wrangeliana*. Both of these leaf beetles are found only west of Bering Strait, both today and in the Pleistocene fossil record (Elias and Kuzmina, 2008). Today they are limited to patches of relict steppe habitat in northeastern Siberia, such as on Wrangel Island (Lozhkin et al., 2001). Table 4 shows other species of leaf beetles found either on both sides of Bering Strait today, or isolated on only one side. The Siberian steppe-associated fauna includes *Galeruca interrupta*, *Hydrothassa hannoveriana*, *Phaedon concinnus*, and two species of *Phratora* (Fig. 3). The only steppe-associated leaf beetle species common to both sides of the Bering Strait is *Phaedon armoraciae* (Fig. 3). The Western Beringian beetle faunas were richer in steppe-associated species than were the Eastern Beringian faunas. Elias and Kuzmina (2008) point out that the steppe–tundra fauna played a dominant role in Western Beringian Pleistocene assemblages, even through interglacial intervals. In contrast to the situation in most of arctic North America, most of northeast Asia's lowlands were free from ice cover during Pleistocene glaciations, allowing unbroken biotic communication between southern and northern Siberia. This, in turn, allowed northern Siberia to be repeatedly invaded by southern steppe species during warm intervals.

There are relict patches of steppe-like habitats on both sides of the Bering Strait today. The modern insect fauna of relict steppe patches in the mountains of the Yukon Territory has been studied by Berman et al. (2001). They found that some species of steppe weevils (family Curculionidae) have managed to survive in these relict patches, such as *Coniocleonus zherichini*. This is a cold-adapted weevil that is mainly found today only in relict steppe localities of northeast Siberia, along the upper Yana and Indigirka river basins. It has also survived in relict steppe environments on south facing slopes of mountains in the Yukon (Fig. 4). Other typical steppe weevils from northeast Siberia, such as *Hypera ornata* and all members of the genus *Stephanocleonus* are absent from North America. These weevils, including *Coniocleonus*, dominated steppe–tundra faunas of Western Beringia during the Pleistocene, but failed

to become established east of the BLB. So some Asian steppe weevils made it across the BLB, while others did not.

The same phenomenon can be observed in the steppe-adapted weevil fauna of Eastern Beringia. The North American weevil *Vitavitus thulius*, a typical steppe–tundra beetle in Eastern Beringia, became established in the Kolyma Lowland and Anadyr River basin of Western Beringia during the Pleistocene, but is not found in Asia today (Fig. 4). Berman et al. (2001) note that this weevil has managed to disperse into formerly glaciated regions of northern Canada in postglacial times, and that it is associated with dry mountain tundra slopes and steppes of the Yukon, although it has not ventured into similar habitats in Alaska during the Holocene, even though it was present there during the Pleistocene. Much of the interior and northern Yukon regions today are quite dry. A total of 19 out of 30 meteorological stations in the Yukon record less than 350 mm of annual precipitation (Environment Canada, 1982), and the average mean annual precipitation (MAP) of these stations is 268 mm. The remaining sites are either situated in mountainous regions, or near the southern boundary, where they are closer to sources of Pacific moisture. However, the same could be said for the interior lowland regions of Alaska, where the MAP for 11 stations is 291 mm (NOAA, 2002).

Other predominantly Eastern Beringian weevils, such as *Lepidophorus lineaticollis*, which dominates many steppe–tundra beetle assemblages from this region, managed to establish a 'beach head' in the easternmost regions of Western Beringia (i.e., coastal Chukotka), but never made it any farther west in Asia (Fig. 4).

