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Human Dispersal from Siberia to Beringia: Assessing a Beringian Standstill in Light of the Archaeological Evidence

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With genetic studies showing unquestionable Asian origins of the first Americans, the Siberian and Beringian archaeological records are absolutely critical for understanding the initial dispersal of modern humans in the Western Hemisphere. The genetics-based Beringian Standstill Model posits a three-stage dispersal process and necessitates several expectations of the archaeological record of northeastern Asia. Here we present an overview of the Siberian and Beringian Upper Paleolithic records and discuss them in the context of a Beringian Standstill. We report that not every expectation of the model is met with archaeological data at hand.

The paleoanthropology of northeastern Asia and Alaska is paramount to understanding initial human dispersal in the Western Hemisphere because of their Late Pleistocene connection by the Bering Land Bridge, the now submerged continental shelf below the Bering Strait between far northeastern Russia and western Alaska. The biogeographical region, called Beringia, extends from the Verkhoiansk Range in eastern Siberia east to the Mackenzie River in northwestern Canada and includes Kamchatka, Chukotka, and the Bering Sea area (Hoffecker and Elias 2007; Hopkins et al. 1982; fig. 1). DNA of ancient human skeletons and living populations indicates direct links between far northeastern Asia and America. This high-latitude migration began after 50 ka and continued through the late glacial, a nearly 40 kyr odyssey through previously uninhabited landscapes characterized by starts and stops (Buvit et al. 2015; Graf 2009, 2010; Hamilton and Buchanan 2010) and involving noticeable responses to extreme conditions, especially 26–20 ka at the last glacial maximum (LGM; see Dennell 2017 for discussion of the ecology of initial dispersals). Though some refer to the entire last glacial stage, or marine isotope stage (MIS) 2, as the LGM (i.e., LGM sensu lato), we consider the LGM sensu stricto most pertinent to Siberian and Beringian human ecology, when Northern Hemispheric glaciers were at their greatest extent and temperatures at their minima, following Clark et al. (2009). Despite temperatures colder than today for Siberia and Beringia during the entire span of MIS 2 (Zazula et al. 2006), various paleoproxy records from these regions indicate even more extreme cold and arid conditions during the LGM (e.g., Kuzmina and Sher 2006; Szpak et al. 2010). Here we consider the archaeological records of Siberia and Beringia in the context of the Beringian Standstill Model (BSM), a hypothesis proposed by geneticists to explain late Pleistocene dispersal of modern humans from Siberia to America. We present basic tenets and archaeological expectations of the BSM, review the region's Upper Paleolithic prehistory, and discuss how well the archaeological record meets these expectations.

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A Hypothesized Beringian Standstill: The Long and Short of It

Genetic studies convincingly demonstrate that Asia gave rise to the first Beringians and Americans. Genetic data from present-day human DNA (mitochondrial, Y chromosomal, and whole genome) link all Native American ancestors to Siberia (Derenko et al. 2007; Karafet, Zegura, and Hammer 2006; Merriwether 2006; Mulligan and Kitchen 2013; Mulligan, Kitchen, and Miyamoto 2008; Perego et al. 2009; Reich et al. 2012; Schurr 2004; Schurr and Sherry 2004; Tamm et al. 2007), and new studies of ancient mtDNA and paleogenomics from early American contexts yield Asian-derived Native American relationships (Gilbert et al. 2008; Kemp et al. 2007; Raff and Bolnick 2014; Raghavan et al. 2014, 2015; Morton Rasmussen et al. 2014, 2015; Smith et al. 2005; Tackney et al. 2015). Paleogenomics indicate that first American population histories were far more complicated than we realized (Skoglund et al. 2015). Despite these advancements, we still do not know precisely when and from where these first American populations emerged or how they dispersed through Beringia and the Americas.

This northern perspective requires considering two events: (1) dispersal from Siberia to Beringia, and (2) subsequent dispersal from Beringia into the Americas. Based on estimates of lineage coalescence as well as placement and dating of the earliest archaeological sites in far northeastern Siberia and Alaska

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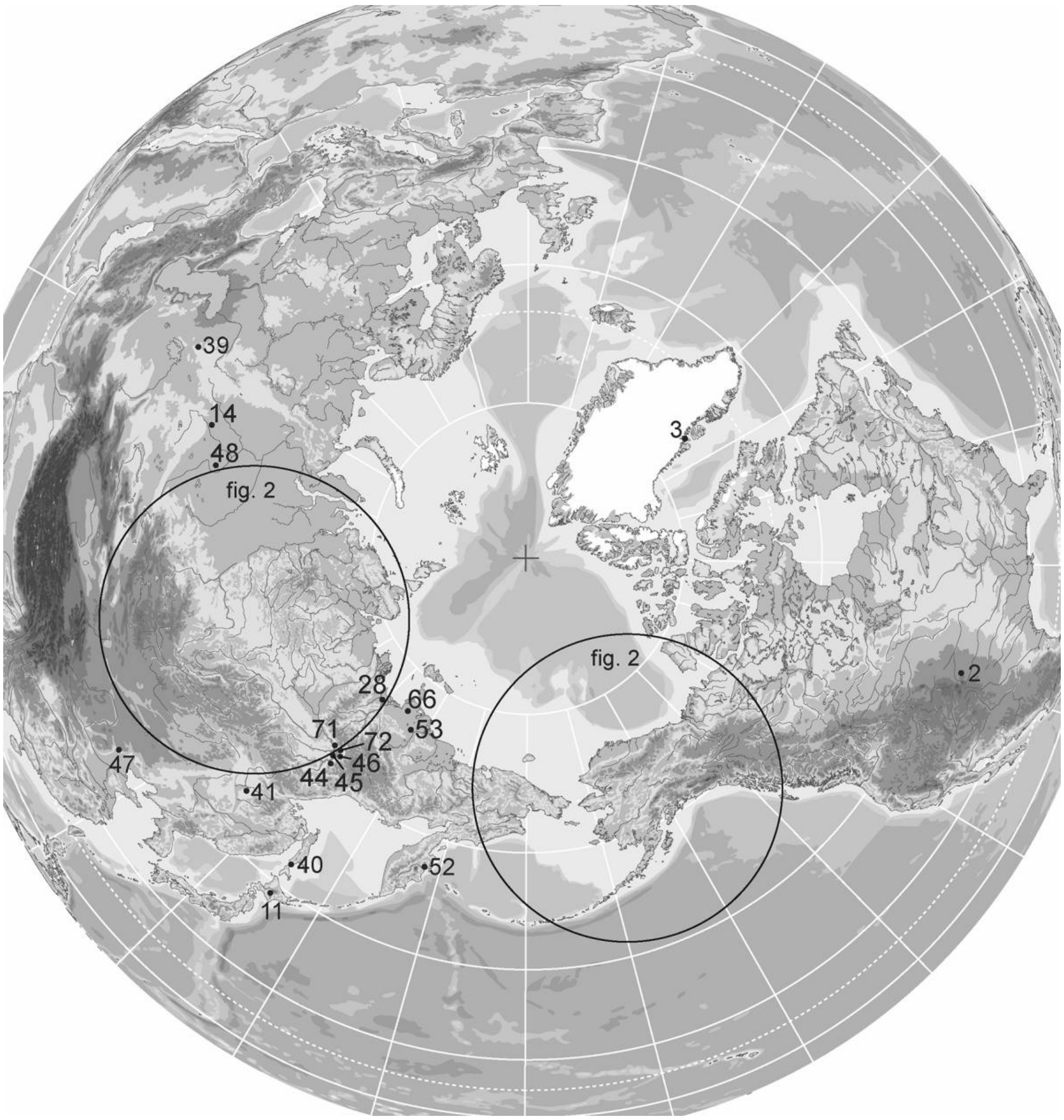

Figure 1. Map showing sites mentioned in the text. 2 (Anzick), 3 (Saqqaq), 11 (Kashiwadai), 14 (Ust' Ishim), 28 (Yana RHS), 39 (Kostenki 14), 40 (Ogon'ki 5), 41 (Ust' Ulma), 44 (Diuktai Cave), 45 (Ust'-Mil), 46 (Verkhne Troitskaia), 47 (Tianyuan Cave), 48 (Cherno'ozere), 52 (Ushki Lake), 53 (Berelekh), 66 (Lake Nikita), 71 (Ikhine), 72 (Ezhantsy). A color version of this figure is available online.

at 33 ka and 14 ka, respectively, most geneticists agree that Native Americans diverged from Asian ancestors either in northeastern Asia or on the Bering Land Bridge just before or immediately following the LGM (Bortolini et al. 2003; Goebel, Waters, and O'Rourke 2008; Hoffecker, Elias, and O'Rourke 2014; Karafet, Zegura, and Hammer 2006; O'Rourke 2009; Raff and Bolnick 2014; Raghavan et al. 2015; Schurr 2004; Schurr and Sherry 2004; Seielstad et al. 2003). Divergence was followed by a period of isolation when today's Native American genetic diversity developed. This incubation or "standstill" was originally hypothesized to have taken 15 kyr (Kitchen, Miyamoto, and Mulligan 2008; Mulligan and Kitchen 2013; Mulligan, Kitchen, and Miyamoto 2008; Tamm et al. 2007), although new studies argue it began later and lasted less than 8 kyr (Raghavan et al. 2015; table 1).

