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Archaeological evidence for two separate dispersals of Neanderthals into southern Siberia

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Abstract

Neanderthals were once widespread across Europe and western Asia. They also penetrated into the Altai Mountains of southern Siberia, but the geographical origin of these populations and the timing of their dispersal have remained elusive. Here we describe an archaeological assemblage from Chagyrskaya Cave, situated in the Altai foothills, where around 90,000 Middle Paleolithic artifacts and 74 Neanderthal remains have been recovered from deposits dating to between 59 and 49 thousand years ago (age range at 95.4% probability). Environmental reconstructions suggest that the Chagyrskaya hominins were adapted to the dry steppe and hunted bison. Their distinctive toolkit closely resembles Micoquian assemblages from central and eastern Europe, including the northern Caucasus, more than 3,000 kilometers to the west of Chagyrskaya Cave. At other Altai sites, evidence of earlier Neanderthal populations lacking associated Micoquian-like artifacts implies two or more Neanderthal incursions into this region. We identify eastern Europe as the most probable ancestral source region for the Chagyrskaya toolmakers, supported by DNA results linking the Neanderthal remains with populations in northern Croatia and the northern Caucasus, and providing a rare example of a long-distance, intercontinental population movement associated with a distinctive Paleolithic toolkit.

Keywords

southern, into, neanderthals, siberia, dispersals, archaeological, separate, two, evidence

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Neanderthals were once widespread across Europe and western Asia. They also penetrated into the Altai Mountains of southern Siberia, but the geographical origin of these populations and the timing of their dispersal have remained elusive. Here we describe an archaeological assemblage from Chagyrskaya Cave, situated in the Altai foothills, where around 90,000 Middle Paleolithic artifacts and 74 Neanderthal remains have been recovered from deposits dating to between 59 and 49 thousand years ago (age range at 95.4% probability). Environmental reconstructions suggest that the Chagyrskaya hominins were adapted to the dry steppe and hunted bison. Their distinctive toolkit closely resembles Micoquian assemblages from central and eastern Europe, including the northern Caucasus, more than 3,000 kilometers to the west of Chagyrskaya Cave. At other Altai sites, evidence of earlier Neanderthal populations lacking associated Micoquian-like artifacts implies two or more Neanderthal incursions into this region. We identify eastern Europe as the most probable ancestral source region for the Chagyrskaya toolmakers, supported by DNA results linking the Neanderthal remains with populations in northern Croatia and the northern Caucasus, and providing a rare example of a long-distance, intercontinental population movement associated with a distinctive Paleolithic toolkit.

Chagyrskaya Cave | Altai Mountains | Siberian Neanderthals | Middle Paleolithic | Micoquian artifacts

The period of existence of Neanderthals, their geographical range, and the timing of their dispersal and extinction are key issues in the study of human evolution and migration. Most Neanderthal remains and associated artifacts have been reported from Europe and western Asia, where they range in age from about 430,000 to 40,000 years ago (kiloannus, or ka) (1, 2). Further east, the unequivocal presence of Neanderthals prior to the last interglacial (which began around 130 ka) until about 50 ka is based on hominin remains (3) and DNA analyses of skeletal remains and sediments at three caves (Okladnikov, Denisova, and Chagyrskaya) in the Altai Mountains of southern Siberia (4–7). Additional evidence is required to support suggestions that Neanderthals had reached eastern and northern China by 125 to 105 and 45 ka, respectively (8, 9). Two genetically distinct Neanderthal populations inhabited the Altai region sometime during the Late Pleistocene (10), but the geographical origin of these populations and the timing of their migrations into the region remain unclear. On current evidence, Neanderthals were present at Denisova Cave between about 200 and 100 ka (11, 12).

Chagyrskaya Cave (51°26′34.6′′ N, 83°09′18.0′′ E) is situated 19 m above the Charysh River in the western piedmont of the Altai Mountains (Fig. 1 and *SI Appendix*, Fig. S1), approximately 100 km west of Denisova Cave (13). The cave consists of two chambers, with a stratigraphic sequence up to 3.5 m thick (*SI Appendix*, sections S1 and S2, Figs. S2–S4, and Table S1). The dense basal deposit (layer 7) is archaeologically sterile and composed mainly of gravel and fine-grained sediments. An erosional contact (unconformity) separates it from overlying layers 6 and 5, which consist of poorly sorted sediments that contain approximately 90,000 Middle Paleolithic (MP) artifacts (including numerous bone tools), 74 Neanderthal specimens, about 250,000 animal fossils, and a range of plant remains (*SI Appendix*, section S3) (14 and 15). The sequence is capped by Bronze Age deposits, with no evidence of Upper Paleolithic (UP) occupation.