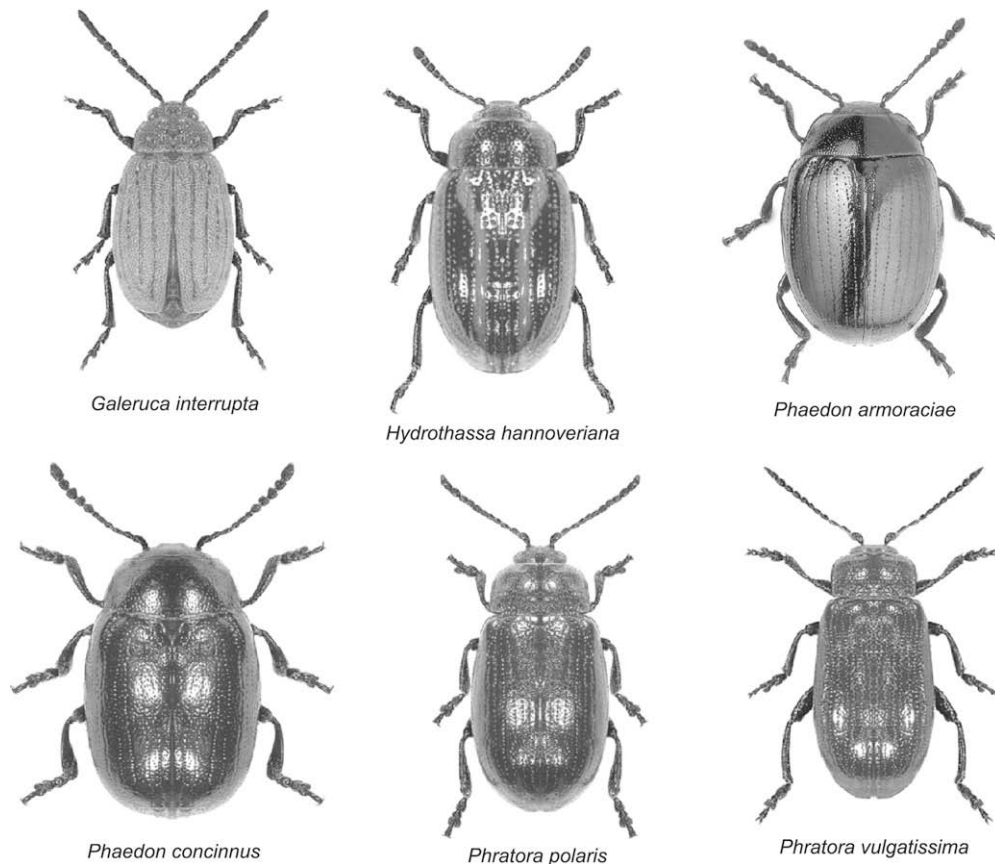
### 2.3. The dispersal of the woolly rhinoceros

The Pleistocene woolly rhinoceros (*Coelodonta antiquitatis* Blumenbach, 1799) was a cold-adapted rhinoceros first known from the Wucheng Formation of northern China 2.5 Mya (Deng, 2008). From here, it migrated northwest across the Palaeartic, reaching western Europe by MIS 12 (Bad Frankenhausen, Germany; Kahlke and Lacomat, 2007). The extent of the woolly rhinoceros' range waxed and waned with the glacial-temperate episodes that characterized the Pleistocene, with its greatest distributions corresponding to the glacial episodes of the late Pleistocene. Perhaps strangely, given the origins of the woolly rhinoceros in northern China and Transbaikalia, woolly rhinoceros is only known from northeastern Siberia during the Last Glaciation (Valdai). The woolly rhinoceros appears to have been relatively unhindered in moving west across the Palaeartic during the Pleistocene, but some form of barrier prevented colonization of northeastern Siberia until the Last Glaciation. In addition to this delay, the woolly rhinoceros also appears to have been prevented from crossing the BLB and colonizing Eastern Beringia at all. It would appear that despite finally colonizing Western Beringia, and being in a position to cross the BLB and migrate onto the North American landmass, a filter restricted the distribution of this taxon to Western Beringia.

The work of Kahlke (1999) shows the distribution of the woolly rhinoceros at the Last Glaciation to be widespread across the Palaeartic region, but never conquering the Scandinavian region or North America. More recently, finds have been recorded from Chukotka, Kamchatka and Wrangel Island in northeastern Siberia (Tikhonov et al., 1999; Boeskorov, 2001). These eastern populations put the woolly rhinoceros on the doorstep of the BLB, yet still it failed to cross despite other members of the same faunal assemblage (*Mammuthus–Coelodonta* faunal complex; Kahlke, 1999) being successful. Chief among these taxa are the previously mentioned woolly mammoth and Pleistocene horses. Proboscideans had their origins firmly in the Old World, yet migrated into the New World via the BLB approximately 1.8 Ma BP (as *Archidiskodon meridionalis*). A second pulse of mammoth migration pushed *Mammuthus primigenius* (woolly mammoth) into North America