Geneticists mostly analyzing mtDNA genome data from living populations propose a long chronology where divergence between Asian ancestors and proto–Native Americans occurred about 40–30 ka as a group left Central Asia and arrived on the Bering Land Bridge by 30 ka. Divergence was immediately fol-

Table 1. Assumptions and archaeological expectations of Beringian Standstill Models (BSM)

BSM and genetic model assumptions	Archaeological expectations
Long-chronology:	
Initial divergence between a Central Asian ancestor population and proto–Native Americans >30 ka	Archaeological sites in eastern Northeast Asia dating 40–30 ka
Migration of proto–Native American population to Beringia by 30 ka	Time-transgressive distribution of sites from south to north with sites in Beringia by 30 ka
15–7.5 kyr isolation period and incubation of Native American suite of genetic variations in Beringia 30–16 ka	Archaeological sites present in Beringia 30–16 ka with new technologies and land-use strategies that differ from contemporary sites in Northeast Asia
Estimated effective population size of 8,000–10,000 individuals at 30–16 ka	Many archaeological sites dating to 30–16 ka in Beringia, reflecting proposed population
Migration of Native American founding population (~1,000 individuals) south along a Pacific coast route into the Americas	Archaeological sites along the Pacific coast dating to 16–13.5 ka
Short-chronology:	
Initial divergence between a Northeast Asian ancestor population and proto–Native Americans by about 23 ka	New archaeological technology and land-use strategy in eastern Northeast Asia by about 23 ka
Migration of proto–Native American population to Beringia immediately after the LGM (23–20 ka)	Time-transgressive distribution from south to north of sites with this new technology and land-use strategy 23–20 ka
<10 kyr isolation period and incubation of Native American suite of genetic variations in Beringia during the Late Glacial (20–14 ka)	Archaeological sites present in Beringia 20–14 ka with new technologies and land-use strategies differing from contemporary sites in Northeast Asia
Migration of Native American founding population south along perhaps both a Pacific coast and interior "ice-free corridor" route into the Americas	Archaeological sites along the Pacific coast and ice-free corridor dating to 16–13 ka

lowed by a long, 15–7.5 kyr isolation period when genetic diversification occurred through the LGM followed by dispersal of founding subclades (A2, B2, C1b, C1c, C1d, C4c, D1, D4h3, X2a) south to the Americas after 16 ka (Mulligan and Kitchen 2013). The long-chronology BSM assumes diversified subclades migrated as distinct populations south along the Pacific coastline carrying all Native American genetic diversity. Subsequent movements were hypothesized for the Holocene with migrations back to East Asia bringing C1a, a sister clade of the American C1 phylogeny, and the American A2a subclade as well as a final west–east dispersal across far-northern North America of the Siberian D2 subclade (Tamm et al. 2007). This version implies that people were in Beringia by 30 ka and that an LGM-aged Beringian biome maintained a viable human population throughout a period of global and regional climatic instability. Accordingly, we expect archaeological sites in high-latitude locations (>60°N) of Siberia from 40 to 30 ka, especially in western Beringia; the earliest archaeological sites on the Bering Land Bridge dating as early as 30 ka and through the LGM; and a Beringian archaeological record dated 30–16 ka, reflecting new tool kits and lifeways used by the new genetically varied founding population that gave rise to Native Americans. Ultimately the founding population would have left archaeological sites along the Pacific coast 16–13.5 ka.

Recently, a short-chronology BSM emerged from comparing ancient and present-day autosomal genome data, including remains from the 24 ka Mal'ta skeleton from the Baikal area (Raghavan et al. 2014), the 12.5 ka Anzick skeleton from Montana (Morton Rasmussen et al. 2014), the 9 ka Kennewick skeleton from Washington (Rasmussen et al. 2015), and the hair from a 4 ka Saqqaq mummy from Greenland (Rasmussen et al. 2010; figs. 1, 2). Raghavan et al. (2015) found genetic ties between all modern and ancient Native American populations sampled to date and Mal'ta, indicating divergence from Asian ancestors not at 40 ka but between 23 and 20 ka, arguing incubation did not last longer than 10 kyr. This is because migration south to the Americas commenced before 13.5–13 ka, the time of Clovis, the earliest unequivocal archaeological tradition in the Americas (Haynes et al. 2007; Waters and Stafford 2007). Short-chronology BSM implies people dispersed to the Bering Land Bridge immediately following the LGM, so no archaeological sites should be expected in eastern Beringia before 20 ka. This version implies that Native American genetic variation emerged rapidly during an early late-glacial standstill.

Several geneticists agree that dispersal from Beringia to the Americas was rapid, occurred after the LGM, and potentially followed the Pacific coast with subsequent interior movements at ~16–14 ka (Fagundes, Kanitz, and Bonatto 2008; Fix 2002; O'Rourke 2009; Wang et al. 2007) and slightly later via an interior "ice-free corridor" at ~14 ka (O'Rourke 2009; Perego et al. 2009; Starikovskaya et al. 2005). A coastal route would have been viable throughout the late glacial (Mandryk et al. 2001); however, an interior route following the Yukon River basin over low divides into the Mackenzie River basin and then south to northern Alberta and Saskatchewan would have been available by about 12.6 ka (Pedersen et al. 2016, but see Munyikwa et al. 2011 and Zazula et al. 2009 for slightly earlier dates). Archaeologically, however, the oldest Pacific coastline evidence dates to the early Holocene (Dixon and Monteleone 2014), and there are no archaeological sites predating Clovis along the ice-

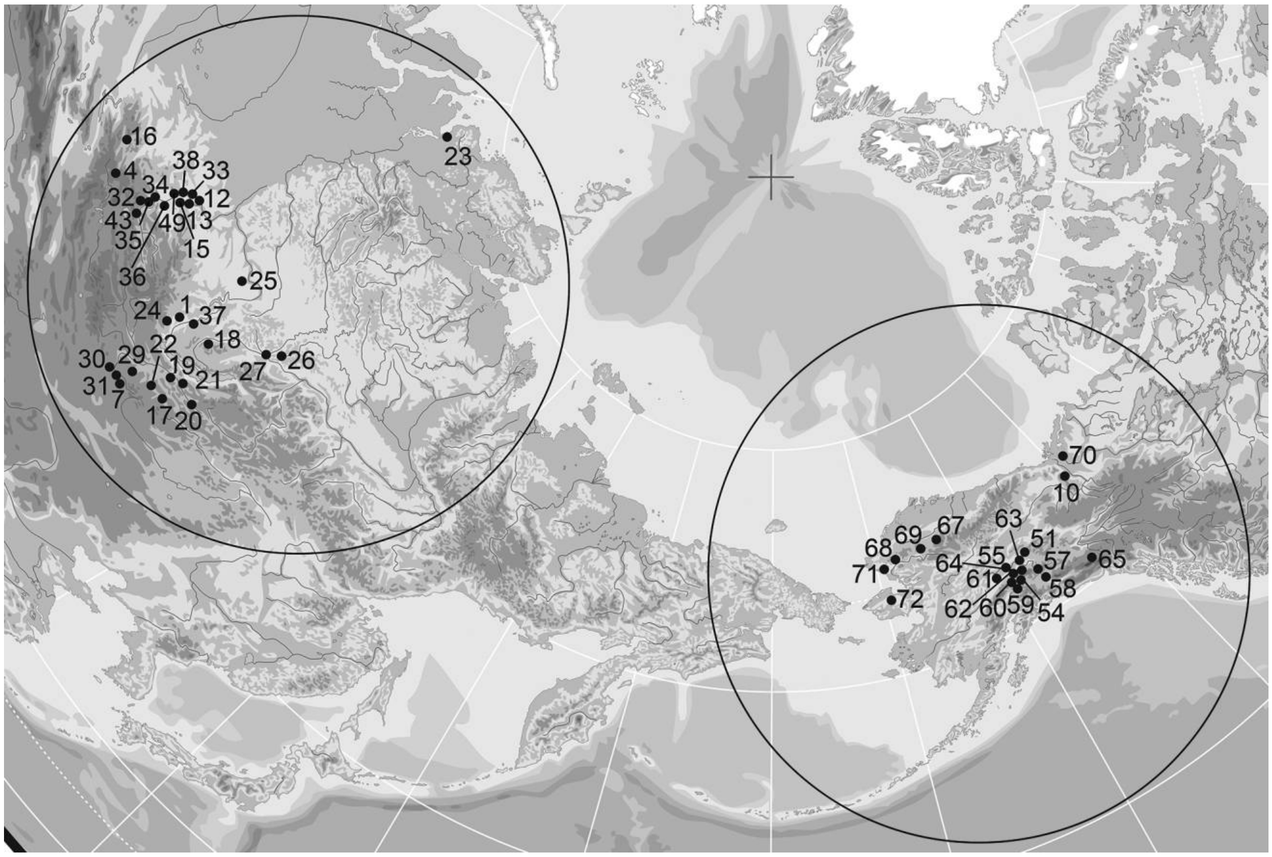

Figure 2. Map showing sites in southern Siberia and Eastern Beringia. 1 (Mal'ta), 4 (Denisova Cave), 7 (Ust'-Menza), 10 (Bluefish Cave), 12 (Afontova Gora), 13 (Listvenka), 15 (Pokrovka), 16 (Kara Bom), 17 (Tolbaga), 18 (Makarovo 4), 19 (Varvarina Gora), 20 (Khotyk), 21 (Kamenka), 22 (Masterov' Kliuch), 23 (Sopochnaya Karga), 24 (Buret), 25 (Ust'-Kova), 26 (Nepa 1), 27 (Alekseevsk), 29 (Kunalei), 30 (Chitkan), 31 (Melnichnoe, Studenoe), 32 (Ui 1), 33 (Novoselovo 13), 34 (Afanaseva Gora), 35 (Kashtanka 1), 36 (Derbina 4/5), 37 (Igeteiskii Log), 38 (Kurtak 4), 43 (Nizhnii Idzhir'), 49 (Kokorevo 1), 51 (Swan Point), 54 (Tangle Lakes), 55 (Moose Creek), 57 (Gerstle River Quarry), 58 (Upward Sun River), 59 (Carlo Creek), 60 (Dry Creek, Panguingue Creek), 61 (Owl Ridge), 62 (Walker Road), 63 (Broken Mammoth), 64 (Linda's Point), 65 (Little John), 67 (Mesa), 68 (Tuluaq Hill), 69 (Irwin Sluiceway), 70 (Engigstciak), 71 (Raven Bluff), 72 (Serpentine Hot Springs). A color version of this figure is available online.

free corridor (Ives et al. 2013), obscuring which route was used and when.

These events are based solely on genetic models. Empirical archaeological evidence is, therefore, critical for testing the long-chronology and short-chronology standstill models and determining precisely when and how humans arrived in the New World. Below we review archaeological records from southern Siberia to central Alaska in the context of both BSMs to establish which is better supported by existing evidence. Finally, in discussion, we place these records in the context of the genetic models.