Results

Site Chronology and Environmental Reconstructions. Optical ages for 23 sediment samples indicate that layer 7 was deposited

Significance

Neanderthals once inhabited Europe and western Asia, spreading as far east as the Altai Mountains in southern Siberia, but the geographical origin and time of arrival of the Altai populations remain unresolved. Excavations at Chagyrskaya Cave in the Altai foothills have yielded 90,000 stone artifacts, numerous bone tools, 74 Neanderthal fossils, and animal and plant remains recovered from 59,000- to 49,000-year-old deposits. The Chagyrskaya Neanderthals made distinctive stone tools that closely resemble Micoquian artifacts from eastern Europe, whereas other Altai sites occupied by earlier Neanderthal populations lack such artifacts. This suggests at least two dispersals of Neanderthals into southern Siberia, with the likely ancestral homeland of the Chagyrskaya toolmakers located 3,000 to 4,000 kilometers to the west, in eastern Europe.

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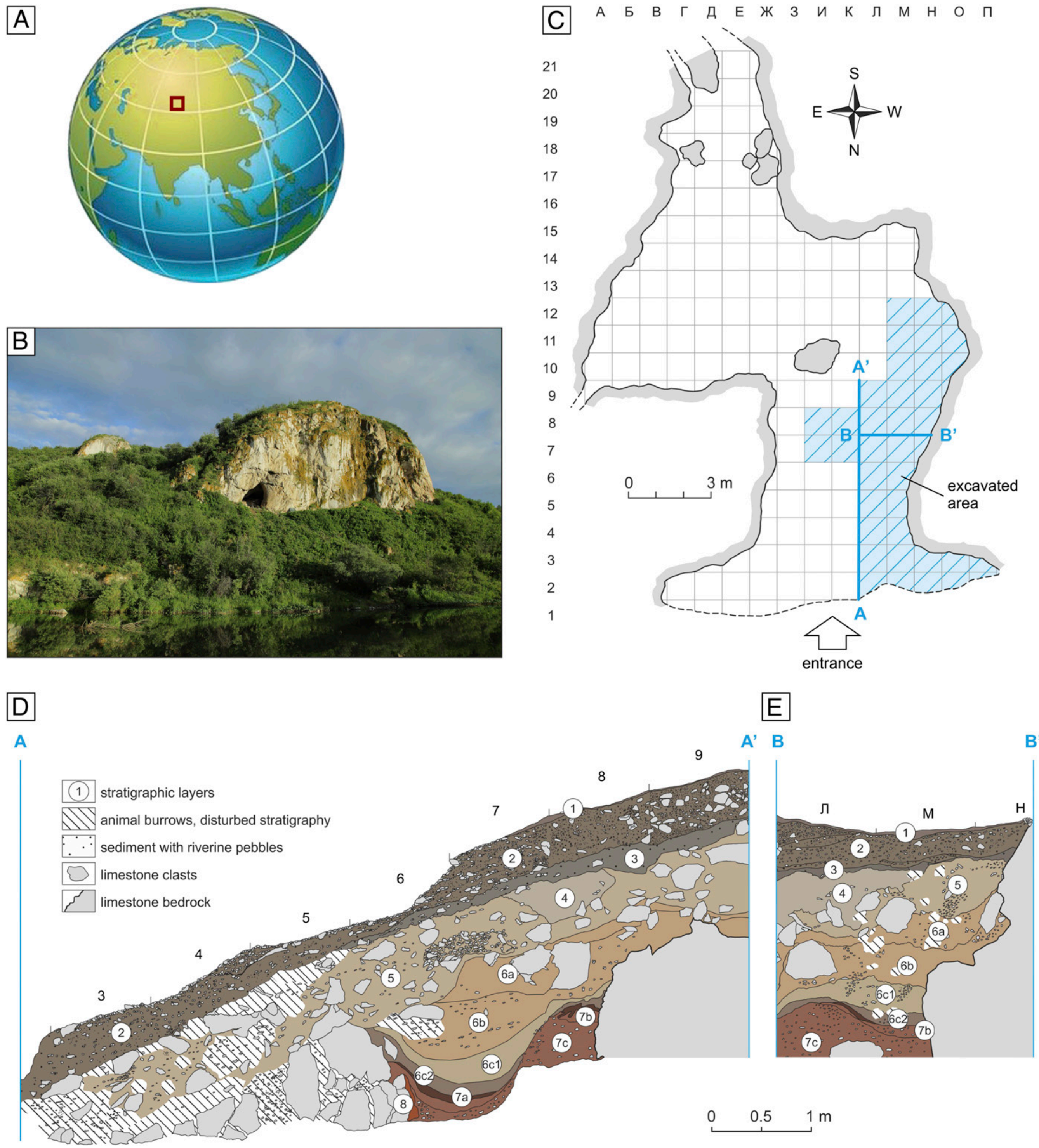

Fig. 1. Chagyrskaya Cave. (*A*) Site location in the Altai region of southern Siberia. (*B*) View of the cave entrance, which faces north. (*C*) Plan of the cave interior showing the excavated area (in blue). (*D* and *E*) Stratigraphic profiles along the two transects (A–A′ and B–B′, respectively) shown in *C*.