**Table 4**  
Comparative species of Western and Eastern Beringian leaf beetles (after Elias and Kuzmina, 2008)

| Western Beringia                              | Eastern Beringia                         |
|---|--|
| <i>Chrysolina arctica</i> Medv.               | <i>Chrysolina basilaris</i> (Say)        |
| <i>Chrysolina brunnicornis wrangelia</i> Vor. |  |
| <i>Chrysolina septentrionalis</i> (Men.)      | <i>Chrysolina septentrionalis</i> (Men.) |
| <i>Phratora vulgatissima</i> L.               | <i>Phratora hudsonia</i> Brown           |
| <i>Phratora polaris</i> Schn.                 |  |
| <i>Phaedon armoraciae</i> L.                  | <i>Phaedon armoraciae</i> L.             |
| <i>Phaedon concinnus</i> Steph.               | <i>Phaedon cyanescens</i> Stal.          |
| <i>Hydrothassa hannoverana</i> F.             | <i>Hydrothassa boreala</i> Sch.          |



**Fig. 3.** Light microscope photographs of leaf beetles (Chrysomelidae) associated with relict steppe habitats in northeast Siberia, Alaska and the Yukon Territory. Photos of *Galeruca interrupta*, *Hydrothassa hannoveriana*, *Phaedon concinnus*, *Phratora polaris* and *Phratora vulgatissima* courtesy of Dr Lech Borowiec, University of Wroclaw, Poland. Photo of *Phaedon armoraciae* courtesy of K. Makarov, Zoological Institute, Russian Academy of Sciences, St Petersburg.

long before the LGM. The bison (*Bison priscus*), another taxon with a broadly similar feeding preference to *Coelodonta*, managed to cross from Asia to Eastern Beringia before the LGM, sometime between MIS 8 and 6 (Shapiro et al., 2004).

Despite originating in northern China and subsequently spreading westwards through Eurasia, the woolly rhinoceros is not known from eastern Siberia before the last glacial episode (Valdai, Weichselian, Devensian). The precise nature of the barrier that prevented the entrance of *Coelodonta* into eastern Siberia prior to MIS 3 is uncertain. There was no extensive land ice in this region during the late Pleistocene (Brigham-Grette, 2001) but the Barents–Kara ice sheet extended as far east as the western margin of the Taymyr peninsula and south onto the Siberian landmass (Hubberten et al., 2004). The woolly rhinoceros was still present in China during the late Pleistocene (Deng, 2006), so if this moderate glaciation present in Taymyr offered any impediment to the eastward spread of European *Coelodonta* populations, there was no similar barrier to the Chinese populations aside from the Altai and Baikal mountains around Lake Baikal. The variability of the climate in this region was possibly a contributory factor, with full arid, glacial conditions reached only during the LGM (Hubberten et al., 2004).

There has been much debate centred around whether variation in vegetation across the BLB, caused by changes in micro-climate (Elias et al., 1997; Guthrie, 2001) together with frequent waterlogged ground, was a sufficient barrier to prevent the woolly rhinoceros from crossing the BLB. The extent of the mesic shrub tundra across the BLB is unknown, a factor largely attributed to incomplete sampling (Elias et al., 1997). The Last Glaciation was the first, and only, opportunity for *Coelodonta* to cross into the New World from Western Beringia, whereas the other components of

the *Mammuthus–Coelodonta* faunal complex had done so much earlier. Taking all the above into consideration leads to a supposition that the woolly rhinoceros arrived in Chukotka too late to take advantage of conditions that made crossing the BLB possible for the other (earlier) taxa. A similar scenario is proposed for the failure of the woolly rhinoceros to colonize Scandinavia, despite the woolly mammoth having already done so. Arriving when it did (>49,000 BP; Boeskorov, 2001), the woolly rhinoceros encountered more mesic and waterlogged conditions. These are the conditions that the woolly rhinoceros would have tried to avoid because of its long coat and gait that were better suited for firmer, flatter ground. The more mesic conditions would have had a corresponding effect on the dominant vegetation, which was unsuited to the derived feeding characteristics of the grazing woolly rhinoceros. The woolly rhinoceros would probably have avoided both deep snow and sodden ground in the same way as the Pleistocene musk ox (*Ovibos moschatus*) would have done (Kahlke, 1999) as their wool would have ceased to have been an effective insulator against the cold if wet and waterlogged. It is interesting to note therefore that the helmeted musk ox (*Bootherium*) had a similar pelage, stance and gait to that of the woolly rhinoceros and it also failed to cross the BLB. *Bootherium* is known from the Eastern Beringian region both before and after the last glacial maximum (Mead and Meltzer, 1984; Guthrie, 2001) but did not manage to cross the BLB to the Old World from America. It is likely that the same barrier of waterlogged ground prevented *Bootherium* from crossing the BLB in the same manner as prevented *Coelodonta*.