The Siberian Record

The Siberian Paleolithic is primarily an archaeological record; however, some human skeletal remains have been recovered. Both archaeological and skeletal remains indicate premodern Neanderthals and Denisovans initially colonized the Altai region of southwestern Siberia more than 50 ka (Buzhilova, Derevianko, and Shunkov 2017; Derevianko 2010; Derevianko and Markin 1998; Derevianko et al. 1998, 2003; Goebel, Derevianko, and Petrin 1993; Green et al. 2010; Krause et al. 2007; Prüfer et al. 2014; Reich et al. 2010; Turner 1990), though one Denisovan specimen may be <50 ka given the difficulty in determining its exact stratigraphic correlation with remains discovered in another part of Denisova Cave (Sawyer et al. 2015; fig. 2). These premodern populations, however, may not have spread north or east of the Altai (Graf 2015, but see Lbova 2000; Tashak 2004). It was not until about 47 ka that Upper Paleolithic archaeological sites began to emerge (table 2). Regionally, they are divided into three chronological phases labeled early, middle, and late (Sapozshnikov 2004; Vasil'ev 1992) and represent dispersal of humans to the north and east, eventually making it across the Bering Land Bridge to Alaska. Only five known sites have preserved paleoanthropological remains from Upper Paleolithic contexts: Mal'ta, Afontova Gora, Listvenka, Pokrovka,

Table 2. Climatic time-stratigraphic units associated with archaeological phases, technologies, and land-use patterns of the Upper Paleolithic in Central and Eastern Siberia

Dates (ka)	MIS	Greenland ice-core climatic intervals (S. O. Rasmussen et al. 2014)	Archaeological phases	Technologies	Land-use strategies
50–34	3	Long Greenland interstadials 14–7 interrupted by short Greenland stadials 13–7	Early Upper Paleolithic	Laminar blade and flake lithic technologies; unifacial blade-tipped osseous projectile technologies	Seasonal use of sites. Too few sites to confidently interpret mobility strategies
34–24	3/2	Long Greenland stades 6–3 interrupted by short Greenland interstadials 6–3	Middle Upper Paleolithic	Blade, bladelet, flake, and bifacial lithic technologies; osseous projectile and sewing technologies; osseous mobile art	Varied site types, including special-task and base-camp sites, indicate familiarity with the landscape and a logistical-mobility strategy
26–20	2	Last glacial maximum long Greenland stades 3–2.1b interrupted by short Greenland interstadials 2.2 and 2.1			
22–12	2	Long Greenland stades 2.1b–1 interrupted by a shorter Greenland interstadial 1 (Bølling-Allerød)	Late Upper Paleolithic	Blade and flake lithic technologies; wedge-shaped microblade core technology and slotted microblade-osseous composite projectile points; osseous sewing technologies	Uniform site types (base camps), behaviors geared toward economizing lithic raw materials and maximizing tool cutting edges suggests a residential-mobility strategy

and Ust' Ishim. Of these, only the remains from Mal'ta, Afontova Gora, and Listvenka were discovered in archaeological excavations and have clear associations with Upper Paleolithic artifacts (Akimova et al. 2005; Astakhov 1999; Gerasimov 1958; Sosnovskii 1935). The other two were found in secondary fluvial settings (Akimova et al. 2010; Fu et al. 2014). All are anatomically modern *Homo sapiens* with complete autosomal genomes sequenced for Mal'ta (Raghavan et al. 2014) and Ust' Ishim (Fu et al. 2014) and some preservation of autosomal material from Afontova Gora (Raghavan et al. 2014). Below we provide a brief review of the Siberian Upper Paleolithic primarily focusing on the record east of the Altai.

Before the Last Glacial Maximum: The Early Upper Paleolithic

Anatomically modern humans appeared in Siberia about 50–45 ka in the Altai but spread into south-central and southeastern Siberia about 45–40 ka, represented by sites from the northern foothills of the Saian Mountains and Lena-Angara Plateau in the upper reaches of the Enisei, Angara, and Lena rivers. In addition to the archaeological remains, a single *Homo sapiens* femur, dating to 45 ka, was found at Ust' Ishim in Western Siberia (Fu et al. 2014).

Early Upper Paleolithic (EUP) sites are in open-air contexts along drainages, a few within alluvium, and others in colluvium or a combination of colluvial and eolian sediments. Dating these early sites has been highly problematic. First, they are situated in complicated depositional settings usually with primary contexts disturbed by LGM cryoturbation. Second, some dates were obtained on pooled bone fragments without proper pretreatment to isolate collagen and to ensure that external contamination was not included. So unless these dates are statistically equivalent to other samples from the same contexts on well-prepared collagen or wood charcoal (see Douka and Higham 2017; Graf 2009), they must be viewed with skepticism. Sites with relatively diagnostic archaeological assemblages, found in understandable stratigraphic contexts with reasonably reliable chronometric dates, are few, suggesting modern humans were first in southern Siberia by about 50–45 ka at Kara Bom (Goebel, Derevianko, and Petrin 1993) and then spread east to the Makarovo 4 site immediately west of Lake Baikal perhaps as early as 45 ka (Goebel and Aksenov 1995). Dates from Varvarina Gora (45–40 ka; Bazarov et al. 1982; Kuzmin 1994), Khotyk (42 ka; Kuzmin et al. 2006), and Kamenka (40–30 ka) east of Lake Baikal suggest more substantial habitation at 45–35 ka (Lbova 2000). Other dates obtained from fauna among the cultural materials at the sites of Masterov Kliuch' (Goebel, Waters, and Mescherin 2000) and Tolbaga (Bazarov et al. 1982; Buvit et al. 2016; Goebel and Aksenov 1995; Goebel and Waters 2001; Kuzmin et al. 2011; Lbova 2005) range from about 48 to 30 ka. These Transbaikal sites are found in colluvial settings, so their long time ranges probably reflect redeposition of materials from various times. At Sopochnaya Karga weather station at 72°N latitude in the lowermost reaches of the Enisei River, a nearly complete mammoth carcass was found with several lesions that Pitulko et al. (2016) contend were made by human hunters; however, neither osseous nor lithic artifacts were found with the remains. From what we know about EUP sites, they fall within the middle part of MIS 3, a paleoclimatic warm period punctuated by several cold intervals (Bezrukova et al. 2010; Kind 1974). Radiocarbon databases, now numbering close to 1,000 dates (Buvit et al. 2016; Kuzmin et al. 2011), signal two possible pulses of EUP occupation, one at ~50–42 ka and a subsequent one after 40 ka, both during warm intervals (GIS-12/11/10 and GIS-9/8) of the mid Upper Pleistocene. Given the limitation of radiocarbon dating near the working limit of the method as outlined by Douka and Higham (2017), we accept these age ranges with some caution.

In addition to sites discussed above, others are included in the EUP on typological and stratigraphic associations of their lithic artifact inventories (fig. 3). Together they illustrate how early modern humans made sophisticated large laminar blade-based technologies with weapons tipped by unifacial points (Derevianko and Shunkov 2005; Derevianko et al. 2005; Goebel 2002*b*; Goebel, Derevianko, and Petrin 1993; Kirillov and Derevianko 1998; Konstantinov 1994; Markin 1998; Vasil'ev and Rybin 2009). The variety of other lithic tools, as well as osseous tools (e.g., needles, awls, retouching implements, and small antler points; Tashak 2007; Vasil'ev and Rybin 2009), indicate humans were undertaking various processing tasks and manufacturing clothing and other perishable items. Evidence from a few EUP sites confirms production of personal adornment on bone and stone (e.g., beads, bead preforms, pendants, bracelets; Derevianko and Rybin 2005; Derevianko, Shunkov, and Volkov 2008; Lbova 2010). Personal ornaments are known from EUP sites across the Old World; however, early sewing implements are known only from the northern contexts of Siberia and Eastern Europe, where they would have been germane in manufacturing warm clothing (Hoffecker 2005). During this time, people were procuring fauna as they encountered them,