329 ± 16 ka (weighted mean age of four samples) and that layers 6 and 5 accumulated sometime between 63 ± 4 and 48 ± 3 ka (weighted mean age of 54.0 ± 2.5 ka; total uncertainty at 1σ). The latter are consistent with the mostly infinite radiocarbon ages obtained for 20 bison (*Bison priscus*) remains (*SI Appendix*, section S4, Figs. S5 and S6, and Tables S2 and S3), but are younger than the DNA-based age estimate of 87 to 71 ka for the "Chagyrskaya Neanderthal" (Chagyrskaya 8) (16, 17), a distal manual phalanx retrieved from the sieved sediments of subunit 6b. This discrepancy may reflect a higher mutation rate in Neanderthals than in modern humans (18) that has not been taken into account and/or the omission of other uncertainties in the genetic age estimates, such as population size and generation interval. Chagyrskaya 8 and Denisova 3 (the youngest Denisovan fossil) share similar proportions of "missing" genetic mutations compared to present-day humans, which suggests that they are

similar in age (16). Denisova 3 has been dated to between 76.2 and 51.6 ka (11, 12), an age range compatible with the optical ages for layers 6 and 5 at Chagyrskaya Cave. An overview of the human remains recovered from Chagyrskaya Cave is given in *SI Appendix*, section S5, Figs. S7–S9, and Table S4.

The subunits of layer 6 have statistically indistinguishable ages, which indicate that these Neanderthal-associated MP deposits accumulated over a few millennia or less, during the final phase of marine isotope stage (MIS) 4 and/or the start of MIS 3. This was a period of cold climate (but warmer than during MIS 4), as indicated by pollen and mammal and bird remains from layer 6 compatible with a dry steppe environment and a rarity or lack of tundra species (*SI Appendix*, section S3) (13–15). Layer 5 was deposited during a period of relatively warm and humid climate, characterized by steppe and forest-steppe vegetation. The main hominin occupation of Chagyrskaya Cave occurred during accumulation of subunit 6c, which represents the primary depositional context of the MP assemblage; subunits 6b and 6a and layer 5 include redeposited MP artifacts, bones, and sediments (*SI Appendix*, sections S1 and S2). Sedimentology and micromorphology analyses support these interpretations of cave use, site formation, and environmental conditions (ref. 13 and *SI Appendix*, sections S1 and S2). Neanderthal hunting activity was focused on bison (juveniles and females in particular) and may have been connected to the seasonal migration of bison herds to and from the mountain foothills (14). Other prey hunted to a lesser extent included horse, reindeer, Siberian ibex, and argali.

Chagyrskaya Cave Lithic Assemblage. A total of 89,539 artifacts have been recovered from layer 6. Detailed lithic analysis of 4,249 artifacts from subunits 6a to 6c indicates that the assemblage represents a single technocomplex, with no marked differences between subunits (*SI Appendix*, section S6). Subunit 6c consists of two sublayers (6c/2 and 6c/1) with indistinguishable optical ages. Sublayer 6c/1 contains more artifacts than does sublayer 6c/2, which is preserved in only a few, spatially restricted, parts of the site. Accordingly, we focus here on the technological and typological characteristics of the 3,021 artifacts from sublayer 6c/1 and on the morphological variability of plano-convex bifacial tools (commonly retouched using bone; Fig. 2) and convergent scrapers in particular.

The lithic assemblage consists of 25 raw materials, including high-quality jaspers, chalcedonites, and porphyrites, which were sourced as pebbles from the nearby riverbed. The assemblage is dominated by debris and chips, with the remaining artifacts characterized by a high proportion of tools and a few cores. Most of the flakes have asymmetrical trapezoidal and rectangular shapes and were manufactured on site using bifacial plano-convex, radial (Levallois centripetal), and orthogonal core-reduction flaking methods; blades occur in low numbers as occasional by-products. Scrapers dominate the toolkit, with a preference for trapezoidal and leaf shapes. Details of artifact production techniques, illustrations of artifacts, the proportions of different artifact types, and the variables used for statistical analysis are given in *SI Appendix* section S6, Figs. S10–S20, and Tables S5–S11.