In summary, it is likely that *Coelodonta* arrived too late in northeastern Siberia to cross the BLB into the Americas. Restricted from entering the Beringian region prior to MIS 3, by the time the





Fig. 4. Map of the Arctic, showing the known modern distributions of three species of weevils (Curculionidae) associated with steppe-tundra environments in the Pleistocene. Data from Berman et al., 2001.

woolly rhinoceros finally arrived in Western Beringia the conditions on the bridge itself had worsened to such an extent as to make it broadly impassable for the woolly rhinoceros. These mesic conditions on the bridge would have made the ground too uneven and too wet for the stocky and woolly *Coelodonta* to cross.

### 3. Discussion

In attempting to reconstruct the glacial environments of the BLB, we are up against several thorny problems. The different lines of evidence (vertebrates, insects, plant macrofossils, and pollen; modern biogeographic patterns versus fossil data) do not always agree. In many ways we are like the committee of blind scientists, asked to describe an elephant. Each researcher gropes along one body part, and assumes that the whole beast is represented by that one part (the small tail, the massive legs, the long, flexible trunk, or the hard, curved tusks). In fact none of them is capable of describing the entire animal, because none of them has seen it in its entirety. This is certainly the case when we attempt to describe the BLB. None of us has enough evidence to get the job done. Nevertheless, we are slowly progressing, and enough has been done to foster a scientific debate.

Ager (2003) concluded that Guthrie's reconstruction of BLB environments (Guthrie, 2001), as well as Yurtsev's similar reconstruction of a band of mesic shrub tundra on the BLB (Yurtsev, 2001), "appear to be based on fossil evidence described by Elias et al. (1996)". In fact both Guthrie and Yurtsev gave careful consideration to several lines of evidence, past and present, when drawing their conclusions about a mesic environment on the land bridge. Guthrie (2001) pointed out that botanists such as Young (1971) commented on an apparent west-east moisture gradient effect in the zonation of the Arctic flora regions. Murray (1995) identified several plant species that have a limited distribution in the Bering Strait region, but are only found on one side or the other. A moisture gradient (higher moisture towards the BLB and lower moisture towards interior Alaska) was discussed by Young, 1982. Anderson and Brubaker (1994) also interpreted a significant east-west moisture gradient across Alaska during glacial intervals. Ironically, it may have been the relative wetness of western Alaska and the BLB that allowed lakes to persist in these regions through the LGM. These lakes, including Imuruk Lake on the Seward Peninsula, Kaiyak Lake and Squirrel Lake near Kotzebue, Zagoskin Lake on St Matthew Island, Flora Lake on St Lawrence Island, and Cagaloq Lake on St Paul Island, persisted through the LGM, yielding

the pollen used by Ager (2003) to argue *against* moist conditions in his study region. Guthrie (2001) noted that nearly all of the sediment cores taken from extant lakes in interior Alaska and the Yukon Territory have basal ages less than 15,000 years old. He concluded that the dry climate of these interior regions of Eastern Beringia made most lakes in this region dry up. Yurtsev (2001) argued that the exposed shelf of the Bering Strait and some adjacent regions received relatively high levels of precipitation, carried by moisture-laden winds from the North Pacific. He likened the spread of steppe–tundra vegetation across the BLB to the populating of an archipelago of small, dry islands.