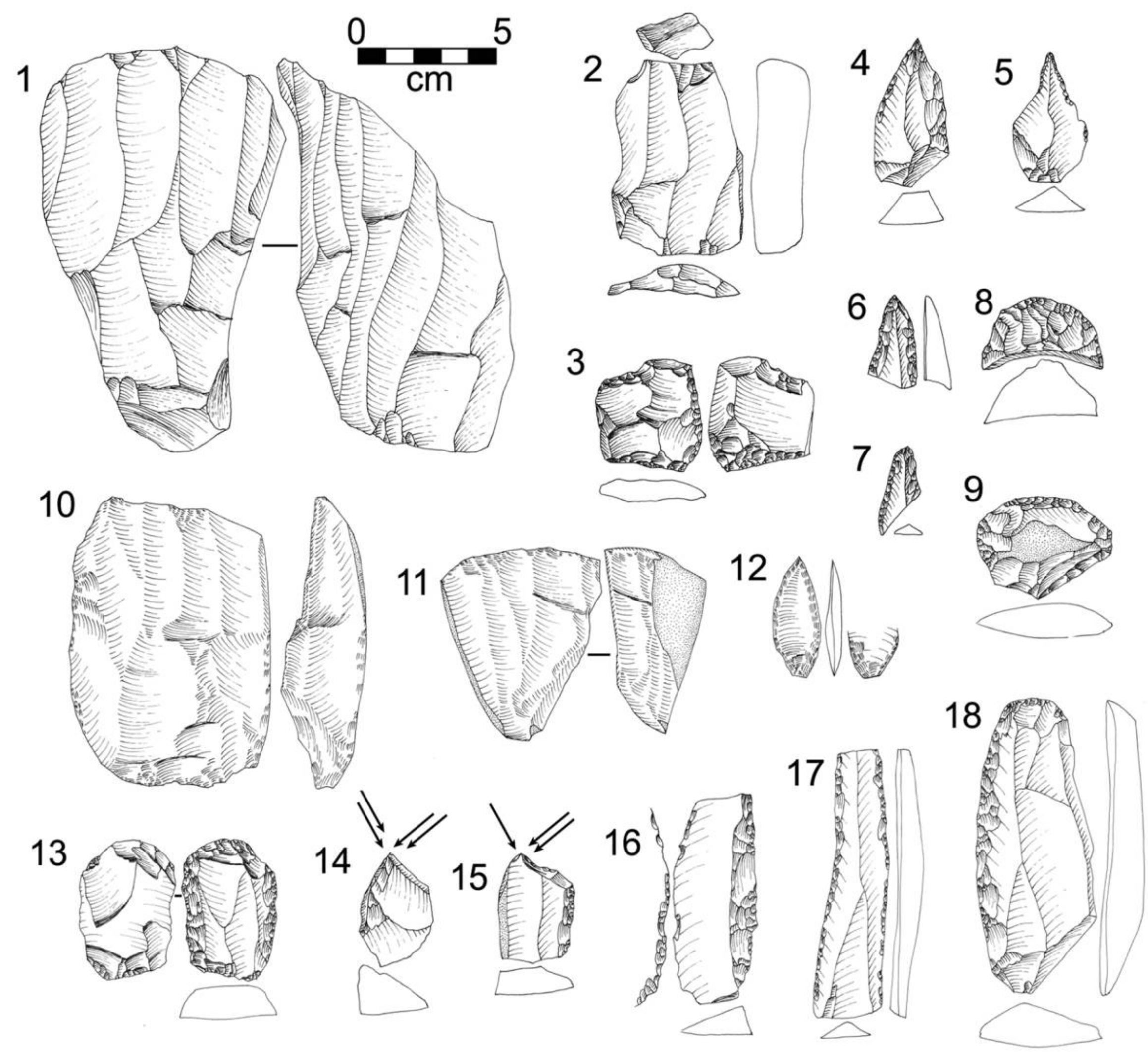

Figure 3. Representative artifacts from early Upper Paleolithic contexts (drawn by T. Goebel). Varvarina Gora: 1 (subprismatic blade core), 2 (laminar, flat-faced blade core), 3 (bipolar core), 4–5 (gravers), 6–7 (points on blades), 8–9 (end scrapers). Makarovo 4: 10 (laminar, flat-faced blade core), 11 (subprismatic blade core), 12 (point on blade). Tolbaga: 13 (bipolar core), 14–15 (burins), 16 (backed blade), 17 (retouched blade), 18 (end/side scraper on blade).

not focusing on any one taxon or type of animal (Goebel 2004*a*; Vasil'ev 2003*a*; Vasil'ev and Rybin 2009). Dense, vertically thick artifact concentrations, dwellings, and storage pits (Konstantinov 2001) indicate people were living at these sites for relatively long periods, maybe seasonally in scheduled base camps. Better seasonality data from faunal assemblages may help sort out these behaviors.

Genome sequencing of the Ust' Ishim individual shows ties to a basal Eurasian population, ancestral to both Europeans and East Asians, without admixture by Denisovans, which make up none of the sequence, and little by Neanderthals, which are only 0.3%–2.3%, a similar range for present-day Europeans and East Asians. This means Neanderthal introgression in the Ust' Ishim individual's ancestral population occurred well before their dispersal to Siberia, perhaps at about 60–50 ka in Southwest or Central Asia (Fu et al. 2014).

The Onset of the Last Glacial Maximum: Middle Upper Paleolithic

The next phase of the Upper Paleolithic is broadly compared with the Gravettian of Central and Eastern Europe (Anikovich et al. 2007; Hoffecker 2002; Roebroeks et al. 2000) because of assemblages based on bladelet production (Lisitsyn 1996), a variety of utilitarian and nonutilitarian osseous technologies including art, high faunal diversity, elaborate site features, and dedicated logistical mobility with sometimes far-reaching raw material procurement (Hoffecker 2002). Russian scholars refer to the Siberian middle Upper Paleolithic (MUP) as the Mal'ta Culture (Derevianko 1998; Lisitsyn 2000; Okladnikov 1968) after the sites of Mal'ta and Buret about 160 km west of Lake Baikal.

Nearly all MUP sites have a similar west–east distribution to the EUP. In fact, MUP material overlies EUP cultural layers at several sites. One difference, however, is that MUP sites extend more than 500 km north to nearly 60°N latitude at Ust' Kova, Nepa 1, and Alekseevsk in the Enisei and Lena River valleys and as far as 71°N latitude at Yana RHS along the lowermost Yana River in northwestern Beringia, representing the oldest (~33–31 ka) MUP site occupation yet found in this far-northern context. Generally, however, Siberian MUP sites exist south of 60°N latitude and range in age from about 34 to 24 ka with at least nine belonging to the relatively warm first half of this age range (34–29 ka), when arboreal taxa are more prevalent in paleoecological records (Bezrukova et al. 2010; Derevianko et al. 2003). The majority, however, date to 29–24 ka, a period when regional conditions began to deteriorate toward the LGM (Graf 2009; Kuzmin 1995; Kuzmin et al. 2011).

MUP assemblages include both flake and blade production but show marked reliance on flake over blade production, and sites such as Mal'ta in the Angara basin; Kunalei, Chitkan, Priiskovoe, and Melnichnoe in the Transbaikal; Ui 1 in the Saian; and Novoselovo 13, Afanaseva Gora, and Kashtanka 1 in the Enisei basin show extensive use of bladelets and small flakes (fig. 4). A few assemblages (Ust' Kova and Derbina 4/5) have bifacial projectile points (Akimova et al. 2003; Goebel 2004*b*; Medvedev 1998*b*), whereas elsewhere most projectile points were constructed of osseous materials. Processing implements include simple retouched flakes and blades and a variety of other small, functional tools (Derevianko 2005; Graf 2008, 2010; Konstantinov 1994; Terry 2010; Terry, Andrefsky, and Konstantinov 2009).

Several MUP assemblages have somewhat elaborate osseous industries compared with EUP and late Upper Paleolithic (LUP) sites. Bone, antler, or ivory implements are unslotted, are rarely decorated, come in various sizes depending on their raw material (i.e., large points made from mammoth or horse vs. smaller points made on cervid antler or bone), and are found in most MUP sites that preserve faunal remains. A few thin, >20 cm long rod-type points have been discovered at Yana RHS, Mal'ta, Buret', and Igeteiskii Log (Medvedev 1998*b*; Pitulko et al. 2013). Sites also produced osseous retouchers, awls, and needles (Abramova et al. 1991; Lisitsyn 2000; Medvedev 1998*b*; Vasil'ev 2000). MUP sites also preserve various forms of nonutilitarian osseous artifacts, mostly carved ivory pieces divided into personal adornment (undecorated and decorated beads, drop, flat-form rectangular, disk-shaped pendants made of ivory, and pendants made of fox canines and cervid incisors) and highly symbolic "mobile" art. Some stone beads and pendants are recorded from Mal'ta, Yana RHS, and Kurtak 4. Mobile art includes engraved ivory plaques or badges, enigmatic rod-shaped pieces, 3-D zoomorphic figurines including mammoths and swans or other birds, 2-D outlines of mammoths carved into ivory, and anthropomorphic forms or "Venus" ivory figurines coeval with most found in western Eurasia. However, unlike western figurines, female characteristics on Siberian examples are carved in 2-D instead of 3-D and occasionally have hooded, full-body winter clothing (Abramova 1995; Drozdov et al. 1990; Medvedev 1998*a*; Pitulko et al. 2012, 2013; Vasil'ev 2000).

Faunal lists include woolly mammoth, woolly rhinoceros, horse, steppe bison, auroch, Irish elk, argali sheep, Siberian mountain goat, saiga antelope, red deer, roe deer, reindeer, arctic fox, red fox, and hare, but unlike the EUP, not all MUP sites contain such a wide variety. Instead, some sites—for example, Ui 1 and Kashtanka 1—contain fauna specific to the geographic location and site function. At the Western Saian upland site of Ui 1, Siberian mountain goat and argali sheep (both upland biota) dominate, and at the lowland hunting camp of Kashtanka 1 in the Minusinsk Basin, reindeer and bison (both gregarious-herd taxa) were preferred (Graf 2015; Vasil'ev 2003*a*). In contrast, base-camp sites tend to have a wide variety of fauna without clear preferences (e.g., 13 taxa in relatively equal frequencies at Mal'ta and a similar pattern at Yana RHS; Medvedev 1998*b*; Pitulko et al. 2013; Vasil'ev 2003*a*). Several MUP sites preserved hearth features and associated dwellings (Konstantinov 2001; Larichev, Khol'ushkin, and Laricheva 1988; Medvedev 1998*b*; Pitulko et al. 2013; Sergin 1996; Vasil'ev 1996, 2003*b*), some more substantial than others, such as the subterranean features proposed at Mal'ta (Gerasimov 1935, but see