Comparison with Other Altai MP Assemblages. The Chagyrskaya toolkit had been previously been grouped with the small artifact assemblage from Okladnikov Cave and named the Sibiryachikha variant (19). Only the remains of Neanderthals have been found in association with this variant, whereas the assemblages found at Denisova Cave and at the open-air sites of Kara-Bom and Ust'-Karakol-1 cannot be related unambiguously to a specific hominin species. Both Neanderthals and Denisovans (a genetically related group of archaic hominins) were present at Denisova Cave during the MP (11, 12), while Kara-Bom and Ust'-Karakol-1 have not yielded any hominin remains. These

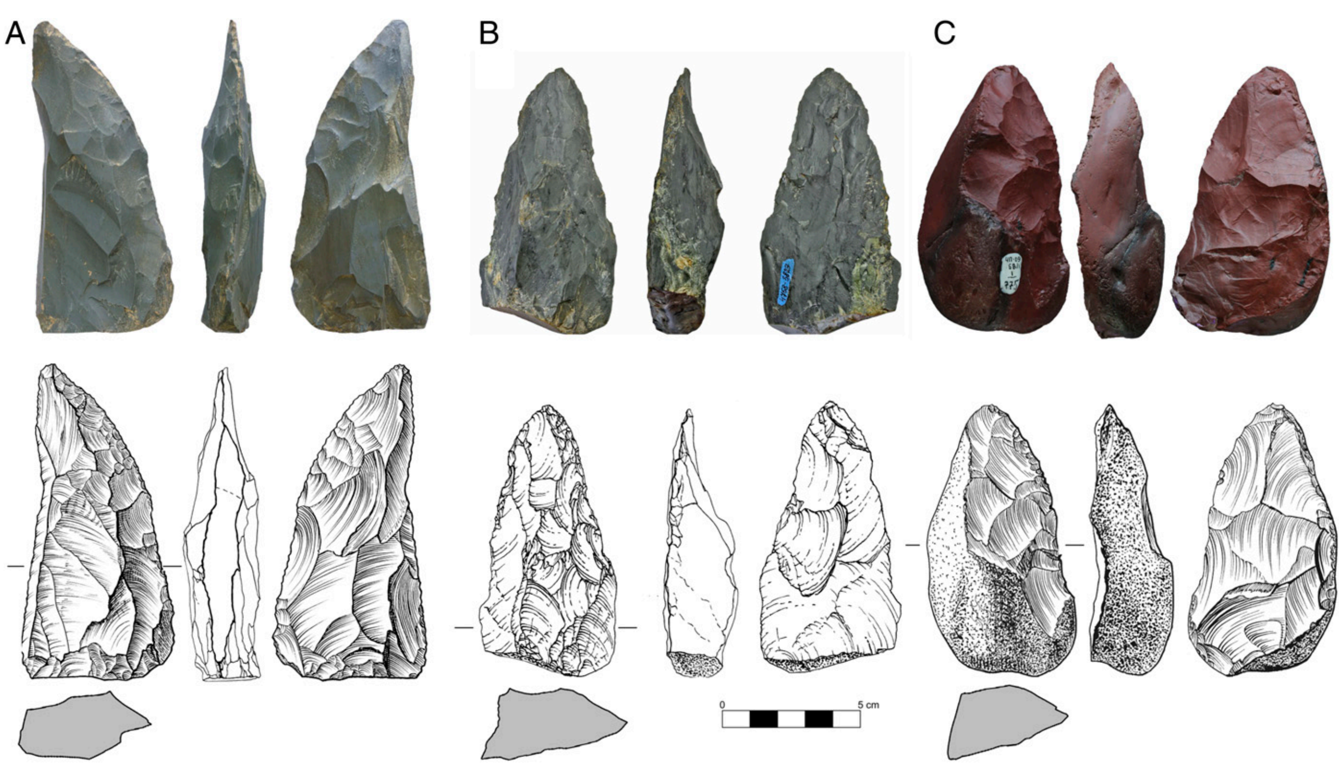

Fig. 2. Stone artifacts from Chagyrskaya Cave, sublayer 6c/1. (*A*–*C*) Photographs, line drawings, and cross-sectional profiles of three plano-convex bifacial tools diagnostic of Micoquian *Bocksteinmesser* and *Klausennischemesser* types. (Scale bar, 5 cm.)