### 3.1. Problems with pollen interpretation

Part of the difficulty in reconstructing ancient Beringian environments from pollen assemblages is the lack of ecological definition of pollen at the generic or family level. Grass pollen is extremely difficult to identify beyond the family level, and so it is generally reported as ‘Poaceae’ or ‘Graminaceae’ in pollen diagrams. But species within this large family have quite variable ecological requirements in Alaska today, and not all of them are indicative of dry environments. In fact, quite the opposite is true for some of the important Arctic grass species. For instance, the dominant Poaceae pollen in modern samples from Barrow, Alaska is *Dupontia fischeri* (Eisner and Peterson, 1998; Elias et al., unpublished). This species grows in wet tundra, often where there is standing water (Hultén, 1968). So arctic Poaceae pollen can be rightly considered just as much an indicator of wet tundra environments (such as on the Arctic coastal plain today) as it might be of dry steppe–tundra conditions. Oswald et al. (2003) were able to discriminate the modern pollen signatures of wet tundra and mesic shrub tundra on the Alaskan North Slope, based on the fact that the former plant community is dominated by the pollen of *Dupontia* and other grasses, while the latter community is dominated by pollen of dwarf shrubs. However, in fossil assemblages it would be impossible to separate *Dupontia* pollen from the pollen of dry-adapted grasses that might have formed part of a steppe–tundra community (see Table 1 for a list of typical steppe–tundra grasses).

Likewise, pollen from the family Cyperaceae is extremely difficult to distinguish at the genus or species level, so it is generally reported as Cyperaceae pollen, but how should this ‘signal’ be interpreted? Most members of this family are sedges (*Carex*), and most sedges grow in damp or waterlogged soils, but the dominant plant on the LGM landscape at Cape Espenberg, based on plant macrofossils, was *Kobresia myosuroides*. This is an upland, dry-adapted species, found today on dry mountain slopes and lichen tundra in Alaska (Hultén, 1968), but the pollen it produces is indistinguishable from that of aquatic sedges. Thus the palaeoenvironmental signals of sedges and grasses may be interpreted backwards from the normal method. At least in some contexts, Poaceae pollen may be taken as an indication of wet tundra and Cyperaceae pollen may be taken as an indication of dry tundra.

### 3.2. Steppe–tundra habitat islands on the land bridge?

As we have alluded to in this review, all of the LGM sites from which steppe–tundra or equivalent vegetation have been interpreted in the central region of Beringia are either on the Alaskan mainland, or on islands in the Bering Sea. The island localities would have been perched well above the elevation of the land bridge plains. Their height above the plain ranged from perhaps 75 to 200 m. These are not enormous heights, but there is at least a possibility that the environment of these uplands may have been sufficiently different to create habitat islands where relatively dry climate allowed steppe–tundra vegetation to persist. Yurtsev (2001) anticipated this reconstruction when he said that the spread

of steppe–tundra vegetation across the land bridge was like the populating of an archipelago of small, dry islands.

### 3.3. Abandoning the broad-brush approach

None of us should take the view that the BLB, or any other large geographic region, was completely dominated by a single type of biological community. All ecosystems, past and present, are made up of patches of varied communities. Certain community types may dominate, but not to the exclusion of others. Palaeoecologists (including Elias) who have attempted to reconstruct BLB environments for the Last Glaciation have too often fallen into the trap of attempting to reconstruct major portions of the land bridge from fossil data from just a few sites. At its height, the BLB covered about 1.5 million km<sup>2</sup>—a region about twice the size of Texas. During the LGM, the distance from the northern margin of the land bridge to the southern margin was 1800 km. Thus far, we have only got a handful of sites from the BLB region from which to draw conclusions. Whole sectors of the land bridge remain unstudied, including the Russian side of the Bering and Chukchi shelf regions. The Bering shelf region between the Pribilof Islands and the Alaskan Peninsula likewise remains unstudied. Parts of the Chukchi shelf have been studied (Elias et al., 1996, 1997), but thus far have not yielded organic-rich sediments dating as far back as the LGM. The few LGM samples from the land bridge plain are both quite near the shore of the Seward Peninsula. As discussed above, the island sites were all perched above this plain, and their fossil pollen signatures may or may not characterize the vegetation of the adjacent lowlands.

On biogeographic grounds, it appears that we can make a case for the presence of some kind of biological filter that blocked the movements of some steppe–tundra plants and animals across the BLB. Dry-adapted plants, some steppe weevils, and some megafaunal mammals failed to get established on one side or the other, and a land-bridge barrier seems the most likely cause.

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