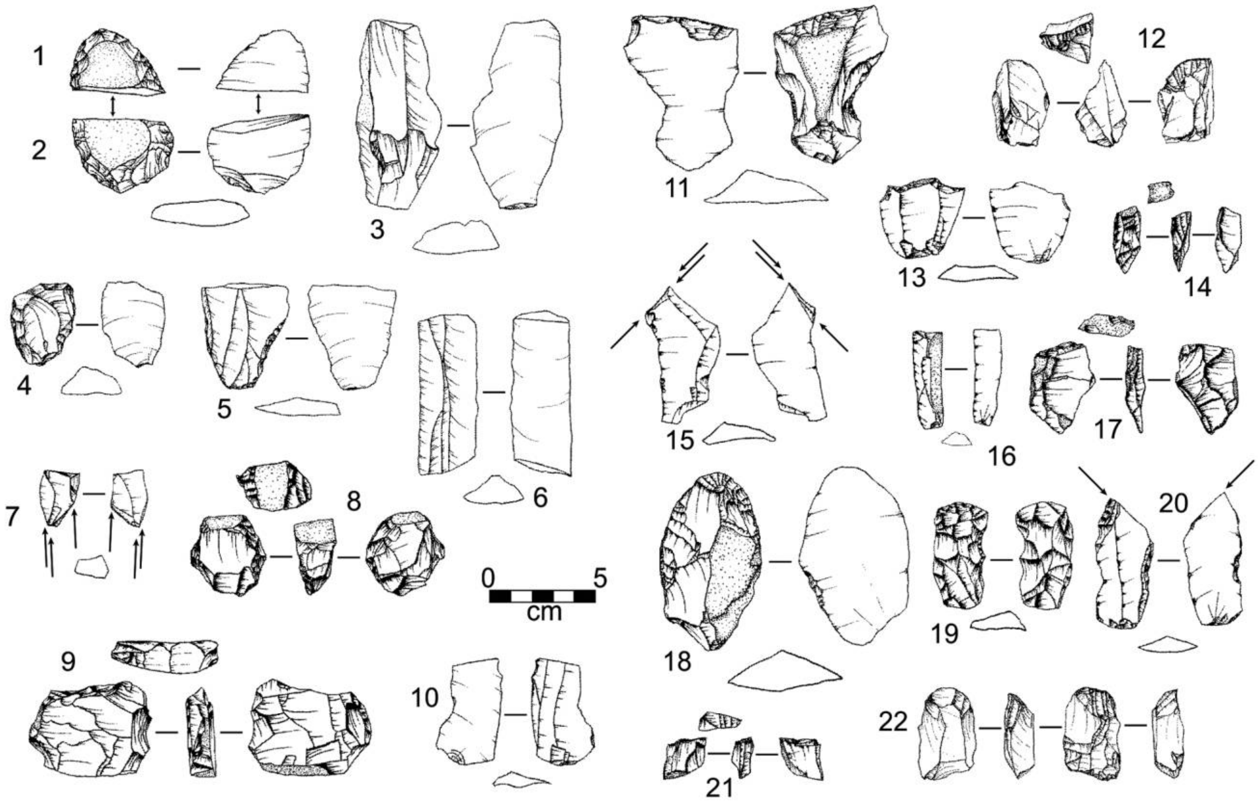

Figure 4. Representative artifacts from middle Upper Paleolithic contexts. Melnichnoe 2: 1–2 (convergent scraper fragments), 3 (blade), 4 (double convex scraper), 5 (concave single side scraper), 6 (medial blade fragment), 7 (burin), 8–9 (flake cores), 10 (proximal blade fragment). Chitkan: 11 (end scraper), 12 (subconical microcore), 13 (double notch on blade), 14 (wedge), 15 (burin), 16 (proximal blade fragment), 17 (retouched core), 18 (end scraper), 19 (irregular bifacial core), 20 (burinated double scraper), 21 (wedge), and 22 (microcore).

Vasil'ev 2000) where there was a child burial and there were storage pits (Gerasimov 1935; Medvedev 1998*b*).

High MUP intersite artifact, faunal, and feature variability indicates a wide variety of site functions with less diverse, smaller artifact assemblages at short-term, logistical camps and with more diverse, more concentrated lithic artifact assemblages and hordes of interesting decorative and artistic pieces at long-term, residential base camps. Faunal assemblage compositions and the types of domestic features also support this interpretation. A variety of sites with different functions indicate a logistically organized land-use strategy with residential bases and associated special-task locations (see Kelly 1983).

Results of genome sequencing of the Mal'ta child signal that people of the Siberian MUP descended from a central Eurasian rather than East Asian population and, therefore, they had already begun to diverge from initial Siberian founding populations (Ust' Ishim) by ~24 ka (Raghavan et al. 2014). In addition, the Mal'ta skeleton shares many derived alleles with the sequenced, 36 ka (early MUP) Kostenki-14 skeleton from the Central Russian Plain (Seguin-Orlando et al. 2014). As expected given its location, the Kostenki skeleton was found to be closely related to present-day Europeans, sharing more derived alleles with Mal'ta than either shared with Ust' Ishim. These results indicate Siberian MUP populations were genetically isolated from East Asians but not each other at some point, and they shared immediate common ancestry with at least some Eastern European MUP populations. Another interesting result from the Mal'ta analyses is its relatively substantial 38%–14% contribution to the Native American genome, with the remainder derived from ancient East Asians, signaling a relatively recent and considerable introgression from MUP Siberia into populations migrating to the Western Hemisphere.

During the LGM: The Times They Were A-Changin'

In the 1970s geologist Tseitlin (1979) proposed Siberian LGM depopulation, specifically between about 23 and 21 ka. Since then, much debate has emerged around this hypothesis with Goebel (1999, 2002*a*, 2004*b*) advancing it based on detailed reviews of Russian excavation reports as well as his own fieldwork at sites chronologically around the LGM (Goebel, Waters, and Mescherin 2000; Goebel et al. 2000). After compiling nearly complete lists of radiocarbon dates from Siberian Upper Paleolithic sites in English, Kuzmin (2008) and colleagues

(Fiedel, Kuzmin, and Keates 2007; Kuzmin and Keates 2005) found no evidence for depopulation. Then, after revisiting original Russian reports on dates in these comprehensive lists, Graf (2005) discovered several inconsistencies in their reporting as well as uncritical acceptance of clearly aberrant ages. When obviously problematic measurements were removed, several >1 kyr gaps emerged that were associated with climatically cold periods including the LGM.

This has led us to conclude that while limited occupation occurred during parts of the global LGM, both the Enisei (Graf 2009, 2015) and Transbaikal (Buvit et al. 2015, 2016) regions were abandoned or reduced to archaeological invisibility for at least 2–3 kyr between about 24.8 ka and 22.7 ka. Calibrated radiocarbon dates from the Altai, Saian, and Angara (Kuzmin et al. 2011) indicate population decline during the LGM, but their gaps and occupations are temporally offset from each other and from gaps and occupations reported in the Enisei and Transbaikal. If this pattern bears out, then it may demonstrate a generally continuous LGM occupation of Siberia but one in which population sizes were low and people moved between these areas, perhaps between uplands and valleys. The question of complete abandonment at some point remains open, but given the archaeological record, LGM environmental factors, sampling, standard-error ranges, and important considerations about site formation, it does seem likely. Where southern Siberians exactly went remains unclear, but with humanity's overall resilience and propensity to migrate instead of perish, likely destinations would have been south and east to more moderate environments. Currently there is no evidence humans avoided inhospitable LGM conditions of southern Siberia by moving north to Yakutia and Beringia.

Recolonization Immediately following the Last Glacial Maximum: Late Upper Paleolithic

Across Siberia are dozens of LUP sites distributed much more broadly than before from Western Siberia to the Russian Far East, Kamchatka, and western Beringia (Abramova 1975; Abramova et al. 1991; Derevianko 1998; Goebel 2002*a*; Kuzmin 2000; Kuzmin and Orlova 1998; Kuzmin et al. 2011). Chronologically, we see a general time-transgressive pattern from south to north, arguably reflecting humans returning from LGM refugia, especially for the eastern half of Asiatic Russia where the LUP may ultimately derive from sites found farther east in pristine depositional contexts and dating to ~27–25 ka in Hokkaido, Japan (Izuho 2013).

Siberian sites with the clearest, earliest, and most trusted evidence of LGM-dated LUP occupations are Studenoe 2 and Ust'-Menza 2 in the Transbaikal. There, hearths from chronologically overlapping, briefly occupied dwelling features were found in vertically accreted alluvium conducive to preservation (Goebel et al. 2000; Konstantinov 1994, 2001; Kuzmin, Jull, and Razgildeeva 2004) and date to 22.7–20.9 ka (Buvit et al. 2016). The next youngest LUP site is Nizhnii Idzhir' from the upper reaches of the Enisei. Lithic artifacts found surrounding a hearth feature in a paleosol formed on eolian deposits date to ~21–20 ka (Asktakhov 2008). Given that the earliest appearance of the LUP has been found at the Kashiwadai site on the southern tip of a peninsula formed by Sakhalin, Hokkaido, and some of the southern Kuril Islands (Paleo-Sakhalin-Hokkaido-Kuril [PSHK]), we expect sites dating to the LGM to be found between Hokkaido and Transbaikal. At Ogon'ki 5, located on Sakhalin Island, five radiocarbon dates on wood charcoal from features in the same cultural layer date to 35–20 ka (Vasilevskii 2005, 2008). These dates span the LGM, but cultural materials and dating samples were found in colluvial deposits and are probably not in a primary context. The Ust' Ulma site, located to the west in the Selemdzha River valley, has LUP artifacts and two radiocarbon dates on wood charcoal from a single hearth feature dated to 23.6–23 ka (Derevianko and Zenin 1995), but similar to Ogon'ki, these materials were found in a colluvial depositional setting. More work is needed in the Russian Far East to bridge the gap between PSHK and Siberia.

The Siberian LUP continues through the end of the Pleistocene, evidenced by scores of sites found in good contexts (Abramova 1986; Abramova et al. 1991; Buvit and Terry 2011; Buvit et al. 2015; Graf 2009; Ineshin and Teten'kin 2011; Konstantinov 1994; Mochanov and Fedoseeva 1996, Slobodin 2011, Vetrov et al. 2007). Conservatively, we can say by about 17–15.5 ka, the LUP spread as far as the middle Aldan River in southwestern Beringia represented at the Diuktai Cave, Ust' Mil', and Verkhne Troitskaia sites (Mochanov 1977; see discussion of dating problems with these sites in Yi and Clark 1985). Unfortunately, there are no well-dated LUP sites found east of the Aldan River in far northeastern Siberia/western Beringia (Slobodin 2011). Investigations of ^{14}C-dated Siberian LUP occupation frequencies through the late glacial illustrate a gradual increase in human populations through time with small spikes during warm intervals (i.e., Bølling, Allerød) and nadirs during intervening cold events (e.g., Oldest Dryas, Older Dryas; Buvit and Terry 2011; Goebel 1999; Graf 2005, 2009; Kuzmin and Keates 2005; Vasil'ev 2011).