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assemblages reflect the local development of Levallois-based industries with Mousterian features (20–22), and they differ markedly from the Sibiryachikha variant, which is dominated by bifacial plano-convex, radial, and orthogonal flaking methods; bifacial tools; convergent scrapers and points; and the absence of Levallois preferential and Levallois convergent core reductions.

Similarities between MP artifacts and associated hominin remains in the Altai, central Asia, and eastern Europe have been proposed (19, 23–26), but limitations in the archaeological and fossil records have precluded firm conclusions. We used a set of statistical methods (including hierarchical cluster analysis, nonmetric multidimensional scaling, and principal component analysis) to compare the technological and typological attributes of the Chagyrskaya artifacts with Levallois-Mousterian MP and UP assemblages in central Asia, and with Micoquian assemblages in central and eastern Europe. The analysis clearly distinguishes the Chagyrskaya assemblage from the central Asian Levallois-Mousterian MP and UP assemblages (Fig. 3 *A* and *B* and *SI Appendix*, section S7, Figs. S21*A* and S22*A*, and Tables S12–S19). Analysis of debitage that has been examined using a technological approach yields the same outcome (*SI Appendix*, Fig. S23 and Table S20). This suggests that the Chagyrskaya assemblage and that from Okladnikov Cave, the age of which is uncertain but is likely also younger than that of the Denisova Neanderthals (4, 19), constitute a separate and unique regional MP variant, technologically and typologically distinct from the Altai Levallois-Mousterian technocomplex.

Comparison with European Micoquian Assemblages. In contrast to the above distinctions, there are strong similarities between the Chagyrskaya assemblage and the Micoquian/*Keilmessergruppen* (KMG) technocomplex, which is based on non-Levallois core-reduction flaking methods and bifacial tool production using plano-convex methods (Fig. 3*B*). Micoquian/KMG sites dating to between approximately 130 and 30 ka have been found across central and eastern Europe (*SI Appendix*, Fig. S24) (27–30). Statistical analysis of the Micoquian/KMG and Chagyrskaya assemblages (using the same methods as above) demonstrates a uniformity of the European assemblages grouped by 26 variables, the most significant of which are related to the plano-convex technological and typological characteristics (Fig. 3 *A* and *C* and *SI Appendix*, section S8, Figs. S21*B* and S22*B*, and Tables S21–S28). All assemblages from Chagyrskaya and central/eastern Europe contain bifacial tools diagnostic of the Micoquian, such as the *Bocksteinmesser* and *Klausennischemesser* types (Fig. 2). The Chagyrskaya assemblage fits most closely with the eastern European Micoquian complexes.

The pronounced similarity of European Micoquian and Chagyrskaya bifacial tools is also supported by a geometric morphometric shape analysis of bifaces, including *Bocksteinmesser* and *Klausennischemesser* types, from the key Micoquian/KMG site of Sesselfelsgrotte (Germany) and Chagyrskaya Cave (*SI Appendix*, Figs. S25 and S26 and Tables S29 and S30). This result suggests the existence of a common design in the technological concept of bifacial production of Micoquian/KMG complexes.

Chagyrskaya 8 genetically resembles Neanderthals from northern Croatia and the northern Caucasus, Vindija 33.19 [radiocarbon age approximately 48 ka cal. B.P. (31)], and Mezmaiskaya 1 (16, 17) [electron spin resonance ages around 70 to 55 ka (32, 33)]. The associated MP assemblage at Vindija Cave is in questionable stratigraphic context (31), but the Micoquian assemblage at Mezmaiskaya Cave is characterized by numerous plano-convex bifacial tools, including *Bocksteinmesser* bifaces, numerous convergent scrapers, retouched/Mousterian points, and angled scrapers (33). We compared the Chagyrskaya assemblage with the combined European Micoquian (including Mezmaiskaya) and Altai/central Asian MP and UP datasets using a more limited number of technological and typological variables common to these technocomplexes. The Chagyrskaya and European Micoquian assemblages cluster together, and the Altai/central Asian assemblages form a separate cluster (Fig. 3 *A* and *D* and *SI Appendix*, Tables S31–S33), thereby replicating the results above.

Discussion

The Chagyrskaya assemblage and the European Micoquian technocomplex overlap chronologically between about 59 and 49 ka and have strong technological and morphological similarities. The Chagyrskaya assemblage can therefore be viewed as a southern Siberian variant of the European Micoquian, and the Sibiryachikha variant seen more broadly as an expression of Micoquian variability across Eurasia. Micoquian populations are commonly considered specialized horse and bison hunters, adapted to steppe and piedmont environments (27, 28). We attribute their presence in the Altai to the eastward migration of Neanderthals from eastern Europe along the Eurasian steppe belt during the cold and arid conditions of MIS 4 (*SI Appendix*, section S9).

DNA recovered from human remains and sediments indicates that Neanderthals first appeared in the Altai before or during MIS 5 (4–7, 10–12). These early populations are not associated with Micoquian artifacts, which appear at Chagyrskaya only toward the end of MIS 4 or the start of MIS 3. It is not possible to distinguish Neanderthal from Denisovan technocomplexes in the cultural sequence at Denisova Cave due to the homogeneous technological and typological characteristics of the lithic assemblages (20). However, the absence of Micoquian-like artifacts at Denisova Cave in deposits dated to between 59 and 49 ka (11) indicates that Denisova and Chagyrskaya Caves were occupied by two distinct Neanderthal populations, most likely at different times given current evidence that Neanderthals were present at Denisova Cave much earlier than at Chagyrskaya Cave (11, 12). Genetic data from Denisova Cave have also revealed several episodes of gene flow between Neanderthals and modern humans (5, 6) and two different Neanderthal components in Denisova 11, the Neanderthal-Denisovan offspring (*SI Appendix*, section S5 and ref. 10).

We therefore propose that Neanderthals entered southern Siberia on at least two separate occasions, with the most recent incursion originating in eastern Europe and the northern Caucasus, which lie 3,000 to 4,000 kilometers to the west of Chagyrskaya Cave. The identification of Micoquian assemblages in all three regions is consistent with the genetic similarities between Neanderthal remains at Chagyrskaya, Vindija, and Mezmaiskaya Caves (16, 17). Our archaeological data support a rarely observed case of long-distance demic dispersal in the Paleolithic and illustrate that artifacts are culturally informative markers of ancient population movements.

Materials and Methods

Stratigraphy and Site Formation. The sedimentary sequence was divided into stratigraphic units—called layers (e.g., layer 6), which were further divided into subunits (e.g., subunit 6c) and sublayers (e.g., sublayer 6c/1)—based on lithological differences and the presence of erosional features. We adopted the stratigraphic scheme used by earlier excavations (13), with further development based on new observations (*SI Appendix*, section S1). Micromorphological analysis of 10 thin sections (prepared from blocks of undisturbed sediment) was used to elucidate the processes responsible for site formation and depositional and postdepositional environments, and to provide context for the archaeological finds (*SI Appendix*, section S2). Sample locations were chosen to maximize the potential for interpreting environmental signals, but were restricted to the stratigraphic profiles exposed in 2014 and 2017.

Radiocarbon Dating of Bone Collagen. Twenty *Bison* bone samples retrieved from layers 5 and 6, including at least 10 humanly modified bones from subunit 6b and sublayer 6c/1, were selected for radiocarbon dating. Collagen was extracted from these samples and the >30-kDa fraction isolated by ultrafiltration to remove contaminants with lower molecular weights (15). The