LUP artifact assemblages are internally consistent with lithic industries based on flake, blade, and wedge-shaped microblade core production with many assemblages containing more flakes than blades (see fig. 5). Microblade-osseous composite projectile technology was nearly ubiquitous throughout the LUP, evidenced by microblade cores, microblades, and slotted points, some with microblades still in place (e.g., at Cherno'ozere in Western Siberia [Petrin 1986] and Listvenka [Akimova et al. 2005] and Kokorevo 1 [Abramova and Grechkina 1985] in the Enisei River valley). This technological strategy, which incorporated microblades detached from diagnostic wedge-shaped cores, resulted in highly standardized products. Moreover, processing tools found in these LUP assemblages (e.g., scrapers, burins) were typically formal with long use-life histories (Graf 2010, 2011; Kuzmin, Keates, and Shen 2007; Terry, Buvit, and Konstantinov 2016). Though production of osseous materials centered mainly on utilitarian implements, items of personal adornment exist, but other art forms do not (although see

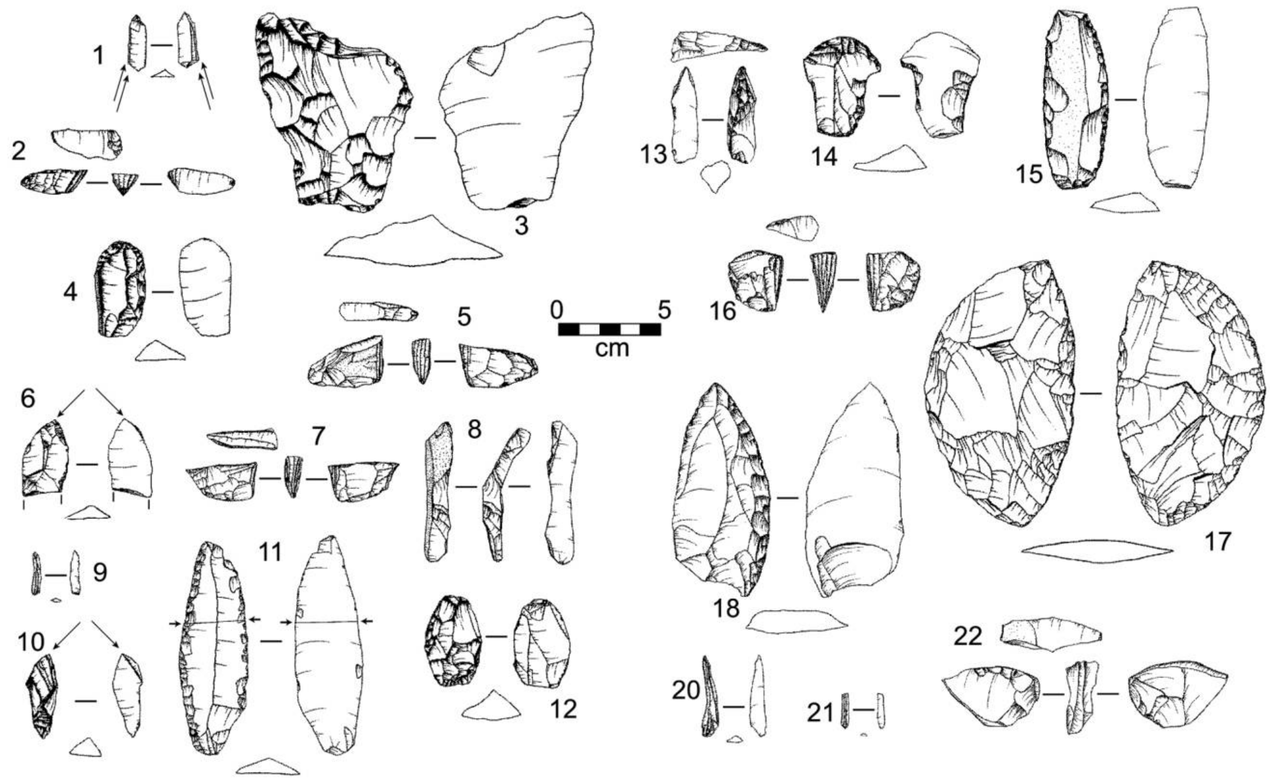

Figure 5. Representative artifacts from later Upper Paleolithic contexts. Studenoe 2: 1 (burin), 2 (subwedge-shaped microblade core), 3 (wedge), 4 (end scraper), 5, 7 (wedge-shaped microblade core), 6 (burin), 8 (ski spall), 9 (microblade), 10 (burin), 11 (convergent scraper), 12 (biface). Ust' Menza 1: 13 (ski spall), 14 (hafted end scraper), 15 (convergent scraper), 16, 22 (wedge-shaped microblade cores), 17 (bifacial foliate), 18 (convergent scraper), 20–21 (microblades).

Vasil'ev 1983 for an example of a small anthropomorphic human statue from the Maina site in the Saian that may date between 16 and 13 ka). The faunal record indicates a focus on specific, primarily large-game, gregarious-herd taxa. This pattern, coupled with a highly standardized and formal lithic technology and the near lack of any long-term dwellings, suggests people of the LUP were on the move, perhaps frequently traveling between sites. Provisioning and tool richness in the Enisei and Transbaikal demonstrate individuals were being outfitted to emphasize group mobility, and most LUP sites reflect short-term residential bases (Graf 2010; Konstantinov 2001; Terry 2010). LUP hunter-gatherers were arguably what Kelly (1983) would characterize as highly mobile, frequently moving residences across the landscape.

Summary of the Siberian Record

All archaeological and aDNA data from the EUP indicate modern humans arrived in southwestern Siberia by about 50–45 ka, spreading from the Altai to the Transbaikal by ~40 ka. Certainly modern humans were present as far north and east as Beijing, China, by this time at Tianyuan Cave (Fu et al. 2013; Shang and Trinkaus 2010). Interestingly, aDNA indicates initial Siberian populations may have been genetically close to the Tianyuan Cave inhabitants; however, they were not directly ancestral to them because Ust' Ishim is equally related to the MUP Mal'ta child who does not share derived alleles with Tianyuan Cave or present-day East Asians. Therefore, ancestors of the initial Siberian population split from early East Asians before arrival in Siberia (Fu et al. 2014; Raghavan et al. 2014). Archaeological materials found above the arctic circle at Yana RHS may represent the endpoint of an EUP dispersal to Beringia (Pitulko et al. 2013); however, elsewhere in Siberia there is at least a 2 kyr gap (and given depositional and pretreatment problems of radiocarbon dates, this may be more like 5–7 kyr) between latest EUP and earliest MUP sites, artifacts from Yana are distinctively MUP, and Siberian paleoecologists have determined the intervening years (40–35 ka) between the EUP and Yana RHS were cold (Bezrukova et al. 2010; Kind 1974). Yana may represent the first far-northern incursion of people using MUP technology at 33 ka during the warm GI-5 (or Lipovo-Novoselovo interstade, 35–30 ka; Bezrukova et al. 2010).

Despite decades of work by Russian archaeologists, the geographical distance between Yana RHS and other MUP sites to the south is probably in part the result of sampling bias because much research to date has been undertaken around current population bases in southern Siberian cities. The taiga of central Siberia, especially in active permafrost conditions of the far north (Pitulko 2008), is logistically difficult for fieldwork, and very few roads into these areas mean far less archaeological survey has been done than southern regions. But the pattern of more and younger MUP sites in southern Siberia is also not surprising given that after 33 ka the Northern Hemisphere was beginning to cool with glaciers expanding from 33 to 26 ka (Clark et al. 2009). Colder, dryer conditions probably kept populations to the south during the onset of the LGM. The MUP record indicates hunter-gatherers were living in base camps and procuring resources relatively nearby. DNA from the Mal'ta child, one member of this MUP population, implies close genetic ties between Siberian and Eastern European MUP populations (Seguin-Orlando et al. 2014), either maintained from a recent common ancestor (45–36 ka) or possibly after occasional aggregation and mate exchange (see Binford 2001; Fix 1999). Given recognized similarities in lithic technologies and symbolic art forms between the Siberian MUP and the Eastern European Gravettian, the latter hypothesis may have more explanatory power, but we must keep in mind that to date we only have one Siberian MUP genome that probably does not represent all genetic variability of the Siberian MUP population.

The lack of archaeological sites dating to 24–21 ka across much of southern Siberia indicates MUP populations living in this region before the LGM were not maintained or that they were quite small and archaeologically unrecognizable. With such little aDNA preservation, we are still uncertain about exactly how the Afontova Gora individual was related to the Mal'ta child or other Upper Paleolithic skeletons. If southern Siberian populations were stressed enough to become archaeologically imperceptible during the LGM and human migrations to escape the inhospitable conditions were localized or had trajectories to the south and east, we find it highly unlikely that humans persisted in the far north.

Toward the end of the LGM, humans using an LUP adaptive strategy based on standardized formal lithic technology, specialized hunting, and high residential mobility arrived in Siberia from the east, where microblades emerged first during the LGM in Hokkaido (Izuho 2013) but perhaps were conceptually conceived from MUP small blade and flake technologies that were present in Siberia, northern China, and Korea just before the LGM (Derevianko et al. 2003; Lee 2015; Lisitsyn 2000; Seong 2011; Terry, Buvit, and Konstantinov 2016; Yi et al. 2016). Although so-called microlithic technology has been found in these places at the onset of the LGM, conceptual techniques and cognitive, technological steps used to make these small blades and flakes are different from techniques and steps to produce Yubetsu and other wedge-shaped microblade core types found in LGM and late-glacial contexts associated with the LUP (Gómez Coutouly 2012; Graf 2008, 2010; Kobayashi 1970; Nakazawa et al. 2005; Takakura 2012; Terry, Buvit, and Konstantinov 2016; Yoshizaki 1961). Despite imperfect resolution of the exact timing and location of its origin, we argue formal, developed microblade technology emerged outside southern Siberia and spread north and west with dispersing human groups at the end of the LGM, continuing the journey into higher latitudes of eastern Siberia as climates ameliorated during the late glacial.

The Beringian Record

To better understand the spread of humans from Northeast Asia to the New World, we now review Beringian archaeology starting with coverage of the two earliest sites, Yana RHS and Swan Point, followed by the late-glacial record (table 3).

The Earliest Beringian Sites: 33 ka and 14 ka

Yana RHS, discovered on the lower Yana River in northwestern Beringia, preserves an MUP component dating to 33–31 ka. Its stone artifacts are characteristically MUP, with flake-core reduction and an elaborate osseous technology of both utilitarian and nonutilitarian symbolic pieces, in some cases incredibly similar to southern Siberian MUP sites (Pitulko et al. 2013). Uncharacteristic of southern Siberian MUP sites, where resource extraction was primarily local, at Yana anthraxolite and amber were procured ≥600 km away. Subsistence pursuits were directed at large (e.g., mammoth, horse, bison) as well as smaller (reindeer and hare) game (Pitulko et al. 2004, 2013). As mentioned above, similarly aged sites exist elsewhere in northern Eurasia (Abramova et al. 1991; Graf 2009; Hoffecker 2002; Kuzmin et al. 2011; Lisitsyn 1996, 2000) but not in eastern Beringia, although questions remain regarding the correlation of humans with modified faunal remains at the Bluefish Caves sites in Yukon, Canada (see Bourgeon, Burke, and Higham 2017; Morlan 2003).