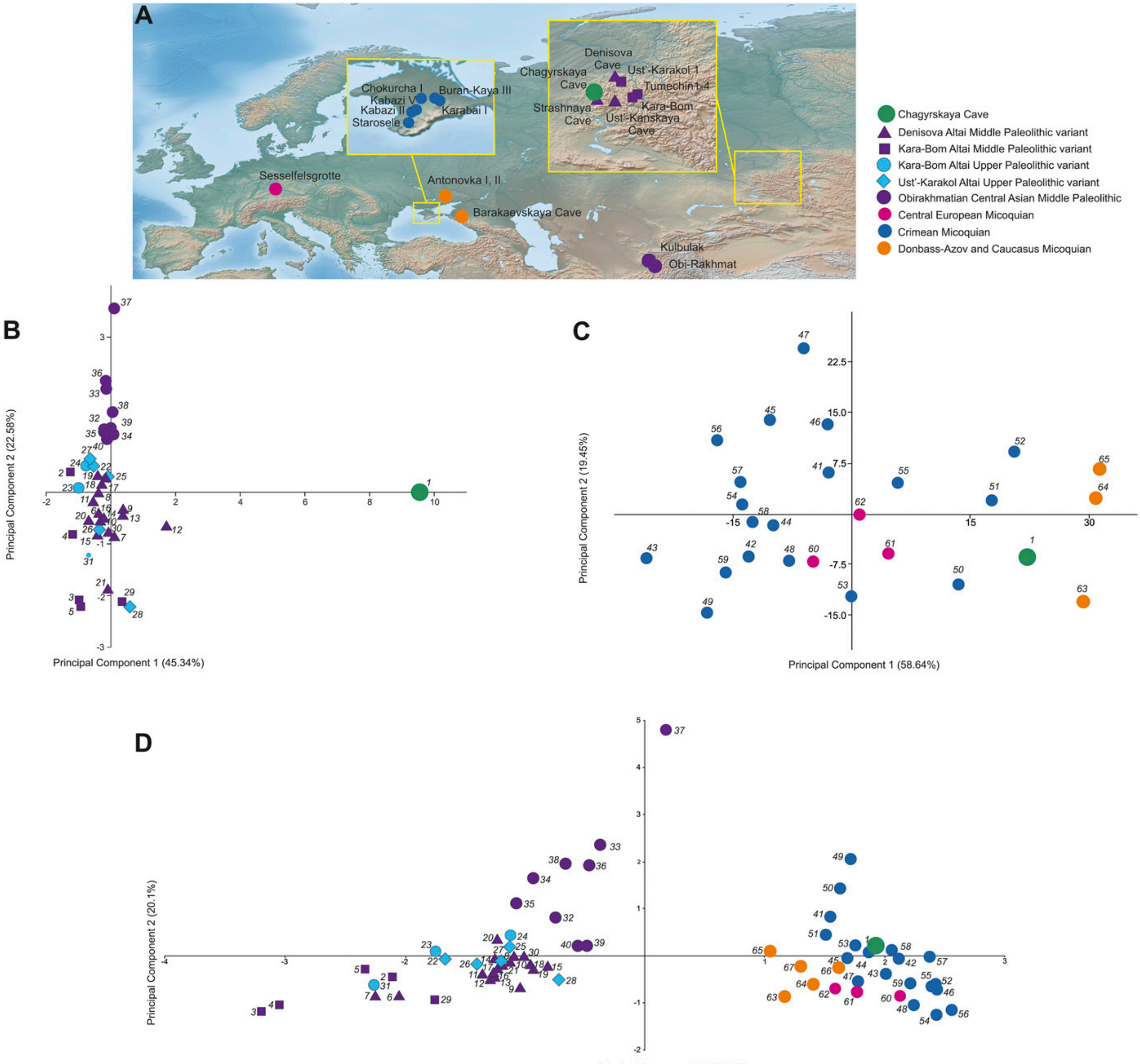

Fig. 3. Site map and principal component analysis of MP and UP lithic assemblages. (*A*) Location of sites with Levallois-Mousterian and Micoquian assemblages used for statistical comparison with Chagyrskaya Cave artifacts. (*B*) Scatterplot of the first two principal components for assemblages from Chagyrskaya Cave, three other Altai sites (Denisova Cave, Kara-Bom, Ust'-Karakol-1), and Obi-Rakhmat in central Asia ($n = 40$). (*C*) Scatterplot of the first two principal components for assemblages from Chagyrskaya and Micoquian sites in eastern Europe (Crimea, Donbass-Azoz, Caucasus) and central Europe ($n = 26$). (*D*) Scatterplot of the first two principal components for assemblages from Chagyrskaya Cave, Levallois-Mousterian sites in the Altai and central Asia, and European Micoquian sites ($n = 67$). The italic numbers correspond to the following sites and assemblages: 1, Chagyrskaya Cave (sublayer 6c/1); 2, Ust'-Karakol-1 (layers 17 to 13); 3, Ust'-Karakol-1 (layer 18); 4, Kara-Bom (layer MP2); 5, Kara-Bom (layer MP1); 6 to 8, Denisova Cave (entrance zone, layers 10 to 8, respectively); 9 to 13, Denisova Cave (main chamber, layers 22, 21, 19, 14, and 12, respectively); 14 to 19, Denisova Cave (east chamber, layers 15, 14, 12, and 11.4 to 11.2, respectively); 20, Strashnaya Cave; 21, Ust'-Kanskaya Cave; 22, Ust'-Karakol-1 UP (layer 11); 23, Kara-Bom UP (layers 6 and 5); 24, Kara-Bom UP (layers 4 to 1); 25, 26, Denisova Cave UP (entrance zone, layers 7 and 6, respectively); 27, Denisova Cave UP (main chamber, layer 11); 28, Denisova Cave UP (east chamber, layer 11.1); 29, Tumechin-1; 30, Tumechin-2; 31, Tumechin-4; 32 to 39, Obi-Rakhmat (layers 21.1, 20, 19.5 to 19.1, and 14.1, respectively); 40, Kulbulak, layer 23); 41 to 45, Kabazi V (subunits I/4A–II/7, III/1, III/1A, III/2, and III/5, respectively); 46, Karabai I (layer 4); 47, 48, Kabazi II (units IIA–III and V–VI, respectively); 49, Kiik-Koba (level IV); 50, Buran Kaya III (layer B); 51, Starosele (level 1); 52, Chokurcha I (unit IV); 53 to 59, Zaskalnaya V (units I, II, IIa, III/1–III/9–1, III/10–III/14, IIIA, and IV, respectively); 60 to 62, Sesselfelsgrotte (units G4–G2, respectively); 63, Antonovka I; 64, Antonovka II; 65, Barakaevskaya Cave; 66, 67, Mezmaiskaya Cave (layers 2B-4 and 3, respectively).