In our opinion there are currently no convincing archaeological sites dating to the LGM in Beringia (but see Pitulko, Pavlova, and Nikolskiy 2017). Instead, the next-oldest, unequivocal Beringian site is Swan Point in the Tanana Valley, central Alaska, dating to 14.1 ka (Holmes 2001, 2011), with a lithic assemblage most similar to the Siberian LUP found in the Aldan sites in southern Yakutia and countless others to the south, especially in southern Siberia (Abramova et al. 1991; Goebel 1999; Graf 2010; Mochanov 1977; Terry 2010) and Hokkaido (Izuho 2013). The 17 kyr hiatus between Yana and Swan Point begs the question, do the two sites represent both ends of early Beringian populations predicted by the long-chronology BSM (Mulligan and Kitchen 2013), or do they represent two separate dispersal events—an early one irrelevant to the peopling of the Americas (which did not reach Alaska) and a later one during the late glacial, possibly supporting a short-chronology BSM (Raghavan et al. 2015)?

At least to some degree we should also consider the hiatus between Yana and Swan Point to be an artifact of sampling—difficulties accessing today's far Northeast Asian, Alaskan, and submerged Bering Land Bridge landscapes (Hoffecker, Elias, and O'Rourke 2014)—or it could mean sustained human set-

Table 3. Climatic time-stratigraphic units associated with archaeological phases, technologies, and land-use patterns of Beringia

Dates (ka)	MIS	Greenland ice-core climatic intervals (S. O. Rasmussen et al. 2014)	Archaeological phases	Technologies	Land-use strategies
33–31	3	Greenland interstadial 5.2	Middle Upper Paleolithic (Yana RHS)	Mostly flake lithic technology; osseous projectile and sewing technologies; osseous mobile art	Large base camp with many tasks represented
31–14.5	3/2	Long Greenland stadials 5–2 interrupted by short Greenland interstadials 5–2			
14.5–14	2	Greenland interstadial 1	Late Upper Paleolithic (Swan Point)	Wedge-shaped microblade technology similar to the Siberian late Upper Paleolithic. No slotted points from the site reported	Camp with hunting-related tasks represented
13.9–12.8	2	Allerød Greenland interstadial 1 interrupted by two to three 200–100 yr cooler events	Nenana Complex	Flake, blade, and bifacial lithic technologies; triangular and teardrop-shaped lithic projectile points	Varied site types, indicating a possible logistical-mobility strategy. More sites needed
12.8–11.7	2	Younger Dryas Greenland stadial 1	Denali Complex	Wedge-shaped microblade core and flake and bifacial lithic technologies; microblade-osseous composite and lanceolate bifacial projectile points	Sites evidence mostly hunting-related activities. Too few sites to confidently identify land-use strategy
12.8–11.7	2	Younger Dryas Greenland stadial 1	North Paleo-Indian	Bifacial and flake lithic technologies; unfluted and fluted lanceolate bifacial projectile points	Sites evidence mostly hunting-related activities. Too few sites to confidently identify land-use strategy

tlement of Beringia only occurred after the LUP adaptive strategy emerged in southeastern Siberia/East Asia during the LGM and spread to northwestern North America afterward (Abramova et al. 1991; Buvit et al. 2015, 2016; Goebel 1999; Goebel and Slobodin 1999; Graf 2013, 2015; Vasil'ev 1992). Indeed, Swan Point contains distinctive Yubetsu microblade and burin technologies similar to Upper Paleolithic sites in eastern Siberia, Japan, and Korea (Andrefsky 1987; Gómez Coutouly 2011, 2012; Hirasawa and Holmes 2017; Holmes 2001, 2011; Mochanov 1977; Morlan 1978; Nakazawa et al. 2005; Yoshizaki 1961). Apart from Swan Point is a series of other late-glacial Beringian sites without microblade and burin technologies—the so-called early Ushki culture in Kamchatka, Berelekh, in northeastern Yakutia, and the Nenana complex in central Alaska, all dating to 14–13 ka (Dikov 1968; Goebel 2004*b*; Mochanov 1977; Pitulko 2011; Pitulko and Pavlova 2010; Powers and Hoffecker 1989). Could these actually represent an autochthonous Beringian population, pre-LGM holdovers predicted to have first inhabited Alaska?

Beringia from 14 to 12 ka

Much lithic variability exists in Beringia after 14 ka, with some late-glacial sites producing microblade technologies but not others (Goebel and Buvit 2011*a*; fig. 6). Although some archaeologists assemble Beringia's varied industries into a single group (i.e., Beringian tradition; Dumond 1977, 1980, 2001; Holmes 2001; Potter, Holmes, and Yesner 2013; West 1996), such lumping masks meaningful behavioral variability (Goebel and Buvit 2011*a*, 2011*b*; Hoffecker and Elias 2007). Others have recognized at least three technological complexes in early Beringia: (1) Denali, with a developed microblade component (Ackerman 2001, 2011; Ackerman, Hamilton, and Stuckenrath 1979; Anderson 1970, 1988; Goebel and Bigelow 1996; Potter et al. 2011; West 1967); (2) Nenana, with a flake and blade technological strategy distinctly without microblade technology (Goebel, Powers, and Bigelow 1991; Goebel et al. 1996; Gore and Graf 2018; Graf et al. 2015; Hamilton and Goebel 1999; Hoffecker, Powers, and Goebel 1993; Pearson 1999; Powers and Hoffecker 1989; Powers, Guthrie, and Hoffecker 2017; Yesner 1996, 2001; Yesner, Crossen, and Easton 2011); and (3) Northern Paleo-Indian, with a variety of bifacial stemmed and lanceolate points (Alexander 1987; Bever 2008; Cinq-Mars et al. 1991; Clark 1981; Rasic 2011; Smith, Rasic, and Goebel 2013).

Originally defined in central Alaska (West 1967) but now known to occur across large parts of Beringia from Kamchatka to southeast Alaska (Ackerman 2001, 2011; Ackerman et al. 1979; Dikov 1968; Dumond 1980; Powers and Hoffecker 1989; West 1996), Denali sites (e.g., Dry Creek component 2, Moose Creek component 2, Tangle Lakes sites, Gerstle River Quarry), typically dating from 12.5 to 10 ka, are generally characterized by wedge-shaped microblade cores, microblades, transverse burins, lanceolate bifacial points, and knives (Hoffecker, Powers,

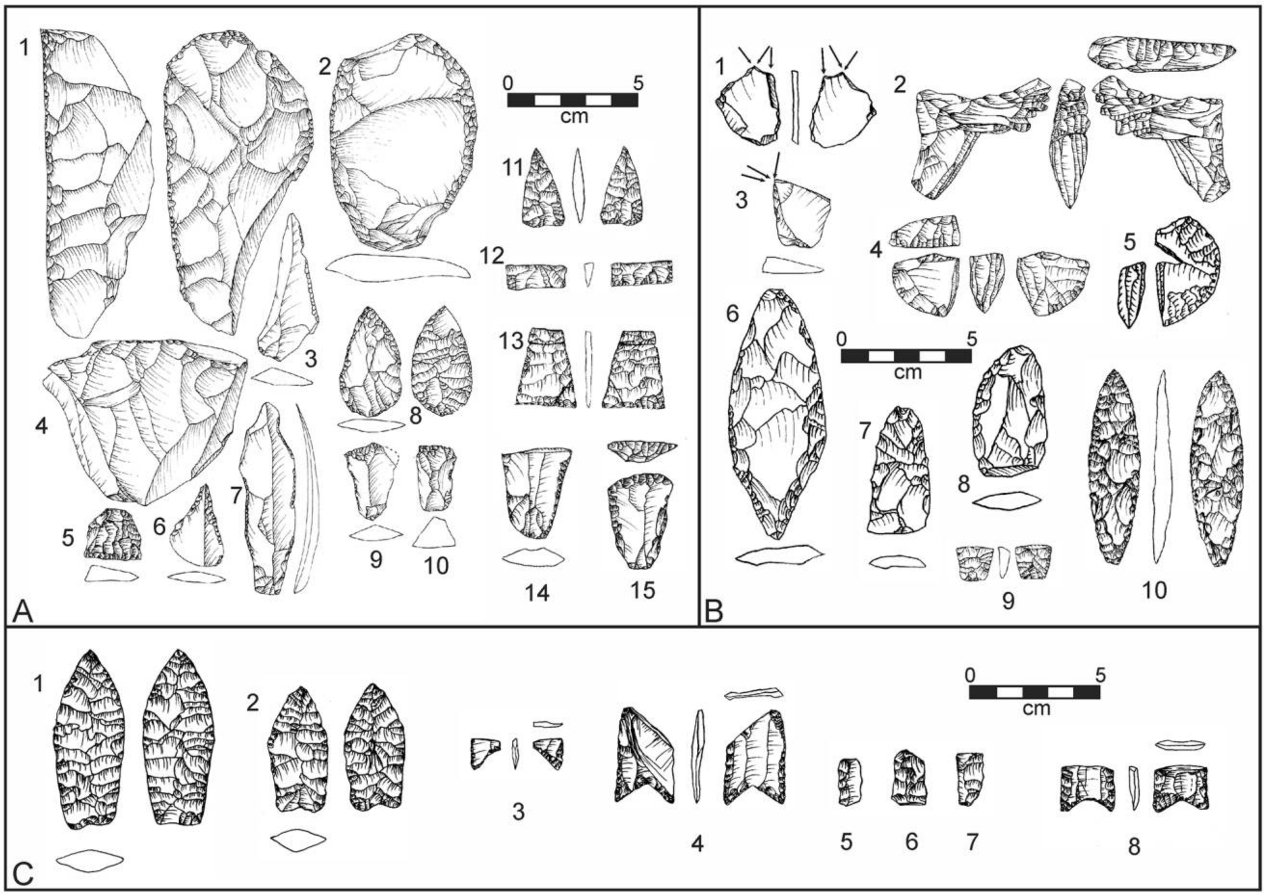

Figure 6. Representative artifacts from eastern Beringia. *A*, Nenana Complex artifacts from Walker Road: 1 (planoconvex cobble tool), 2 (unifacial side scraper), 3, 7 (utilized bladelike flakes), 4 (subprismatic blade core), 5 (bipolar flake core), 6 (bifacial drill), 8 (teardrop-shaped bifacial point), 9–10 (unifacial end scrapers; modified from Goebel and Buvit 2011); Dry Creek: 11–12 (triangular-shaped bifacial points), 14 (retouched blade), 15 (end scraper on blade; redrawn from Hoffecker, Powers, and Bigelow 1996); Owl Ridge: 13 (triangular-shaped bifacial point). *B*, Denali Complex artifacts from Donnelly Ridge: 1 (burin), 5 (wedge-shaped microblade core), 6–8 (bifaces; modified from Goebel and Buvit 2011); Dry Creek: 2 (wedge-shaped microblade core refit with a ski spall and core tablets), 3 (burin), 4 (wedge-shaped microblade core), 9 (bifacial lanceolate point base; redrawn from Hoffecker, Powers, and Bigelow 1996); Owl Ridge: 10 (bifacial lanceolate point). *C*, Northern Paleo-Indian projectile points from Mesa: 1–2 (lanceolate bifacial points; modified from Goebel and Buvit 2011); Serpentine Hot Springs: 3–4 (fluted bifacial point base), 5–7 (flute (channel) flakes); Raven Bluff: 8 (fluted bifacial point base).

and Goebel 1993; Potter 2007; Powers and Hoffecker 1989; West 1967). Occasionally, Denali occupations lack microblades (e.g., Carlo Creek component 1, Panguingue Creek component 1, Upward Sun River; Bowers 1980; Goebel and Bigelow 1996; Graf and Bigelow 2011; Potter et al. 2011).

Several sites stretching from western to eastern Beringia share a common technological complex reflecting an adaptive strategy different from the Siberian LUP. Based on stratigraphic correlation and a suite of radiocarbon ages from the lowest components of the Dry Creek, Owl Ridge, Moose Creek, and Walker Road sites in the Nenana River valley (Goebel, Powers, and Bigelow 1991; Graf and Bigelow 2011; Graf et al. 2015; Pearson 1999; Powers and Hoffecker 1989), Nenana complex sites date to 13.5–13 ka. These lithic industries lack microblade and burin technologies but include blade and flake cores, small teardrop-shaped and triangular Chindadn points on flake blanks, and unifacial tools such as end scrapers, side scrapers, and gravers on flakes and blades (Goebel, Powers, and Bigelow 1991; Gore and Graf 2018; Graf et al. 2015; Hoffecker, Powers, and Goebel 1993; Powers, Guthrie, and Hoffecker, 2017). The lowest cultural components at the Broken Mammoth and Linda's Point sites in the middle Tanana River valley (Alaska) and Little John site in the upper Tanana River valley (Yukon) date about 13.5–13 ka and may be attributable to Nenana (Yesner 1996, 2001; Yesner, Crossen, and Easton 2011; Younie 2015; Younie and Gillespie 2016). Three sites in western Beringia—Lake Nikita and Berelekh (14–13.5 ka) on the lowermost Indigirka River, and cultural layer 7 at the Ushki Lake sites (13 ka) in central Kamchatka (Dikov 1968; Goebel, Waters, and Dikova 2003; Goebel, Slobodin, and Waters 2010; Kuzmin and

Tankersley 1996; Pitulko 2011; Pitulko and Pavlova 2010)—are contemporaneous and share similar lithic industries with Nenana. These assemblages seemingly form a cohesive Beringian-wide complex dating to a relatively short, 1 kyr interval with very similar technological strategies.

The Northern Paleo-Indian tradition includes sites found across the northern reaches of eastern Beringia from the Seward Peninsula to the Yukon. These sites contain finely flaked, lanceolate bifacial points that are sometimes end thinned or even fluted. Alaskan fluted points similar to Paleo-Indian varieties in temperate North America at 12.5 to 11.5 ka clearly postdate Clovis and have been found in datable contexts at sites such as Serpentine Hot Springs on the Seward Peninsula and Raven Bluff in the western Brooks Range of northern Alaska (Ian Buvit, William Hedman, Steven Kuen, and Jeff Rasic, "Formation, age, and depositional environments of the Raven Bluff fluted point site, northwest Alaska," unpublished manuscript; Goebel et al. 2013). Unfluted lanceolate bifacial points have been found at the sites of Tuluaq Hill, Irwin Sluiceway, and Mesa in the Brooks Range and Engigstciak in far northwestern Yukon. These all date to ~12.5–11 ka, with the exception of the Tuluaq Hill with dates of ~13–12.8 ka (Kunz, Bever, and Adkins 2003; Rasic 2011; Smith, Rasic, and Goebel 2013).

Beringian archaeologists recognize much variability among late-glacial sites even within the three complexes considered here. In central Alaska, for example, some early Denali sites lack microblades but still have signature lanceolate bifacial points and transverse burins. In northern Alaska, Mesa (Bever 2008) and Raven Bluff (Ian Buvit, William Hedman, Steven Kuen, and Jeff Rasic, "Formation, age, and depositional environments of the Raven Bluff fluted point site, northwest Alaska," unpublished manuscript) have microblades stratigraphically associated with otherwise Paleo-Indian-looking assemblages. Explanations of the patterns of variability generally fall into three working hypotheses: (1) different populations or cultural groups, (2) different technological activities or seasonal use of sites within a single adaptive strategy, or (3) diachronic changes in adaptive strategies as early Beringians responded to climate change (Goebel and Buvit 2011*a*, 2011*b*; Graf and Bigelow 2011; Potter, Holmes, and Yesner 2013).

Discussion: An Archaeological Test of the Beringian Standstill Models

Does archaeological evidence support a long-chronology BSM? The Siberian Upper Paleolithic archaeological record indicates that the peopling process of this vast region was episodic and punctuated by inclement climatic events such as the LGM (Graf 2008, 2009, 2010; Hamilton and Buchanan 2010). As mentioned above, paleoecological proxy records from Siberia and Beringia indicate both regions similarly experienced very extreme cold and arid conditions during the LGM. This means that despite humans pushing as far as the Yana RHS site in western Beringia during the warm GI-5 event, populations across the north decreased during the LGM to archaeologically imperceptible levels (Buvit et al. 2015; Graf 2009, 2015; see also Mussi 2015 for evidence for LGM abandonment of Europe). Therefore, the current Siberian and Beringian archaeological records do not support expectations of the long-chronology BSM: no archaeological sites date to the LGM, demonstrating maintained human populations in far-northern Siberia and Beringia from 30 to 16 ka.

Does archaeological evidence support a short-chronology BSM? Considering Siberian and Beringian depopulation during the LGM as we do, the initial dates in the Transbaikal of the sudden presence of formal microblade technology as part of an LUP adaptive strategy and a subsequent time-transgressive spread of this technology and way of life north and west through eastern Siberia, we maintain that a population of people dispersed north from East Asia on the heels of the LGM as climate began to ameliorate. The aDNA of Mal'ta and its relationship to Native Americans suggests at least one introgression event into some East Asian populations after 24 ka coincidental with reintroduction of microblades and dispersal of this technology north to Beringia (Graf 2013; Raghavan et al. 2014, 2015). We hypothesize introgression may have occurred somewhere between the PSHK and Lake Baikal. During the LGM, the MUP population dwindled in southern Siberia, but remnants may have persisted farther east, possibly toward the coast of the Sea of Japan or on PSHK, where conditions were much more conducive to human habitation than they were farther inland (Igarashi 2016; Momohara et al. 2016). During the late stages of the LGM, an East Asian population with some western admixture utilizing an LUP lifeway, technologically focused on microblades, pushed west into the Transbaikal region by 22.7 ka and eventually north to Yakutia by about 17–15.5 ka when LUP sites appear in the Aldan River valley. Subsequent dispersal east could have placed humans, with a highly mobile LUP-based land-use strategy, in Alaska 2 kyr later, by ~14 ka, when the Swan Point site was inhabited. Exact locations of events remain unknown, but filling the geochronological and technological gaps and making a direct connection between Diuktai and Swan Point seem more tenable than filling gaps and directly linking Yana with Swan Point. Further, the marked archaeological variability that emerged in Beringia following initial occupation at Swan Point is temporally patterned. We contend it resulted from human response to late-glacial climatic and environmental changes. After initially arriving in Beringia as a genetically diverse population equipped with "institutional knowledge" of Siberian flake, blade, and microblade forms, these first Americans switched between technological and food-procuring strategies in response to environmental and associated resource distribution changes.

Currently, archaeological records best fit the short-chronology BSM for timing, but we predict the incubation event did not take place in Beringia but in the Russian Far East or on PSHK during the LGM before dispersal back into Siberia. The sudden emergence and rapid spread of the LUP lifeway as well as the proposed genetic makeup of Asian ancestors of first Americans may support this hypothesis with inland migration to Beringia and the Americas; however, more skeletons are needed to test a Northeast Asian standstill.

Conclusions and Future Directions

The peopling of Siberia and Beringia was episodic, taking tens of thousands of years and with more than one dispersal attempt evidenced. We know from emerging LGM records that humans did not continuously occupy the far north above 60°N latitude until after 15 ka. No LGM-aged archaeological sites have yet been found on the Bering Land Bridge, but after initial arrival of humans after the LGM, the Beringian archaeological record becomes highly diverse through the late glacial as the immediate ancestors of the first Americans adapted to fluctuations in resource availability. Siberian and Beringian archaeological records thus support Raghavan et al.'s (2015) short-chronology BSM.

Future research to confirm or refute the BSMs requires a continued search for archaeological sites providing not only artifacts, features, and ecofacts but also human remains in the hard-to-reach regions between Lake Baikal and Alaska/Yukon where it is predicted by the models that either LGM or post-LGM sites exist. Similarly, when possible, excavations need to be carried out with the goal of answering questions about formation processes, prehistoric lifeways, and site function. Every effort should be made to revisit key sites (esp. Aldan sites in Yakutia and Bluefish Caves in Yukon) to resolve questions about chronology, prehistoric landscapes, and stratigraphic associations. These sites and others may provide important links between southern Siberia and North America and empirical evidence for the location of the standstill or homeland of the genome of first Americans.

We also need to better characterize the relationship between Beringian and LUP lithic assemblages of southern Siberia, the Far East, PSHK, and Paleo-Honshu with more sophisticated analytical techniques that allow for comparable results, such as recent morphometric analyses to explain cultural transmissions of artifact forms (Davis et al. 2015; Smith, Smallwood, and DeWitt 2014). These, in addition to detailed, systematic investigations of lithic raw material sourcing and technological provisioning and organization studies (Coffman and Rasic 2015; Gore and Graf 2018; Graf 2010; Kuzmin et al. 2008; Nakazawa and Yamada 2015; Reuther et al. 2011; Terry, Andrefsky, and Konstantinov 2009) will help link together the strategies employed from southern Siberia to eastern Beringia.

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