extent of collagen preservation was assessed from measurements of collagen yields, stable isotope ratios, and carbon-to-nitrogen (C:N) atomic ratios. Samples were graphitized and their radiocarbon contents measured by accelerator mass spectrometry. The measured ages were considered reliable only if the bones contained more than 1% weight collagen and had C:N ratios between 2.9 and 3.5. For samples that yielded finite conventional ages, calendar-year ages (and the corresponding 68.2% and 95.4% confidence intervals) were estimated using the IntCal13 calibration dataset (*SI Appendix*, section S4).

Optical Dating of Sediments. Twenty-seven sediment samples were collected from layers 5, 6, and 7 for optical dating (34, 35). For most of these samples (23 from layers 5 and 6, and 2 from layer 7), the equivalent dose values were estimated from measurements of the infrared stimulated luminescence signals emitted by individual sand-sized grains of potassium-rich feldspar. Each single-grain dose distribution was examined for any patterns in the data, the coefficient of variation was calculated, and the finite mixture model or central age model was used, as appropriate, to obtain the final dose value for age determination. The equivalent doses of the two other samples from layer 7 were determined using a multiple-aliquot infrared stimulated luminescence procedure. The external environmental dose rate for each sample was estimated from measurements of the beta and gamma emissions from uranium-238, uranium-235, and thorium-232 (and their decay products) and potassium-40, and the small contribution from cosmic rays. Beta dose rates (including the contribution from the decay of potassium-40 and rubidium-87 inside the grains) were determined from laboratory measurements, whereas the gamma dose rate was measured in situ at each sample location. The external dose rate components were adjusted for water content and the optical ages calculated directly in calendar years. Sample collection, preparation, measurement, and data analysis procedures followed those used for optical dating of sediments from Denisova Cave (11, 12), with additional details given in ref. 36 and *SI Appendix*, section S4.

Artifact Technology and Typology. The technological and typological characteristics of the Chagyrskaya artifacts are based on detailed studies of the lithic assemblage from sublayer 6c/1 (*SI Appendix*, section S6). Typological studies of the Crimean Micoquian collections and European Micoquian artifacts from Sesselfelsgrotte (Germany) were made by author V.P.C. The central Asian Levallois-Mousterian assemblages came from published sources (*SI Appendix*, section S7), as did the assemblages from Antonovka I and II and Barakaevskaya Cave (*SI Appendix*, section S8). We incorporated Gladilin's typology (37) into the attributive analysis of the Chagyrskaya assemblage to account for the typological variability and methods used to work the raw materials. Key attributes included ratios of categorized lithic artifacts, characteristics of primary knapping, core-reduction models, bifacial production, and degree of raw material reduction. The characteristic feature of this method is the analysis of each artifact as a set of technologically significant and multiple, interrelated morphometric characteristics. We studied bifacial tools using scar pattern analysis to reconstruct the sequence of biface manufacture from the existing negatives on the biface.

Statistical Analysis of Lithic Assemblages. SPSS Statistics software (v.18) and the PAST program were used for hierarchical cluster analysis, nonmetric multidimensional scaling (nmMDS), and principal component analysis (PCA). Hierarchical agglomerative clustering was accomplished using the centroid linkage method with squared Euclidean distance, which computes the dissimilarity between the centroids of several clusters. nmMDS is a nonparametric ordination method that computes a similarity/distance matrix for a set of items and locates each item in low-dimensional space. PCA provides a composite view of the variability among technological and typological assemblages. All data used for nmMDS and PCA were scaled using z-score standardization. PERMANOVA, a nonparametric multivariate statistical test, was used to compare groups of items and to assess which variables have the greatest influence. Further details of statistical methods are given in *SI Appendix*, sections S7 and S8.

Geometric Morphometric Shape Analysis. A quantitative description of shape variability within and between groups of bifaces from Chagyrskaya Cave and Sesselfelsgrotte (the key Micoquian site in central Europe) was created using the Artifact GeoMorph Toolbox 3-D (AGMT3-D) software package for landmarks-based geometric morphometric shape analysis (38).

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